PATTERNS AND PROCESSES OF SPECIES DIVERSITY IN FRAGMENTED NORTHERN HARDWOOD FORESTS

BY

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ABSTRACT

Twenty-four upland hardwood forests were examined to determine the influence of plant dispersal and environmental heterogeneity on the composition and richness of species in the forest understory. Patterns in the dispersal attributes of established plants were evaluated in relation to associated plant traits, microhabitats on the forest floor, and measured or inferred gradients in the availability of moisture, nutrients and light.

Plant attributes that maximally explained differences in species richness were mode of dispersal, habitat affinity, life form, shade tolerance, and moisture affinity. Environmental variables that maximally explained species richness were stand structure, soil moisture and soil parent material. Species richness was strongly influenced by sugar maple abundance and declined sharply on mesic, calcium-rich soils.

In this study, modes of dispersal were strongly correlated with plant traits and habitat factors that govern germination, establishment and persistence. The contribution of dispersal and environmental processes to species richness could not be distinguished, statistically.

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I dedicate this thesis to my life-long partner, and friend, Linda Galen.

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1.0 INTRODUCTION

The question, "Why do some places have more species than others?", has attracted attention throughout the history of ecology. One reason for this is that the answer one gives both reflects, and informs, one's understanding of the fundamental processes that govern the distribution and abundance of organisms. A core issue since the late 1950's has been the identification of processes that allow numerous species to coexist in the same environment. Classical models of species interactions (Grinnell 1904, Volterra 1926, Gause 1934) predict that two similar species cannot coexist indefinitely on a single limiting resource in a uniform environment. In the presence of such conditions, one species should eventually displace the other and the assemblage should be reduced to a single species (Hutchinson 1957, 1959; Hardin 1960). How is it, then, that so many natural habitats are species-rich?

One productive approach to this question has been to examine the assumptions of the classical models: what happens if species are not "similar", if interactions do not proceed to equilibrium, if there is more than one limiting resource, or, if the environment is not spatially or temporally uniform. This research effort has generated a vast literature and many alternative explanations (see Chapter 4 and reviews by Connell 1978, Huston 1979, Pickett 1980, Sousa 1984, Petraitis *et al.* 1989, Hart and Horowitz 1991, Tilman and Pacala 1993, Ricklefs and Schluter 1993, Huston 1994, Palmer 1994, Heywood 1995, Grace 1999). Despite this effort, a synthetic understanding that applies at all spatial and temporal scales has not been achieved.

In terrestrial plant communities, a broad consensus has emerged that the environment is not spatially and temporally uniform. Under these conditions, heterogeneity in limiting resources is expected to promote species coexistence by increasing the probability that there will be some place, or time, where one's competitors perform poorly or do not survive and where populations of one's own kind may expand (Hutchinson 1961, Levin 1974, Warner and Chesson 1985, Comins and Noble 1985, Hurtt and Pacala 1995). Implicit in this perspective is the expectation that differences in plant traits will lead to pattern in the distribution of species and variability in the composition and dynamics of plant assemblages (Whittaker 1956, Grubb 1977, Tilman 1982, Chesson 1986).

The spatial and temporal scales at which heterogeneity contributes to species diversity, and to species coexistence, have not been resolved (cf. Pacala and Silander 1985, Ricklefs 1987, Cornell and Lawton 1992, Holmes and Willson 1998, Cain *et al.* 2000). A long-standing presumption has been that interactions among local species and the physical environment are the principal means by which plant and animal assemblages are structured (Ricklefs 1987). If true, then the composition and richness of a given assemblage may be explained solely by reference to processes operating within the local patch. The diversity of species, however, often fails to converge under similar conditions, suggesting that regional and historical processes, as well as unique events and circumstances, are important contributors to community structure (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993).

One spatial process that is expected to influence the composition and richness of plant assemblages is dispersal. Dispersal is predicted to have profound consequences for populations and communities since it governs the size and composition of the seed rain (Clark and Yi 1995), affects the probability that diaspore will land in a site suitable for germination (Harper 1977, Sorensen 1978, Venable and Levin 1985), determines the initial conditions that seeds and seedlings must confront (Schupp and Fuentes 1995), affects the initial spatial array of individuals in a population (Thiede and Augspurger 1995), determines who interacts with whom and with what intensity (Schmida and Ellner 1984, Pacala 1986, Silander and Pacala 1990, Rees 1996, Rees *et al.* 1996), influences local extinction rates by affecting the probability that declining or extirpated populations are rescued (Brown and Kodric-Brown 1977, Holt 1993), influences the rate at which plants colonize new habitat (Halpern *et al.* 1990, Matlack 1994, Kotanen 1997, Brunet and von Oheimb 1998) and the sequence in which they arrive (Drake 1991, Fastie 1995), and, influences the level of gene flow within and between populations and thus the degree to which neighboring plants are related (Williams and Guries 1994) and genetic variation is structured spatially (Levin 1981, Hamrick and Godt 1997, Hamrick *et al.* 1993).

The contribution of dispersal to observed differences in the composition and richness of individual habitats and plant assemblages, however, is poorly understood. One reason for this is the logistic

challenge of monitoring the dispersal of seeds and spores. Diaspores are typically released through time and often by means and over distances that cannot be readily observed. Despite a concerted effort to determine the dispersal reach of species (Appendix 11), uncertainty remains regarding the proportion of diaspores that land beyond the immediate vicinity of the maternal plant (Portnoy and Willson 1993) and regarding the frequency and importance of longer-distance dispersal events (Cain *et al.* 2000).

One way forward has been the use of indirect measures, such as the proportion of established taxa dispersed by a given mode, to characterize the dispersal spectra associated with particular habitats (Dansereau and Lems 1957, Frenkel 1970, Pojar 1974, Lutensteiner 1979, Ellner and Shmida 1981, Hoehne 1981, Morton and Hogg 1989, Willson *et al.* 1990) and plant traits (Westoby *et al.* 1990, Hughes *et al.* 1994, Leishman *et al.* 1995, Mabry *et al.* 2000). The data from these studies, while limited, have found pattern in the relative frequency of dispersal modes and broad similarities in the dispersal spectra of similar habitats. In the temperate forests of eastern North America, dispersal by animal ingestion, unassisted means, and wind is typically more frequent than dispersal by ants, animal adhesion and mechanical expulsion (Table 1.1.). The taxa of wetland and disturbed habitats, in contrast, may typically be dispersed by the wind.

The use of indirect measures, however, makes it difficult to determine whether the pattern in the distribution and composition of species is due to the failure of seeds to land there (dispersal limitation), germinate there (recruitment limitation), or, persist there (survival limitation) (Schupp and Fuentes 1995). This creates a measure of uncertainty with respect to causation and ambiguity with respect to the contribution of plant traits that may be correlated with dispersal. Pattern in the dispersal attributes of established plant assemblages, therefore, may be inherently ambiguous with respect to the mechanisms that give rise to it.

Those who wish to examine the contribution of dispersal at the scale of habitats and landscapes reluctantly accept such ambiguity in the expectation that pattern revealed through the use of indirect methods will provide a starting point for future research with more revealing methods.

Table 1.1 Comparison of dispersal spectra in plant communities of broadly similar structure in eastern North America. Cell entries = mean percent of flora (references 1, 2, 3, this study); median percent of flora (reference 4) . n = number of stands. Modes of dispersal: AI=animal ingestion, AA=animal adhesion, AC=animal conveyance (ants), A(*s.l.*)=animal dispersed; ME=mechanical expulsion, U=unassisted, O=other (man). Sources: 1. Dansereau and Lems 1957; 2. Hoehne 1981; 3. Morton and Hogg 1989; 4. Willson *et al.* 1990. See original sources for details regarding size and attributes of the sampled flora.

Community	Mode of Dispersal								
	AI	AA	AC	A (*s.l.*)	Wind	ME	U	Water	O
Deciduous Forests:									
Illinois, Michigan, Tennessee[4] (n=4)	29	7	10	46	18	3	36	-	-
Quebec: climax[1] (n=3)	-	-	-	39	43	-	17	-	-
Quebec: disturbed[1] (n=3)	-	-	-	26	62	-	12	-	-
Wisconsin: forest islands 1951[2] (n=4)	23	15	3	41	15	4	19	5	-
Wisconsin: forest islands 1975[2] (n=4)	26	9	11	46	3	3	35	6	-
This Study (n=24)	17	13	10	40	31	5	22	-	-
Conifer Forests:									
Minnesota[4] (n=1)	22	3	7	32	31	2	34	-	-
Quebec[1] (n=1)	-	-	-	29	71	-	-	-	-
Island Flora:									
Ontario[3] (n=1)	42	24	-	64	23	-	-	63	6

Table 1.1 Comparison of dispersal spectra in plant communities of broadly similar structure in Eastern North America (cont'd).

Community	Mode of Dispersal								
	AI	AA	AC	A (*s.l.*)	Wind	ME	U	Water	O
Old Field									
Quebec[1] (n=1)	-	-	-	17	83	-	-	-	-
Bluegrass Meadow									
Quebec[1] (n=1)	-	-	-	13	87	-	-	-	-
Alder Thicket									
Quebec[1] (n=1)	-	-	-	40	60	-	-	-	-
Fen									
Quebec[1] (n=1)	-	-	-	12	83	-	5	-	-

The principal motivation for this thesis has been to gain a clearer understanding of the roles of dispersal and environmental heterogeneity in structuring the composition and richness of species in the forest understory. The forests in this study are isolated fragments of the pre-settlement forest of the Huron-Ontario Section of the Great Lakes - St. Lawrence Forest Region (Rowe 1972). The effects of forest fragmentation are considered only briefly, however, since the methods of the thesis cannot readily distinguish their effects from the effects of within-patch processes.

Objectives of the Thesis

i) To characterize the dispersal profile of established plants in the understory of sampled forest patches;

ii) To identify the environmental factors and plant traits that best explain observed differences in the composition and richness of established plants in the understory of sampled forest patches;

iii) To compare the degree to which environmental factors and plant traits explain observed differences in species richness in the understory of sampled forest patches.

General Approach

In keeping with recent studies, the principal method for investigating the influence of dispersal on plant assemblages will be the comparison of the proportion of taxa dispersed by a given mode in contrasting habitats and environmental states. Ambiguity with respect to causal factors remains but has been minimized by recording the distribution of species in relation to uniform microhabitats and by considering the contribution of associated plant traits that may independently influence the distribution of species or constrain the mode of dispersal. The latter method draws on long-standing initiatives to identify and evaluate pattern in relation to species groups with similar structural or functional traits (e.g. Raunkiaer 1934, Root 1967, MacArthur and Wilson 1967, Grime 1977, Noble and Slayter 1980, Willson *et al.* 1990, Leishman and Westoby 1992, Smith *et al.* 1997).

The first objective of the thesis was achieved by conducting a spring and summer survey of twenty-four forest patches in the general vicinity of Peterborough, Ontario, and, by characterizing the apparent mode of dispersal of 413 species of vascular plants in relation to the morphology and known properties of the diaspore. Plant traits that may independently influence the distribution of species or modes of dispersal were also characterized with reference to published sources.

The vegetation survey was conducted in relation to a field-based classification of microhabitats that characterized uniform conditions within each 10m x 10m quadrat with respect to canopy closure, soil moisture, substrate, and disturbance. This approach provided insight into the scale of spatial heterogeneity within the forest and the degree to which this heterogeneity was associated with differences in species composition, richness, and functional traits.

The second objective of the thesis was achieved by collecting soil samples and field data to characterize the moisture and fertility of forest soils, the composition and structure of forest trees, and site disturbance. The base cation status, soil pH and percent soil organic matter were determined by laboratory analysis; percent canopy closure was determined by hemispherical photography. Pattern in the composition and distribution of species and plant traits was evaluated by detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). The degree to which environmental variables and plant traits explained differences in species richness in 10m x 10m quadrats was determined by simple linear regression.

The third objective of the thesis was achieved by multiple linear regression and detrended correspondence analysis (DCA). The latter analysis, suggested by Dr. R. Hansell, Institute of Environmental Studies, University of Toronto, provided a graphical method for determining the degree to which environmental and dispersal variables accounted for the same fraction of variance summarized by multiple linear regression.

Structure of the Thesis

Chapter 2 describes the sampling protocol and methods associated with the vegetation survey and

environmental inventory; summarizes the relationships among key environmental variables; and, identifies the environmental factors and plant traits that influence the distribution and composition of species in the forest understory.

Chapter 3 describes the procedure for classifying modes of dispersal and plant traits; and, identifies patterns in the distribution of dispersal modes in relation to life form, life history, provenance, modality, fruit type, taxonomic rank, habitat affinity, environmental gradients, microhabitats, species frequency class, species richness class, plant cover class, patch size, and, patch isolation.

Chapter 4 describes the methods for identifying and comparing the contribution of variables to species richness; and, identifies the degree to which environmental variables and plant traits individually, and collectively, explain observed differences in species richness in 10m x 10m quadrats.

Chapter 5 presents the principal findings and conclusions of the thesis.

Chapter 6 summarizes the cited literature.

Appendices: Supporting information original to the thesis is presented in Appendices 1 to 10. Contextual information compiled from secondary sources is presented in Appendices 11 to 14.

2.0 ENVIRONMENTAL PATTERNS

2.1 Introduction

Spatial and temporal heterogeneity in conditions that govern the germination, establishment, growth and reproduction of plants is a striking feature of natural environments. In the presence of heterogeneity, differences in plant traits are expected to create pattern in the distribution of species and variability in the composition and dynamics of plant assemblages (Whittaker 1956, Levin 1974, Grubb 1977, Tilman 1982, Chesson 1986). Variation in the availability of limiting resources is expected to promote species coexistence by increasing the probability that there will be some place, or time, where competitors perform poorly or do not survive and where populations of low abundance may expand (Hutchinson 1961, Levin 1974, Warner and Chesson 1985, Comins and Noble 1985, Hurtt and Pacala 1995). Coexistence under these circumstances requires that species be ecologically distinct since the populations of rare species cannot otherwise expand in the presence of species that are more abundant (Chesson 1991, Pacala and Tilman 1994).

In the temperate forests of eastern North America, environmental heterogeneity may be created at a variety of spatial and temporal scales. Influential processes that operate at large spatial or temporal scales include glaciation (Hills 1952, Peet and Christensen 1980, Howell and Vankat 1981), pedogenesis (McFadden *et al.* 1994, Reich *et al.* 1997), plant migration (Davis 1981a), succession (Glenn-Lewin *et al.* 1992), forest stand development (Oliver and Larson 1996), periodic outbreaks of pathogens (Davis 1981b, Perry and Moore 1987), periodic storm events (Oliver and Stephens 1977, Frelich and Lorimer 1991), periodic extremes in precipitation and temperature (Tilman and Downing 1994), periodic fire events (Nowacki *et al.* 1990, Reich *et al.* 1990), chance colonization events and sequences (Drake 1991, Fastie 1995), vegetation and soil feed-back processes (Watt 1947, Fox 1977, Pastor *et al.* 1984, Frelich *et al.* 1993), and, past land use practices (Pettit *et al.* 1995, Motzin *et al.* 1996).

In contrast, processes that operate at small spatial scales, and over short time frames, are typically plant-based processes such as the uptake of moisture and nutrients (Tilman 1982, 1988; Roberston *et al.* 1988), dispersal (Levin 1976, Roughgarden 1977, Pacala 1987, Portnoy and Willson 1993),

germination (Grubb 1977, 1986), recruitment (Hurtt and Pacala 1995), the creation of space through plant death (Chesson and Warner 1981, Tilman 1994), competitive interactions (Goldberg and Barton 1992, Gurevitch *et al.* 1992, Bengtsson *et al.* 1994), and, herbivory (Whitney 1984).

In the northern hardwood forest, an important source of heterogeneity is the forest canopy. Canopy trees influence the quantity, spectral quality and phenology of light received at the forest floor (Minkler and Woerhiede 1965, Horn 1971, 1975, Brewer 1980, Messier and Bellefleur 1988, Canham *et al.* 1990, Canham and Burbank 1994), the availability of nutrients and moisture in the rooting zone of forest soils (Aber *et al.* 1991, Pastor and Post 1986, Zinke 1962, Crozier and Boerner 1984,1986, Leininger and Winner 1988, Boerner and Koslowsky 1989), the quantity and quality of coarse woody debris on the forest floor (Harmon *et al.* 1986, Hale and Pastor 1998), the probability and size of tree pits created during wind-throw events (Putz *et al.* 1983), and the timing and size of gaps in the forest canopy (Lorimer *et al.*1988, Lorimer 1989, Frelich and Lorimer 1991). Mechanisms that contribute to these effects include differences in canopy architecture (Horn1971), seasonal patterns of development and senescence (Brewer 1980), tissue and leaf litter chemistry (Vitousek 1982, Melillo *et al.* 1982), mechanical firmness (Mergen 1954), response to wind-throw (Beatty and Stone 1986), and life span (Lorimer 1989).

The spatial scale at which heterogeneity contributes to species coexistence is influenced by the dispersal properties of potentially competing plants. For most plants, the fraction of propagules dispersed beyond the immediate vicinity of the parent declines sharply with distance, creating seed dispersal curves with long tails (Portnoy and Willson 1993). Most propagules travel only metres to tens of metres from the parent plant and the most important dispersal outcome may be achieved within 1-2 canopy diameters of the maternal parent (Appendix 11; Hughes *et al.* 1994). At this distance, dispersal is a non-limiting process and pattern in the distribution and composition of species is governed primarily by factors governing germination, establishment and persistence.

Recent studies suggest that dispersal over this distance may be an important precondition for the coexistence of species (Atkinson and Shorrocks 1981; Shmida and Ellner 1984; Pacala 1986, 1987; Pacala and Silander 1987; Rees *et al.* 1996). Rather than interact with a number of individuals in

a plant assemblage, and thereby experience the average density of the population, plants interact primarily with individuals that lie within a canopy or root crown diameter (Harper 1977, Pacala and Silander 1985, Venable and Brown 1993). In the forest understory, this means that the distance over which most plants competitively interact is on the order of centimetres to metres. When the dispersal distance of plants is short, siblings tend to aggregate into monospecific clumps and competing species become segregated spatially. Under these circumstances, individuals tend to compete more with their own kind than with others and thus create the primary conditions for coexistence(Schmida and Ellner 1984, Pacala 1987, Lavorel *et al.* 1994).

When the dispersal reach of plants extends beyond the neighborhood in which plants compete, an increasing number of seeds land in environments that are less favorable than the home patch, and, a declining number of conspecific seeds land in close proximity to one another. These conditions reduce the tendency for monospecific clumping by favoring small founding populations and low fecundity. Under these circumstances, coexistence is facilitated by the spatial segregation of competitors when seeds land in empty but suitable environments (Hurtt and Pacala 1995, Holmes and Wilson 1998), and, by reversals in relative competitive strength when more widely dispersed seeds germinate next to weaker competitors or to stronger competitors weakened by less favorable settings (Chesson and Case 1986).

Pattern in the response of species to environmental variation has been examined at a variety of spatial and temporal scales. One pattern that has attracted increasing attention in recent years is the response of forest plants on contrasting geological substrates (Curtis 1959, Buell *et al.* 1966, Peet and Christensen 1980, Howell and Vankat 1981, Pregitzer and Barnes 1982, Pastor *et al.* 1984, Zak *et al.* 1986, Host *et al.* 1988, Palmer 1990, Whitney 1991, Host and Pregitzer 1992, McFadden *et al.* 1994, Kobe *et al.* 1995, Kobe 1996, Reich *et al.* 1997, van Breeman *et al.* 1997, Hutchinson *et al.* 1999). Marked contrasts in the composition and richness of species observed within the forest canopy, and on the forest floor, have typically been attributed to gradients in moisture and fertility associated with differences in the bedrock, soil parent material, and degree of soil weathering (soil order).

The relative importance of moisture and nutrients to differences in forest composition and productivity is a long-standing issue that has been critically re-examined in several recent papers (cf. Pastor *et al.* 1984, Pastor and Post 1986; Reich *et al.* 1997; Kobe *et al.* 1995, Kobe 1996, van Breeman *et al.* 1997). This research has contributed to a rethinking of the relative importance of plant and soil based processes to nutrient dynamics in north temperate forests, and, has stimulated research into the relative importance of nitrogen and base cations to the distribution and relative abundance of important canopy trees such as sugar maple.

The calcium-based explanations proposed by Kobe *et al.* (1995) and Kobe (1996) to account for the marked decline in juvenile sugar maple mortality on calcium-rich soils in northwestern Connecticut (see Section 2.4) have broad phytogeographic and ecological importance since they provide a mechanistic basis for the predominance of sugar maple in the Maple-Basswood, and Beech-Maple, forest regions (Braun 1950), and, for the greater shade tolerance of sugar maple, and red spruce (McLaughlin *et al.* 1991), on calcium-rich soils.

Study Objectives: The principal objective of this chapter is to identify the environmental factors that influence the distribution and composition of plants in the understory of sampled forest patches. Plant response is examined in relation to inferred gradients in limiting resources and to apparent microhabitats in the forest understory. Pattern in the distribution of dispersal modes in relation to microhabitats and environmental gradients will be examined in Chapter 3. The contribution of environmental and dispersal factors to species diversity will be compared in Chapter 4.

2.2 Methods

2.2.1 Selection of Study Sites

Twenty-four forest patches (Appendix 1) were chosen to reflect a range of patch sizes in two landscapes of contrasting forest fragmentation (Table 2.1). The forest patches were second-growth deciduous stands in the vicinity of Peterborough, Ontario. Sampled areas within patches were standardized, where possible, with respect to topographic relief, soil texture, soil moisture, forest cover type, and disturbance. The intent was to sample upland sugar maple stands on sites with low

Table 2.1. Size distribution of sampled forest patches.

Landscape I (15% forest cover)[1]			Landscape II (35% forest cover)[1]		
Size Class (ha)[2]	# Patches	% (N=12)	Size Class (ha)[2]	# Patches	% (N=12)
10-20	1	8.3	10-20	2	16.7
21-50	3	25.0	21-50	1	8.3
51-100	5	41.7	51-100	3	25.0
101-500	3	25.0	101-500	5	41.7
>500	0	0	>500	1	8.3
Total	12	100.0	Total	12	100.0

Notes:

1. M. Austen, Long Point Bird Observatory, *pers. com.* Digitized forest cover map derived from LANDSAT TM satellite imagery.
2. Source: Forest stand maps (1:10,000 scale), Forest Resource Inventory, Ontario Ministry of Natural Resources (1978, 1979, 1980).

topographic relief (< 2%), mesic soils, sand or loam textures, and low disturbance. In practice, the moisture regime of sampled areas varied with soil parent material, landscape position, and microtopography, and therefore ranged from dry-mesic to wet.

The chosen patches, with one exception, were selected from among sixty-three forest patches previously surveyed by the author (1995) for the Woodlands Biodiversity Project, Long Point Bird Observatory (Austen *et al.*, unpublished). The study sites established by the Long Point Bird Observatory (one circular quadrat, 35.4 m radius, per patch) were accepted for this study. The exceptions were study sites O9 and GG1, which were moved to more level terrain to satisfy the relief criterion for this study, and study site DD1, which was established *de novo* to balance the sampling design for soil texture. The protocol for establishing quadrats within study sites is presented below (Section 2.2.2).

The study sites are situated within the Huron-Ontario Section of the Great Lakes-St. Lawrence Forest Region (Rowe 1972), also known as the Great Lake Section of the Hemlock-White Pine-Northern Hardwoods Forest Region (Braun 1950). The forest patches have developed on sand and loam soils of the Brunisolic, Luvisolic and Gleysolic orders, overlying glacio-fluvial, calcareous till, calcareous outwash, or lacustrine parent materials, on Ordovician limestone of the Trenton formation (Weber and Morwick 1946, Gillespie and Acton 1981, Hoffman and Acton 1974). The climate of the region is humid, mesothermal, with little or no water deficiency (Energy, Mines and Resources Canada 1990a,b). The mean annual temperature (1964-1990) at Peterborough is 6.0 ^{o}C, with a mean daily temperature of -9.4 ^{o}C in January and 20.0 ^{o}C in July. The mean annual precipitation is 882.2 mm. (Environment Canada 1993).

2.2.2 Sampling Methods

Eight 10m x 10m quadrats were located within each 0.4 ha study site in relation to a stratified random sampling design. At each study site, a sketch map was prepared showing the location and estimated area of each microhabitat (see Microhabitat Variables, Section 2.2.3.5). Quadrats were located at random within each microhabitat in relation to the following sampling design: for

extensive microhabitats, such as closed, seasonally dry, forest floors, quadrats were located with reference to coordinates (bearing and pacing from the site centre) drawn from a random number table; for small microhabitats (features less than 10m in each direction), such as tip-up mounds, tree pits, seeps, and most canopy gaps, quadrats were centred on the feature which was chosen at random from a numbered set of such features; for linear microhabitats (features longer than 10m in one direction), such as seepage tracks, access lanes and associated ditches, quadrats were centred on the feature at a random number of paces initiated from the feature's edge. Stumps and logs were sampled passively in relation to the microhabitats in which they were found. The number of quadrats located in a given microhabitat was proportional to its area within the quadrat, subject to the constraint that each microhabitat type be sampled at least once.

Quadrats were located within study sites (rather than within forest patches) in order to clarify the contribution of environmental heterogeneity to species richness within a sampling space of arbitrary but constant area (0.4 ha). A sample area of constant size was used to avoid passive sampling effects which inflate species richness when the sampled area is proportional to patch size (Connor and McCoy 1979).

2.2.3 Environmental Variables

The environmental variables for this study are summarized in Table 2.2. Brief descriptions of the rationale for inclusion, criteria for classification, field or laboratory methods, and sources for published data sets, are presented below. Data collected in the field but not included in analyses are summarized in Section 2.2.3.7.

2.2.3.1 Soil Variables

Soil Parent Material: an indicator of the composition, sorting, and stratification of soil materials (Flint 1971; Bloom 1978); in this study, an indicator of regional differences in the inherent moisture retention and fertility of sampled soils. The inferred order of moisture retention capacity was lacustrine>calcareous till>calcareous outwash>glacio-fluvial, based on the declining abundance of fine particles. This ordering of parent materials also reflected inherent differences in soil fertility,

Table 2.2. Summary of environmental variables.

Variable	Attribute	Source
soil parent material	1. glacio-fluvial 2. calcareous till 3. calcareous outwash 4. lacustrine	Weber and Morwick (1946) Gillespie and Acton (1981) Hoffman and Acton (1974)
soil order	1. brunisol 2. gleyed brunisol 3. luvisol 4. gleyed luvisol 5. gleysol	Weber and Morwick (1946) Gillespie and Acton (1981) Hoffman and Acton (1974) field observation
soil moisture class	1. seasonally wet depressions 2. seasonally moist depressions 3. seasonally dry depressions	field observation
soil organic matter	continuous variable	laboratory observation
soil pH	continuous variable	laboratory observation
base cations	1. available calcium 2. calcium:magnesium ratio 3. potassium:magnesium ratio	laboratory observation
tree diameter class, breast height	1. 0-30 cm: 2 cm increments 2. > 30.0 cm: continuous values measured to nearest 0.1 cm	field observation
tree height class	1. < 1 m 2. 1-3 m 3. 3-10 m 4. 10-15 m 5. 15-25 m 6. > 25 m	field observation
forest stratum	1. herb layer (<1 m) 2. shrub layer (1-3 m) 3. subcanopy (3-15m) 4. canopy (>15 m)	field observation

Table 2.2 Summary of environmental variables (cont'd).

Variable	Attribute	Source
canopy cover type	1. oak, no sugar maple 2. oak + sugar maple 3. sugar maple 4. sugar maple + wet-mesic or wet tree taxa 5. wet-mesic + wet tree taxa	field observation
canopy closure	continuous variable (%)	field observation
cover class (herb layer)	1. solitary individual (+) 2-5 individuals (r) 2. <1% 3. 1-5% 4. 6-15% 5. 16-25% 6. 26-50% 7. 51-75% 8. 76-100%	field observation
habitat affinity	1. forest 2. forest + open 3. open + forest 4. open	Voss (1972, 1985, 1996)
coefficient of wetness	-5 obligate wetland -4 facultative wetland -3 facultative wetland -2 facultative wetland -1 facultative 0 facultative +1 facultative +2 facultative upland +3 facultative upland +4 facultative upland +5 obligate upland	Oldham *et al.* (1995)
microhabitat type	see Table 2.4	field observation
# microhabitats	continuous variable	field observation

Table 2.2 Summary of environmental variables (cont'd).

Variable	Attribute	Source
patch interior area class	1. 0-5 ha 2. 6-10 ha 3. 11-20 ha 4. 21-50 ha 5. 51-100 ha 6. 101-200 ha 7. 201-500 ha 8. 501-1000 ha	M. Austen, *pers. com.*
patch area	continuous variable	Ontario Ministry of Natural Resources (1978, 1979, 1980)
patch isolation	continuous variable	NTS map sheets (1:50,000)
forest cover	continuous variable	NTS map sheets (1:50,000)

based on an inferred decline in cation exchange capacity (Brady 1990) and soil pH (Dancer *et al.* 1993). However, soils on the lacustrine parent materials were saturated seasonally and thus subject to periodic denitrification (Ponnamperuma 1972) and to lower rates of ammonification (Patrick and Mahaptera 1968, Ponnamperuma 1972). The presumed order of fertility, based on the joint influence of contributing factors, was calcareous till ≥calcareous outwash>lacustrine>glacio-fluvial. Quadrats were classified in relation to published soil survey maps and reports (Weber and Morwick 1946, Gillespie and Acton 1981, Hoffman and Acton 1974).

Soil Order: an indicator of the effects of the dominant soil-forming processes on soil properties (Canada Soil Survey Committee 1978); in this study, an indicator of regional differences in the inherent fertility of sampled soils. The inferred order of soil fertility was Luvisolic>Brunisolic> Gleysolic, based on the presence/absence of a Bt horizon and the degree of periodic or prolonged reducing conditions associated with saturated soils. Soils in quadrats with seasonally moist or wet depressions were classified as gleyed Brunisolic, and gleyed Luvisolic, if mottling observed during a previous field assessment (1995) was observed within 50 cm of the mineral surface (Canada Soil Survey Committee 1978). Quadrats were classified in relation to published soil survey maps and reports (Weber and Morwick 1946, Gillespie and Acton 1981, Hoffman and Acton 1974).

Soil Moisture Regime: in this study, an indicator of the duration and intensity of moisture deficit in the soil (Patterson 1978). In contrast to measures of soil moisture, soil moisture regime is an indicator of variations in the soil moisture supply through time (± 100 years) (Pierpoint 1978). The former is a direct measure of soil moisture content, whereas the latter is assessed in relation to physical soil properties and soil profile characteristics (Ontario Institute of Pedology 1985).

In 1995, the moisture regime at the centre of each study site was determined with reference to the depth and properties of soil mottles, and, the texture of mineral soil in the upper B horizon (Ontario Institute of Pedology 1985). This method was not used for the 1996 field season owing to difficulties in determining the depth to mottles during the late August assessment. The moisture regime of quadrats was therefore classified in relation to the moisture status of forest depressions, a supplementary, planned, assessment that was initiated at the beginning of the spring survey.

Quadrats with standing water in depressions during the spring and/or summer vegetation survey (see Section 2.2.3.3) were classified as "seasonally wet". Quadrats with moist depressions (soil dark and moist to the touch when compared to the adjacent forest floor) during the spring and/or summer vegetation survey were classified as "seasonally moist". Quadrats with dry depressions during both the spring and summer vegetation survey were classified as "seasonally dry". This method, while lacking the rigor of the Ontario Institute of Pedology procedure, was deemed sufficient to characterize major differences in soil moisture within and between forest patches, when applied with reference to the results of the 1995 survey.

Soil Organic Matter (SOM): a general indicator of soil quality but not useful for predicting nitrogen mineralization (Nadelhoffer *et al.* 1983); in this study, an indicator of soil moisture retention capacity (Brady 1990), and, of seasonally saturated soils when organic matter content was greater than 30% (Canada Soil Survey Committee 1978).

Ten soil cores to 15 cm depth were removed with a slot-tube soil sampler from each 10m x 10m quadrat in relation to a stratified sampling design and placed in plastic freezer bag. The cores were taken in a hap-hazard manner in proportion to the type and area of microhabitat present. Loose leaf litter was removed prior to taking the core; litter ramified with fungal mycelia was left undisturbed and included in the core. Each sample was air-dried prior to storage and subsequently mortared and pestled, passed through a 4.00 mm sieve, placed in a drier oven, and dried overnight at 105°C (David 1988, Karam 1993). Approximately 10-15 grams of dried soil, from which macro charcoal and large roots had been removed, were placed in a crucible of known weight and subsequently ashed in a muffle furnace for 12 hours at 430° C (Nelson and Sommers 1982, Davies 1974) (550° C for soils with high apparent soil organic matter; Karam 1993). The furnace temperature was increased to the loss-on-ignition temperature over a three hour period (four hours for organic soils) to avoid flash combustion of organic matter and to minimize transient surges due to thermal lag. Following cooling (approximately 8 hours), samples were removed and weighed on an OHAUS Precision Plus digital balance. Percent soil organic matter was calculated as:

$$\% \text{ SOM} = [(\text{"soil"} - \text{"ash"}) / \text{"soil"}] \times 100$$

Replicates were not taken owing to the loss of sixty soil samples during storage.

Soil pH: in this study, an indicator of conditions favoring nitrification (Dancer *et al.* 1973). Five grams of soil (previously dried at 105°C and stored 3.5 years), and 15 ml of de-ionized water, were placed in a small plastic beaker, stirred vigorously for 60 seconds on a mechanical stirrer, and let stand for at least 15 minutes. The 1:3 ratio of soil to de-ionized water was increased to 1:6 for soils with > 30% soil organic matter to achieve wet slurry conditions. The pH_{water} reading was taken with a glass electrode, Corning pH Meter, Model 7, calibrated to buffer pH 7.0. The pH of soil samples was determined for quadrats 1-24, 34-40, 49-56, 61-192, only, since the original soil samples for quadrats 1-60 were lost during storage, and, changes in land use prevented replicates from being taken at each location.

Base Cations: in this study, a measure of the concentration of available calcium, exchangeable magnesium, and exchangeable potassium, in the upper 15 cm of the soil profile. Free calcium carbonate was not purged from soil samples, in order to determine the concentration of calcium "available" for plant uptake. Results were therefore reported as "available calcium" since the recorded concentration will include both "exchangeable" calcium, and free calcium carbonate, when the latter is present in the soil profile.

Twenty grams of soil, passed through a 1mm sieve, and one teaspoon of silica, were placed in a plexiglass leaching tube containing approximately 1 cm of tightly packed glass wool, a one-hole rubber stopper, and rubber tubing. After adding a teaspoon of silica to cover the soil surface, the leaching tube was suspended between a 300 ml flask containing 250 ml of 1 N, pH 7.0, ammonium acetate, and, a labeled, empty 300 ml flask. The outflow rate of leachate was subsequently adjusted to a slow drip, approximately 10 drops per 60 seconds, so that the leaching process would last at least 4 hours.

The concentration of calcium, magnesium, and potassium cations was subsequently determined by atomic adsorption spectrophotometry in a Perkin Elmer Atomic Absorption Spectrometer, Model 3100. The leachate was diluted, as required, with a 3% solution of lanthamum chloride, with the aid

of a Nichiryo AutoDilutor. The following equation was used to calculate the concentration of base cations:

$$\frac{\text{spectrometer reading x 50 (dilution factor) x 250 (ml leachate)}}{\text{20 (grams of soil)}} = \text{ppm base cations in soil}$$

The concentration of cations was subsequently expressed in centimoles (10^{-2} moles) per kg of soil (cmol/kg). The atomic adsorption spectrophotometry was conducted by Dr.Teng, Department of Forestry, University of Toronto.

The calcium:magnesium ratio, and, potassium:magnesium ratio, were also calculated to clarify the degree to which cation uptake may be affected by an imbalance among base cations (Ouimet and Camire 1995). Soil samples were reacted with 0.1N hydrochloric acid to assess the degree to which free calcium carbonates was present. Soils that "fizzed" upon reaction were classified as "reactive".

2.2.3.2 Forest Stand Structure Variables

Tree Diameter Breast Height (dbh): in this study, an indicator of the time since last disturbance (Henry and Swan 1974, Oliver and Stephens 1977, Lorimer 1980). The diameter of live and standing dead stems > 1 m tall was measured with a diameter tape and recorded in 2 cm increments, for stems 0-30 cm dbh.; stems > 30 cm dbh were measured to the nearest 0.1 cm in continuous increments. The diameter of stems in the 0-2 cm and 2-4 cm size classes was estimated visually in stands with many stems. Stems < 1 m tall were recorded as seedlings and assigned to one of eight cover classes.

Tree Height Class: in this study, an indicator of forest stand development (Oliver and Larson 1996). Tree height was measured during leaf flush with the aid of a Suunto clinometer and 30 m tape. Stems were assigned to the following height classes: <1 m, 1-3 m, 3-10 m, 10-15 m, 15-25 m, and >25 m. Stems <1 m tall were recorded as seedlings and assigned to one of eight cover classes. Representative stems in each height class were measured and subsequently used as visual standards for assigning stems to the appropriate size class.

Forest Stratum: in this study, an indicator of forest stand development (Oliver and Larson 1996), and, a datum used to classify forest cover type and selected microhabitat types. Four strata were recognized in this study: herb layer (<1 m), shrub layer (1-3 m), subcanopy (3-15 m), and canopy (>15 m). The threshold values for each stratum were measured for representative trees with the aid of Suunto clinometer and a 30 m tape.

Forest Cover Type: in this study, an indicator of recurring tree assemblages, soil moisture regime (Maycock 1963), available light (Messier and Bellefleur 1988, Canham *et al.* 1990), and litter quality (Pastor *et al.* 1984, Reich *et al.* 1997). Five cover types were recognized, based on their association with increasing soil moisture, and, the presence/absence of sugar maple: i) red or white oak (no sugar maple, no wet-mesic or wet taxa); ii) sugar maple + red or white oak; iii) sugar maple (no red or white oak, no wet-mesic or wet taxa); iv) sugar maple + silver maple, black ash, red ash, balsam poplar, or American elm; v) silver maple, black ash, red ash, balsam poplar, or American elm (no sugar maple, no red or white oak). Cover types were assigned to quadrats based on the presence/absence of indicator species in the shrub, subcanopy or canopy layer. This approach accommodated variability in species composition and stand structure caused by recent disturbance, and, revealed differences in moisture conditions more accurately than a classification based solely on the predominant species in the canopy layer.

Canopy Closure: in this study, an indicator of the quantity and quality of solar radiation received at the forest floor (Messier and Bellefleur 1988, Canham *et al.* 1990). Canopy closure was defined as the proportion of the sky hemisphere covered by leaves, branches and stems. High canopy closure therefore corresponds to low levels of red-shifted solar radiation received at the forest floor. Percent canopy closure was calculated by "HEMIPHOT" (ter Steege 1994) from digitized, hemispherical, 35 mm photographs taken with a Nikon F3 camera that was fitted with a Nikkor 8 mm *f*2.8 "fish-eye" lens, and, a Nikon DR-3, right-angle view finder. A high contrast black and white film, Kodalith High Contrast Ortho Film, ASA 12, Eastman Kodak, was used to maximize the contrast between sky and canopy (Chan *et al.* 1986).

A hemispherical photograph of the forest canopy was taken from the centre of each quadrat. The

camera was mounted on a Manfrodo tripod, set at 1.0 m above ground level, oriented to 0^{0} north, and leveled in the vertical and horizontal planes with the aid of pocket spirit level. An exposure setting was chosen that would maximize the contrast between sky and canopy. The canopy and visible sky were metered with the aid of a Minolta M spotmeter and an *f*-stop was selected that was at least two stops higher than the value for open sky. Brightly illuminated spots in the canopy were metered to ensure that the sky value was at least two stops greater than the highest value recorded for the canopy. For greater security, this exposure value was bracketed by one stop. Inspection of the developed images revealed that the middle exposure best represented the status of small and large canopy openings.

This approach was field tested to confirm that canopy vegetation was not mis-classified as "sky". Field testing revealed that under high canopy closure conditions (low light), the edge of the exposed image could not be differentiated from the film base. Experimentation subsequently determined that by taping a white plastic arrow to the rim of the lens at each cardinal direction, sufficient light would be reflected to the film plane to reveal the reveal the edge of the exposed image. The north arrow was made larger than the other arrows to ensure proper orientation of the digitized image. The arrows were cut from a white plastic container. The projecting portion of the E, S, and W arrows was 8 mm wide x 5 mm high; the projecting portion of the N arrow was 14 mm wide x 8 mm high.

The developed images (5 cm x 5cm) were digitized with a SCANJET IIC, Hewlett Packard, scanner. Images were scanned at 200 DPI at contrast setting 250 and brightness setting 125. The digitized images were processed in HEMIPHOT with a fixed radius of 195 units.

The radius over which light was collected in each image varied with canopy height and was typically on the order 20-25 metres.

2.2.3.3 Vegetation Variables

Species Composition: The plant inventory was conducted 7 May 1996 to14 June 1996 (spring survey) and 20 June 1996 to 25 July 1996 (summer survey). The boundary of each 10m x 10m

quadrat was marked by yellow propylene rope and sampled intensively by walking close interval (approximately 1.5 m) line transects. Taxa were recorded by microhabitat to facilitate analyses of compositional trends in relation to environmental factors. Known taxa were identified to species rank in the field with the aid of 10x hand lens; voucher specimens were collected for unknown taxa, and, for taxa requiring more than 10x magnification of diagnostic characters. Voucher specimens were identified with the aid of a dissecting microscope and with reference to the following authorities: trees (Barnes and Wagner 1981; Farrar 1995), willows (Argus 1992), shrubs (Voss 1985, Soper and Heimburger 1982), ferns and fern allies (Cody and Britton 1989), grasses (Voss 1972, Dore and McNeill 1980), sedges (Voss 1972, Gleason 1952, Webber and Ball 1984), herbs (Voss 1972, 1985, 1996; Gleason 1952, Gleason and Cronquist 1991), Asteraceae (Fisher 1988, Semple and Ringius 1983, Semple and Heard 1987). Identifications of difficult taxa were reviewed by specialists in the Ontario flora. *Carex* and Poaceae identifications were reviewed by M.J. Oldham, Natural Heritage Information Center, Ontario Ministry of Natural Resources; *Carex*, Section Ovales, identifications were reviewed by Dr. P.W. Ball, Erindale College, University of Toronto; selected grass specimens were identified by Dr. S.J. Darbyshire, Agriculture and Agri-Food Canada; selected fern identifications were reviewed by Dr. D.M. Britton, Professor Emeritus, University of Guelph. Twenty-five specimens could not be identified to species.

Cover Class: in this study, an indicator of plant abundance. The abundance of each species, and overall plant cover, within a 10 m x 10 m quadrat was estimated visually with the aid of one-metre swag sticks and marked quadrat diagonals. Plant abundance was recorded in relation to eight cover classes: i) solitary individual (+), 2-5 individuals (r); ii) < 1%; iii) 1-5%; iv) 6-15%; v) 16-25%; vi) 26-50%; vii) 51-75%; viii) 76-100%.

2.2.3.4 Plant Attribute Variables

Habitat Affinity: in this study, an indicator of the habitats in which a species is typically found and thus an indicator of transient and permanent residents in the forest understory. Four habitat types were recognized based on the apparent affinity for closed vs open canopy conditions: i) "forest": species found exclusively in closed forest habitats; ii) "forest + open": species found primarily in

closed forest habitats but also present in forest openings and thickets; iii) "open + forest": species found primarily in open habitats such as marshes, old fields, thickets, forest edges, but also present in closed forest habitats; iv) "open": species found exclusively in open habitats or disturbed sites in forest habitats. Species were assigned to one habitat type based on the habitat descriptions summarized by Voss (1972, 1985, 1996) for the State of Michigan, U.S.A.

Coefficient of Wetness: the probability of finding a species in a wetland habitat (Oldham *et al.* 1995); in this study, an indicator of the moisture affinity of surveyed species. Plants in southern Ontario were classified by Oldham *et al.* (1995) in relation to the following categories: i) "obligate wetland": species almost always occurs in wetlands under natural conditions, >99% probability of being found in a wetland habitat; ii) "facultative wetland": species usually occurs in wetlands but occasionally found in non-wetland habitats, 67-99% probability of being found in a wetland habitat; iii) "facultative": species equally likely to occur in wetlands or non-wetlands, 34-66% probability of being found in a wetland habitat; iv) "facultative upland": species occasionally occurs in wetlands but usually occurs in non-wetland habitats, 1-33% probability of being found in a wetland habitat; v) "obligate upland": species almost never occurs in wetlands under natural conditions, <1% probability of being found in a wetland habitat.

2.2.3.5 Microhabitat Variables

Microhabitat: in this study, a dimension of environmental heterogeneity, and, an indicator of uniform conditions, at the quadrat scale, with respect to canopy closure, soil moisture, substrate, and disturbance. Thirty-nine microhabitats were recognized (Table 2.3). The core features in the classification are forest floors, depressions, tip-up mounds, tree pits, stumps, logs, canopy gaps, seeps, raised root mats, and, features created by human disturbance, such as lanes, access roads, ditches, and regenerating fields. The moisture status for selected features is not recorded in Table 2.3 to reduce the number of elements in the classification. The moisture status of seep, riparian marsh, and riparian thicket is "seasonally wet"; the moisture status of riparian meadow is "seasonally moist"; the moisture status of mounds and regenerating fields is "seasonally dry". The moisture status of stumps, logs, raised root mats, and lane/access roads varies from seasonally dry to

Table 2.3. Definition and areal extent of forest microhabitats. Notes: "seasonally dry" = forest floor or depression free of standing water or moist soil during spring and summer survey; "seasonally moist" = forest floor or depression has moist soil during spring or summer survey; "seasonally wet" = forest floor or depression has standing water during spring or summer survey; "forest floors, *sensu stricto*" = that portion of the forest floor free of seasonally moist or wet depressions, tip-up mounds, tree pits, logs, stumps, raised root mats, seeps, lane/access roads, regenerating fields, riparian meadows, riparian marshes and riparian thickets; "-cc"= feature under a closed canopy of trees, saplings or tall shrubs; "-oc" = feature under an open canopy (feature has a clear view to the sky); % SA = % of sampled area (19,200 m^2).

Microhabitat	% SA	Description
seasonally dry forest floors-cc	54.3	forest floors, *sensu stricto*, that are seasonally dry and under a closed canopy
seasonally dry forest floors-oc	6.8	forest floors, *sensu stricto*, that are seasonally dry and under an open canopy
seasonally moist forest floors-cc	3.0	forest floors, *sensu stricto*, that are seasonally moist and under a closed canopy
seasonally moist forest floors-oc	3.0	forest floors, *sensu stricto*, that are seasonally moist and under an open canopy
seasonally moist forest depressions-cc	4.1	forest depressions (depression in forest floor <20 cm deep) that are seasonally moist and under a closed canopy
seasonally moist forest depressions-oc	0.2	forest depressions (depression in forest floor >20 cm deep) that are seasonally moist and under an open canopy
seasonally wet forest floors-cc	0.6	forest floors, *sensu stricto*, that are seasonally wet and under a closed canopy
seasonally wet forest depressions-cc	4.0	forest depressions (depression in forest floor >20 cm deep) that are seasonally wet and under a closed canopy
seasonally wet forest depressions-oc	1.0	forest depressions (depression in forest floor >20 cm deep) that are seasonally wet and under an open canopy

Table 2.3. Definition and areal extent of forest microhabitats (cont'd).

Microhabitat	% SA	Description
seep-cc	0.9	depressions in the forest floor that are under a closed canopy, are saturated for most of the growing season, and, have an organic horizon (soil organic matter >30% by weight)
seep-oc	0.3	depressions in the forest floor that are under an open canopy, are saturated for most of the growing season, and, have an organic horizon (soil organic matter >30% by weight)
seasonally dry gap-cc	2.2	forest floors, *sensu stricto*, that are seasonally dry, and under a closed canopy of trees, saplings or tall shrubs; canopy stratum (>15 m) missing
seasonally dry gap-oc	6.8	forest floors, *sensu stricto*, that are seasonally dry, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (>15 m) missing
seasonally moist gap-cc	0.5	forest floors, *sensu stricto*, that are seasonally moist, and under a closed canopy of trees, saplings or tall shrubs; canopy stratum (>15 m) missing
seasonally moist gap-oc	3.0	forest floors, *sensu stricto*, that are seasonally moist, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (>15 m) missing
seasonally wet gap-oc	1.0	forest floors, *sensu stricto*, that are seasonally wet, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (>15 m) missing
mound-cc	3.6	a raised mass of earth that has been deposited by soil eroding from the roots of a wind-thrown tree, and, under a closed canopy; *sensu stricto*, the portion of a pit-mound complex lying above the plane of the forest floor

Table 2.3. Definition and areal extent of forest microhabitats (cont'd).

Microhabitat	% SA	Description
mound-oc	0.4	a raised mass of earth that has been deposited by soil eroding from the roots of a wind-thrown tree, and, under an open canopy; *sensu stricto*, the portion of a pit-mound complex lying above the plane of the forest floor
seasonally dry pit-cc	1.5	a depression in the forest floor that has been created by the uprooting of a wind-thrown tree, and, that is seasonally dry and under a closed canopy; *sensu stricto*, the portion of a pit-mound complex lying below the plane of the forest floor.
seasonally dry pit-oc	0.1	a depression in the forest floor that has been created by the uprooting of a wind-thrown tree, and, that is seasonally dry and under an open canopy; *sensu stricto*, the portion of a pit-mound complex lying below the plane of the forest floor.
seasonally moist pit-cc	0.3	a depression in the forest floor that has been created by the uprooting of a wind-thrown tree, and, that is seasonally moist and under a closed canopy; *sensu stricto*, the portion of a pit-mound complex lying below the plane of the forest floor.
seasonally wet pit-cc	0.2	a depression in the forest floor that has been created by the uprooting of a wind-thrown tree, and, that is seasonally wet and under a closed canopy; *sensu stricto*, the portion of a pit-mound complex lying below the plane of the forest floor.
seasonally wet pit-oc	0.1	a depression in the forest floor that has been created by the uprooting of a wind-thrown tree, and, that is seasonally wet and under an open canopy; *sensu stricto*, the portion of a pit-mound complex lying below the plane of the forest floor.
log-cc	0.5	a tree bole (> 4 cm dbh) that is in contact with the earth and under a closed canopy
log-oc	0.2	a tree bole (> 4 cm dbh) that is in contact with the earth and under an open canopy

Table 2.3. Definition and areal extent of forest microhabitats (cont'd).

Microhabitat	% SA	Description
stump-cc	0.2	the upright remnant of a cut or wind-thrown tree that is under a closed canopy
stump-oc	0.1	the upright remnant of a cut or wind-thrown tree that is under an open canopy
raised root mat-cc	1.3	the root mat of a partially wind-thrown tree, typically associated with seasonally moist or wet soils, and, a deep (>15 cm) humus layer; or, the elevated ball of soil and roots at the base of shrubs on seasonally moist or wet soils; canopy closed (defined here as ≥60% canopy closure)
raised root mat-oc	0.6	the root mat of a partially wind-thrown tree, typically associated with seasonally moist or wet soils, and, a deep (>15 cm) humus layer; or, the elevated ball of soil and roots at the base of shrubs on seasonally moist or wet soils, canopy open (defined here as ≤ 60% closure)
stone-cc	<0.1	exposed, limestone, boulders, under a closed canopy
lane/road-cc	2.3	a farm lane, or forest access road, under a closed canopy
lane/road-oc	1.3	a farm lane, or forest access road, under an open canopy
ditch-cc	0.3	a ditch associated with a farm lane or forest access road, under a closed canopy
ditch-oc	<0.1	a ditch associated with a farm lane or forest access road, under an open canopy
regenerating field-cc	1.3	a plowed, farm field that is undergoing forest succession and presently is under a closed canopy of saplings or tall shrubs
regenerating field-oc	1.3	a plowed, farm field that is undergoing forest succession and presently is in the "old field" stage, under an open canopy

Table 2.3. Definition and areal extent of forest microhabitats (cont'd).

Microhabitat	% SA	Description
riparian meadow-oc	0.7	a seasonally flooded, riparian meadow, on mineral soil, under an open canopy that has been maintained by periodic cutting
riparian marsh-oc	0.4	a seasonally flooded, shallow marsh, on organic soil
riparian thicket-oc	0.1	a seasonally flooded thicket swamp, on mineral soil, under an open canopy that has been maintained by periodic cutting

seasonally wet depending on the feature and the quadrat surveyed. Forest depressions were defined as depressions in the forest floor >20 cm deep and were measured with the aid of painted swag sticks (alternating black and tan bands 20 centimetres wide) and a pocket spirit level.

 # Microhabitats: in this study, an indicator of environmental heterogeneity. The value represents the number of recognized habitats in a 10 m x 10 m quadrat.

2.2.3.6 Landscape Variables

Patch Interior Area: in this study, an indicator of forest fragmentation; the area (ha) of continuous forest that is more than 100 m from the forest edge (Austen *et al.* unpublished). Interior area was calculated from digitized LANDSAT TM satellite imagery by the geographic information system, ARC-INFO (S. Hounsell, Ontario Hydro, *pers. com.*). This data set is the property of the Long Point Bird Observatory (LPBO) and has been used in the thesis with their permission (M. Austen, *pers. com.*). Forest patches were assigned by the LPBO to one of eight area classes: 0-5 ha, 6-10 ha, 11-20 ha, 21-50 ha, 51-100 ha, 101-200 ha, 201-500 ha, 501-1000 ha.

Patch Area: in this study, an indicator of forest fragmentation; the area (ha) of continuous forest within a forest patch. Patch area was calculated from the stand data recorded on forest stand maps, 1:10,000 scale (Ontario Ministry of Natural Resources 1978, 1979, 1980). In contrast to the previous data set, patch area is a continuous variable that accounts for the total area of continuous forest in the patch.

Patch Isolation: in this study, an indicator of forest fragmentation. Patch isolation was defined as the mean distance (m) to the nearest forest patch in eight 45^{o} arcs radiating from the site centre. The distance from patch edge to patch edge was measured to the nearest 50 metres on a 1:50,000 scale National Topographic Service (NTS) map sheet with the aid of a Staedtler-Mars ratio scale.

Forest Cover: in this study, an indicator of forest fragmentation. Forest cover was defined as the percent forest cover within a 5 km x 5 km square centred on the study site. In contrast to the

previous data set. this approach includes forest cover within the sampled patch and thus accounts for total forest cover within the vicinity of the vegetation sample. The forest cover on a 1:50.000 scale National Topographic Service (NTS) map sheet was calculated with the aid of a dot grid.

2.2.3.7 Supplementary Data

The following data was recorded in the field but not used in analyses reported in this thesis.

Decomposition Status: an indicator of time since death. The status of logs and standing dead stems was recorded in relation to the following classification: i) bark firm; ii) bark loose; iii) stem bare. firm; iv) stem mossy. firm; v) stem soft. bare; vi) stem soft. mossy.

Reproductive Status: The reproductive status of species was recorded in relation to the following classification: i) vegetative; ii) flowering (flower in bud or open); iii) fruiting.

Phenology: a datum that enables the reproductive status of plants to be correlated with canopy conditions. Reproductive status at the time of sampling was recorded in relation to the following classification: i) trees in bud or leaf flush; ii) trees with immature leaves. iii) trees with mature leaves; iv) trees with senescing leaves.

Herbivory Status: the herbivory status of plants was recorded in relation to the following classification: i) leaf tip bitten; ii) leaf with holes; iii) leaf with ragged edge; iv) leaf with fungal dots; v) leaf with egg cases; vi) plant decapitated. The intensity of herbivory was recorded in relation to the following classification: i) "low":one to few leaves per plant. <1% of population; ii) "intermediate": few to many leaves per plant. 1-10% of population; iii) "high": few to many leaves. >10 % of population.

2.2.4 Analytical Methods

2.2.4.1 Overview

The objectives of this thesis have been achieved by means of a series of comparative. mensurative.

experiments (Hurlburt 1984) in which a system property (species richness, species composition, species attribute) has been measured repeatedly in treatment space (environmental states, environmental gradients, microhabitats, forest patches). The experimental units in each experiment were the physical locations at which the system property was measured (Hurlburt 1984).

In mensurative experiments, pseudoreplication may arise when the sample space in which system properties are measured is smaller than the inference space implicit in the hypothesis being tested (Hurlburt 1984). In this chapter, the inference space is second-growth northern hardwood stands on Ordovician limestone in the vicinity of Peterborough, Ontario. Sample space is commensurate with this inference, since system properties were measured in treatment space across the region.

The degrees of freedom for determining a treatment effect varied with the experimental treatment since treatment conditions were rarely present in each quadrat or forest patch, or, were not statistically independent: $n \leq 192$ for system properties measured in relation to environmental states, gradients and microhabitats; $n \leq 24$ for system properties measured in relation to forest patches.

The statistical independence of samples was more apparent for some analyses than for others. While it is clear that replication within patches should not contribute degrees of freedom when testing for a treatment effect among patches, the statistical independence of two or more quadrats within a patch is less transparent when testing for a treatment effect among environmental states, gradients, or microhabitats. At issue is whether differences in disturbance history at the micro-scale sufficiently influence the composition of the seed rain, germination success, resource availability, competitive interactions, or plant persistence, for quadrats to be regarded as independent samples. Since this could not be determined, *a priori*, each quadrat was permitted to contribute one degree of freedom when testing for a treatment effect among environmental states, gradients or microhabitats. The effects of patch membership, if present, were subsequently removed by treating patch membership as a co-variable in multivariate analyses.

2.2.4.2 Distribution of Species on Environmental Gradients

Analysis #1: The tendency for the composition of species to be more similar within, than among, forest patches was investigated in order to evaluate the relative influence of local processes, such as short-distance dispersal and competitive exclusion, and regional processes, such as glaciation and pedogenesis.

Similarities in species composition were investigated by detrended correspondence analysis (DCA) (Jongerman *et al.* 1987). The degree to which quadrats were clustered within patches was assessed visually. The contribution of patch membership to the dispersion of quadrats was evaluated in canonical correspondence analysis (CCA) by the Monte Carlo permutation test (n=1000 permutations), after fitting all remaining environmental variables as co-variables. DCA was the preferred method for the pattern analysis since the dispersion of quadrats is governed by species relations with the underlying environment rather than with the set of variables chosen for study. DCA was preferred to correspondence analysis (CA) since the latter ordination displayed a pronounced arch that distorted the order of quadrats along the second axis. All analyses were performed in CANOCO Version 3.12 (ter Braak 1991). The DCA ordination diagram is presented Figure 2.1.

Analysis # 2: The distribution of species on environmental gradients was examined by canonical correspondence analysis (CCA) in order to determine which environmental variables exerted the greatest influence on the composition of herb assemblages. Patch membership was treated as a co-variable in this analysis to minimize the contribution of replicate samples within patches when testing for an overall treatment effect on the dispersion of species in ordination space. The variable "number of live tree stems >1m" was omitted from the analysis due to high collinearity (variance inflation factor =36.6) with the variable "number of stems 0-4 cm dbh". Ordination scores were scaled in relation to scaling mode 2 (i.e. species scores are weighted mean sample scores) since the primary interest was the dispersion of species rather than quadrats (ter Braak 1994). Species in ordination space are therefore situated at the centroid of the quadrats (not shown) in which they occur. The relative importance of each environmental variable is represented by an arrow that points

in the direction of maximum influence and that is scaled to reflect the strength of the correlation between the variable and the fitted abundance of the plotted species (ter Braak 1994). The scaled co-ordinates for the head of each arrow are the biplot scores for the first and second axis (ter Braak 1994). An overall test of significance of the species ordination was determined by the Monte Carlo permutation test (n=9.999 permutations). All analyses were performed in CANOCO version 3.12 (ter Braak 1991). The scatter plot was created in S-Plus. Version 4.5 (Mathsoft Inc.1998) and annotated in Publisher 98 (Microsoft Corporation 1998). The CCA ordination diagram is presented in Figure 2.2.

Analysis #3: The relative importance of environmental variables was examined further by determining the percentage of the total inertia explained by each variable. The percent inertia explained was computed as the (Σ canonical eigenvalues for each variable $\div$ Σ unconstrained eigenvalues for the ordination) x 100. Since most environmental variables interacted with at least one other variable, the fraction of inertia that was uniquely explained by each variable was also determined by fitting all remaining variables as co-variables. The significance of the latter value was determined by the Monte Carlo permutation test (n=1,000 permutations), after Bonferroni correction for n=16 tests ($p<0.003$). All analyses were performed in CANOCO, Version 3.12 (ter Braak 1991). The results of this analysis are presented in Table 2.13.

Analysis #4: The distribution of species on the principal environmental gradients was examined further to determine if species were restricted to a particular edaphic condition, forest cover type, or disturbance state. This analysis was conducted in relation to variables that had the highest inter-set correlations with the first or second axis of the CCA ordination. The percentage of taxa restricted to a given soil parent material, soil order and forest cover type was evaluated at the quadrat spatial scale; the percentage of taxa restricted to a given moisture condition and disturbance class was evaluated at the quadrat scale. The analysis was performed in JMP Version 3.2.2. (SAS Institute Inc. 1997); results are presented in Table 2.14.

Analysis #5: The variance explained by environmental variables in Analysis # 2 was decomposed

(Quinghong and Brakenhielm 1995) to determine the relative contribution of edaphic variables, patch variables, and landscape variables, to the dispersion of species scores in ordination space. This was undertaken to clarify the relative importance of local versus regional processes (*sensu* Ricklefs and Schluter 1993) in the distribution of understory herbs.

The method of Quinghong and Brakenhielm (1995) enables one to determine the degree of interaction among variables, and, to determine the independent (unique) contribution of each variable. For this analysis, regional processes such as glaciation and pedogenesis are considered to be the primary contributors to properties of the edaphic variables (soil parent material, soil order, soil moisture class, percent soil organic matter, and soil pH), and, plant migration is considered to be the principal means by which propagules are distributed across the landscape. Recruitment limitation is considered to be a consequence of regional processes when due to soil based factors. Local processes, such as short-distance dispersal, competitive interactions, and heterogeneity arising from the death or removal of canopy trees, are considered to be the primary contributors to patch dynamics and to local species composition. The "patch scale" variables for this analysis were forest cover type, percent canopy closure, stem diameter class, number of tree species, number of tree stems, number of microhabitats, open microhabitats, disturbed microhabitats, and patch membership. Landscape variables (patch isolation and patch size) were considered to reflect the degree of migration constraint inherent in the spatial configuration of forest patches in the present-day landscape.

The results of this analysis were summarized in a Venn diagram that displays the percentage of the explained variance uniquely, and jointly, accounted for by edaphic, patch, and matrix (landscape) variables. The analysis was performed in CANOCO Version 3.12 (ter Braak 1991). The Venn diagram, presented in Figure 2.3, was created in Publisher 98 (Microsoft Corporation 1998).

2.2.4.3 Distribution of Species in Forest Microhabitats

Analysis #1: The response of species to the pragmatic classification of microhabitats was investigated by detrended correspondence analysis (DCA). At issue was the degree to which the

composition of species differed among habitat types. The significance of the ordination was assessed in relation to the criterion that habitats separated by 4 or more standard deviation units on the first or second axis should have few if any species in common (ter Braak 1987). The Monte Carlo permutation test cannot be performed on DCA scores in CANOCO Version 3.12. CCA was not suitable for this analysis since the habitat categories represented a nested set of environmental states within microhabitats rather than discrete or continuous variables within quadrats. The analysis was performed in CANOCO Version 3.12 (ter Braak 1991). The DCA ordination diagram is presented in Figure 2.4; the number of habitats occupied by surveyed taxa is presented in Table 2.15.

Analysis #2: The species composition of canopy gaps was investigated further to determine the influence of canopy-opening size on species composition. Ten size classes were established for the ordination analysis: 0-10 m^2, 11-20 m^2, 21-30 m^2, 31-40 m^2, 41-50 m^2, 51-60 m^2, 61-70 m^2, 71-80 m^2, 81-90 m^2, 91-100 m^2. The species composition of small gaps was expected to be similar to that of closed, seasonally dry, forest floors. If gap size were the primary determinant of species composition in canopy openings, then gaps of a given size should cluster in ordination space, and, gaps of increasing size should cluster at increasing distance from the reference condition. Gaps that were separated by 4 or more standard deviation units were expected to have few if any species in common (ter Braak 1987).The analysis was performed in CANOCO Version 3.12 (ter Braak 1991). The DCA diagram is presented in Figure 2.5.

Analysis #3: The distribution of species across habitats was assessed to determine the degree to which environmental heterogeneity in the forest understory has been utilized by plants. A restricted distribution pattern was considered support for the view that heterogeneity increases the species richness of forest patches primarily through the provision of novel resources, whereas, a pattern of widespread use was considered support for the view that heterogeneity maintains the richness of forest patches primarily through the spatial segregation of competing species.

Four broad habitat categories were established for the analysis: closed dry forest floors, *sensu stricto*; natural disturbance features (canopy gaps, tree pits, tip-up mounds, stumps, logs); human disturbance

(regenerating fields, lanes, ditches); and moist or wet habitats (forest floors, depressions, seeps, riparian meadow, riparian marsh and riparian thicket). The distinction between natural and human disturbance is somewhat forced since many of the stumps and canopy gaps in this study were created by selective logging. The effect on the forest canopy, however, is similar to natural tree fall. The analysis was performed in JMP Version 3.2.2. (SAS Institute Inc. 1997) and EXCEL Version 7.0a (Microsoft Corporation 1996). The results of this analysis are presented in Figure 2.6.

2.2.4.4 Distribution of Sugar Maple on a Moisture-Fertility Gradient

Analysis #1: Species richness in sampled forest stands was inversely correlated with sugar maple abundance (Chapter 4.0). This pattern was especially evident on mesic soils overlying calcareous till where sugar maple abundance explained 63.0% of the variance in species richness in undisturbed stands. The distribution and abundance of sugar maple at small spatial scales has recently been attributed to differences in the availability of calcium ions in the soil profile (Kobe *et al.* 1995, Kobe 1996). The structure of sugar maple stands in this study was subsequently examined on a gradient of increasing calcium availability to determine if there was evidence of increased sugar maple survivorship on calcium rich soils.

The analysis was initially restricted to undisturbed stands on Brunsolic and Luvisolic soils, overlying calcareous till, in order to standardize samples with respect to soil parent material, soil moisture, and recent site disturbance. Soils with free calcium carbonate in the upper 15 cm of the soil profile (positive reaction to 0.1N HCl) were excluded from this analysis in order to standardize samples with respect to exchangeable calcium (see contrasting treatment in Analysis 2). The analysis was further restricted to quadrats with forest cover type 2 (sugar maple + red or white oak) and forest cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, trees) in order to standardize samples with respect to forest cover. N = 29 10m x 10m quadrats in 7 forest patches.

Stand structure was evaluated in relation to four size classes: 0-4 cm, 4-10 cm, 10-30 cm, and >30 cm, dbh. Sugar maple abundance was evaluated in relation to absolute and relative abundance. The relationship between sugar maple abundance and calcium availability was evaluated in simple linear

regression. The analysis was performed in JMP Version 3.2.2. (SAS Institute Inc. 1997). The results are presented in Figure 2.7.

Analysis #2: The relationship between stand structure and calcium availability was re-examined in undisturbed stands on Brunisolic soils in order to standardize samples for soil parent material (calcareous till), soil order (Orthic Melanic Brunisol) and soil series (Otonabee loam). Soils with free calcium carbonate in the upper 15 cm of the soil profile were included in this analysis, in order to standardize samples with respect to *available* calcium. This analysis, as before, was restricted to quadrats with forest cover types 2 and 3, in order to standardize samples with respect to forest cover. This sample (N = 17 quadrats in 3 forest patches) provided the most uniform subset of quadrats in which to assess the response of sugar maple to differences in available calcium.

Stand structure was evaluated in relation to four size classes: 0-4 cm, 4-10 cm, 10-30 cm, and >30 cm, dbh. Sugar maple abundance was evaluated in relation to absolute and relative abundance. The relationship between sugar maple abundance and calcium availability was evaluated in simple linear regression. The analysis was performed in JMP Version 3.2.2. (SAS Institute Inc. 1997). The results are presented in Figure 2.8.

Analysis #3: The response of shade tolerant and intolerant herbs to increasing calcium availability and sugar maple abundance was examined in order to test the presumption of declining light levels on calcium rich soils. This analysis was extended to determine the calcium affinity of understory plants in relation to flowering phenology. Of interest was the degree to which life histories attributed to shade avoidance, early spring flowering and an ephemeral life history, were associated with calcium rich soils. Early spring flowering plants with persistent shoots were contrasted with mid to late season flowering plants to determine if calcium affinity were associated with the degree to which the life cycle was completed after canopy closure. Ephemeral and early spring flowering plants were classified in relation to Rogers 1982, and, to flowering data collected during the spring and summer vegetation survey. June 1st was taken to be the transition date between early and mid to late season flowering. Although leaf expansion may proceed as late as the summer solstice, the

forest canopy was typically well developed by June 1st.

As in Analysis # 1, this analysis was restricted to undisturbed stands on Brunisolic and Luvisolic soils, overlying calcareous till, in order to standardize samples with respect to soil parent material, soil moisture, and recent site disturbance. Soils with free calcium carbonate in the upper 15 cm of the soil profile were excluded from the analysis in order to standardize samples with respect to exchangeable calcium. The analysis was restricted to quadrats with forest cover type 2 (sugar maple + red or white oak) and forest cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, trees) in order to standardize samples with respect to forest cover. N = 29 10m x 10m quadrats in 7 forest patches.

Shade tolerance was evaluated by simple linear regression; calcium affinity in relation to flowering affinity was evaluated by Wilcoxon rank sum test. The analyses was performed in JMP Version 3.2.2. (SAS Institute Inc. 1997). The results are presented in Figures 2.9 and 2.10.

2.2.4.5 Distribution of Plant Attributes on Environmental Gradients

The distribution of selected plant attributes on environmental gradients was examined in order to determine the degree to which the distribution of species may be explained by life form, life history, provenance, habitat affinity, shade tolerance and moisture affinity.

Analysis #1: The degree to which the selected attributes explained the dispersion of species scores in ordination space was investigated in CCA. The response variable was the proportion of taxa in a 10m x 10m quadrat with the attribute of interest. The significance of each contribution was determined by the Monte Carlo permutation test (n=1000 permutations). The analysis was performed in CANOCO Version 3.12 (ter Braak 1991). The results of the analysis are presented in Tables 2.16, 2.17 and 2.18.

Analysis #2: The distribution of provenance, habitat affinity and moisture affinity was summarized by microhabitat to provide contextual information for the interpretation of dispersal modes in

Chapter 3. The response variable was the proportion of taxa (all life forms) in each habitat with the attribute of interest. The analysis was performed in JMP, Version 3.2.2. (SAS Institute Inc. 1997). The results are presented in Table 2.19.

2.3 Results

The tendency for species to be associated with particular environmental states and gradients will be reported in relation to the following headings: vegetation survey, relationships among environmental variables, species response to environmental gradients, species response to forest microhabitats, response of sugar maple and understory herbs to available calcium, local versus regional processes, and plant attributes.

2.3.1 Vegetation Survey

A summary of surveyed taxa by taxonomic rank, life form, life history and provenance is presented in Table 2.4. A summary of plant attributes by species is presented in Appendix2; a cross-referenced list of species codes is presented in Appendix 3. The distribution of species by soil parent material, soil moisture and canopy closure is presented in Appendix 4. A listing of species by microhabitat is presented in Appendix 5. The distribution of species by microhabitat is presented in Appendices 6 and 7.

The sampled flora was composed of 413 species, 208 genera, 78 families and 45 orders. Twelve species occurred in ≥50% of the quadrats surveyed: *Acer saccharum* (91.1%), *Trillium grandiflorum* (71.9%), *Maianthemum canadense* (67.8%), *Epipactis helleborine* (67.8%), *Prunus virginiana* (64.1%), *Carex pensylvanica* (62.5%), *Tilia americana* (55.7%), *Erythronium americanum* (55.7%), *Dryopteris carthusiana* (55.7%), *Galium triflorum* (54.7%), *Taraxacum officinale* (52.0%) and *Arisaema triphyllum* (50.5%). The three most species rich genera were *Carex* (43 taxa), *Viola* (10 taxa), and *Aster* (9 taxa). The three most genus rich families were Asteraceae (24 genera), Poaceae (21 genera) and Rosaceae (10 genera). The three most family rich orders were: Polypodiales (5 families), Ranunculales (4 families) and Solanales (4 families).

Table 2.4. Summary of surveyed taxa by taxonomic rank, life form, life history and provenance. Life history: annual *s.s* = annual; biennial *s.l.*= biennial, annual/biennial; perennial *s.l.* = perennial, annual/perennial, biennial/perennial.

Plant Attribute	# Taxa	% (n=413)
TAXONOMIC RANK		
species	413	100.0
genus	208	-
family	78	-
order	45	-
LIFE FORM		
tree	30	7.3
shrub	55	13.3
vine	9	2.2
fern	23	5.6
fern ally	8	1.9
grass	36	8.7
herb	252	61.0
LIFE HISTORY		
annual *s.s.*	13	3.1
biennial *s.l.*	22	5.3
perennial *s.l.*	372	90.1
unclassified	6	1.5
PROVENANCE		
native	349	84.5
alien	58	14.0
unknown	6	1.5

Herbs were the most abundant life form (61.0% of surveyed taxa), followed by shrubs (13.3%), grasses (8.7%), trees (7.3%) and ferns (5.6%). The least abundant life forms were vines (2.2% and fern allies (1.9%). Most taxa were perennials (90.1%). Plants with biennial life histories (5.3%) were more abundant than plants with annual life histories (3.1%). The provenance of most taxa was native (84.5%) .

The cover class of surveyed taxa in 10m x 10m quadrats is summarized by life form, life history, provenance, and habitat affinity in Table 2.5. The median cover for each element in the analysis was cover class 2 (0.5-1.0% cover). The maximum cover recorded was cover class 7 (50-75% cover). The life forms with the highest mean cover were the grasses (2.40) and fern allies (2.37). Plants with annual life histories had significantly greater mean cover (2.65) than plants with perennial (2.08) or biennial (1.88) life histories. The mean cover class of native taxa (2.12) was significantly greater than alien species (1.82). Plants with an affinity for "forest + open" habitats had a signficantly higher mean cover (2.20) than plants with affinities for other habitats (1.79-2.11). Overall, plants with the lowest mean cover were plants with affinity for "open" habitats (1.79), alien species (1.82) and plants with biennial life histories (1.88).

The habitat affinity rating assigned to understory species is reported in Appendix 2. Species classified as occurring exclusively in forested habitats ("F") included: *Arisaema triphyllum*, *Maianthemum racemosa*, *Caulophyllum thalictroides*, *Solidago flexicaulis*, and, *Carex arctata*. Species classified as occurring primarily in forested habitats ("F+O") included: *Trillium grandiflorum*, *Erythronium americanum*, *Dryopteris carthusiana*, *Carex pedunculata*, and *Corylus cornuta*. Species classified as occurring primarily in open habitats ("O+F") included: *Carex pensylvanica*, *Taraxacum officinale*, *Impatiens capensis*, *Fragaria virginiana*, and *Poa pratensis*. Species classified as occurring exclusively in open habitats ("O") included: *Ranunculus acris*, *Asclepias syriaca*, *Daucus carota*, *Lactuca serriola*, and *Vicia cracca*.

A checklist of surveyed taxa is presented in alphabetical order by family in Table 2.6.

Table 2.5. Cover class of surveyed taxa in herb layer in10m x 10m quadrats by life form, life history, provenance and habitat affinity. Life history: annual *s.s* = annual; biennial *s.l.*= biennial, annual/biennial; perennial *s.l.* = perennial, annual/perennial, biennial/perennial. Cover class: 1=<0.5% cover, 2=0.5-1.0% cover, 3=1.0-3.0% cover, 4=3-15% cover, 5=15-25% cover, 6=25-50% cover, 7=50-75% cover, 8=75-100% cover. Highest value in bold when difference among attributes within category significant at p<0.05, after Bonferroni correction for n=16 tests. Wilcoxon rank sum tests, by column, independent samples.

	Cover Class		
Plant Attribute	Mean	Median	Range
LIFE FORM			
tree	1.95	2	1-7
shrub	2.05	2	1-7
vine	1.80	2	1-5
fern	2.21	2	1-6
fern ally	2.37	2	1-5
grass	**2.40**	2	1-6
herb	2.11	2	1-7
LIFE HISTORY			
annual *s.s.*	**2.65**	2	1-7
biennial *s.l.*	1.88	2	1-4
perennial *s.l.*	2.08	2	1-7
PROVENANCE			
native	**2.12**	2	1-7
alien	1.82	2	1-6
HABITAT AFFINITY			
forest	2.11	2	1-7
forest + open	**2.20**	2	1-7
open + forest	2.09	2	1-7
open	1.79	2	1-6

Table 2.6. Check list of surveyed taxa by family (alphabetical order).

ACERACEAE

Acer negundo L.

Acer rubrum L.

Acer saccharinum L.

Acer saccharum Marshall ssp. *saccharum*

Acer saccharum Marshall ssp. *nigrum* (Michaux f.) Desmarais

Acer spicatum Lam.

ANACARDIACEAE

Rhus radicans L. ssp. *negundo* (E. Greene) McNeill

Rhus typhina L.

APIACEAE

Cicuta bulbifera L.

Cicuta maculatum L.

Cryptotaenia canadensis (L.) DC.

Daucus carota L.

Osmorhiza claytonii (Michaux) C.B. Clarke

Sanicula marilandica L.

Sanicula trifoliata Bickn.

Sanicula species

APOCYNACEAE

Apocynum androsaemifolium L. ssp. *androsaemifolium*

ARACEAE

Arisaema triphyllum (L.) Schott ssp. *triphyllum*

ARALIACEAE

Aralia nudicaulis L.

Panax quinquefolium L.

ARISTOLOCHIACEAE

Asarum canadense L.

ASCLEPIADACEAE

Asclepias incarnata L. ssp. *incarnata*

Asclepias syriaca L.

ASTERACEAE

Achillia millefolium L. ssp. *millefolium*

Ambrosia artemisiifolia L.

Antennaria neglecta E. Greene

Arctium minus (Hill) Bernh. ssp. *minus*

Aster ciliolatus Lindley

Aster cordifolius L.

Aster ericoides L.

Aster lanceolatus L.

Aster lateriflorus (L.) Britton

Aster macrophyllus L.

Aster novae-angliae L.

Aster puniceus L.

Aster umbellatus Miller

Bidens frondosa L.

Carduus acanthoides L.

Carduus nutans L.

Chrysanthemum leucanthemum L.

Cirsium arvense (L.) Scop.

Cirsium vulgare (Savi) Ten.

Conyza canadensis (L.) Cronq.

Erigeron annuus (L.) Pers.

Erigeron philadelphicus L. ssp. *philadelphicus*

Erigeron strigosus Muhlenb. ex. Willd.

Erigeron species

Table 2.6. Check list of surveyed taxa by family (alphabetical order).

Eupatorium maculatum L.

Eupatorium perfoliatum L.

Eupatorium rugosum Houtt.

Euthamia graminifolia (L.) Nutt.

Hieracium aurantiacum L.

Hieracium caespitosum Dumort. ssp. *caespitosum*

Lactuca canadensis L.

Lactuca serriola L.

Lactuca species

Onopordon acanthium L.

Prenanthes species

Rudbeckia hirta L.

Solidago altissima L.

Solidago caesia L.

Solidago canadensis L.

Solidago flexicaulis L.

Solidago gigantea Aiton

Solidago juncea Aiton

Solidago nemoralis Aiton

Solidago rugosa Aiton ssp. *rugosa*

Sonchus arvensis L.

Sonchus oleraceus L.

Taraxacum officinale G. Weber

Tragopagon dubius Scop.

Tussilago farfara L.

BALSAMINACEAE

Impatiens capensis Meerb.

BERBERIDACEAE

Caulophyllum thalictroides (L.) Michaux

Podophyllum peltatum L.

BETULACEAE

Alnus incana (L.) Moench ssp. *rugosa* (Duroi) Clausen

Betula alleghaniensis Britton

Betula papyrifera Marshall

Corylus cornuta Marshall

Ostrya virginiana (Miller) K. Koch

BORAGINACEAE

Hackelia virginiana (L.) I.M. Johnston

BRASSICACEAE

Cardamine diphylla (Michx.) A. Wood

Cardamine pensylvanica Muhlenb. ex Willd.

CAMPANULACEAE

Lobelia inflata L.

Lobelia species

CAPRIFOLIACEAE

Diervilla lonicera Miller

Lonicera canadensis Bartram

Lonicera dioica L.

Lonicera hirsuta Eaton

Lonicera oblongifolia (Goldie) Hook.

Sambucus canadensis L.

Sambucus racemosa L. ssp. *pubens* (Michaux) House

Triosteum aurantiacum E. Bickn.

Viburnum acerfolium L.

Viburnum lentago L.

Viburnum opulus L.

Viburnum trilobum Marshall

Table 2.6. Check list of surveyed taxa by family (alphabetical order).

CARYOPHYLLACEAE

Cerastium fontanum Baumg. ssp. *triviale* (Link) Jalas

Dianthus armeria L.

Silene vulgaris (Moench) Garcke

Stellaria longifolia Muhlenb. ex Willd.

CELASTRACEAE

Celastrus scandens L.

CLUSIACEAE

Hypericum perforatum L.

CONVOLVULACEAE

Calystegia sepium L.

CORNACEAE

Cornus alternifolia L.f.

Cornus foemina Miller ssp. *racemosa* (Lam.) J.S. Wilson

Cornus rugosa Lam.

Cornus stolonifera Michaux

CUCURBITACEAE

Echinocystis lobata (Michaux) Torrey & A. Gray

Sicyos angulatus L.

CUPRESSACEAE

Thuja occidentalis L.

CYPERACEAE

Carex albursina E. Sheldon

Carex alopecoidea Tuckerman

Carex arctata Boott

Carex backii F. Boott

Carex bebbii (L. Bailey) Olney ex Fern.

Carex blanda Dewey

Carex brevior (Dewey) Mackenzie ex Lunell

Carex cephaloidea Dewey

Carex communis L. Bailey

Carex crinita Lam.

Carex cristatella Britton

Carex deweyana Schwein.

Carex digitalis Willd.

Carex gracillima Schwein.

Carex granularis Muhlenb. ex Willd.

Carex hirtifolia Mackenzie

Carex hitchcockiana Dewey

Carex intumescens Rudge

Carex lanuginosa Michaux

Carex laxiflora Lam.

Carex peckii Howe

Carex pedunculata Muhlenb. ex Willd.

Carex pensylvanica Lam.

Carex plantaginea Lam.

Carex platyphylla J.Carey

Carex prairea Dewey

Carex projecta Mackenzie

Carex pseudo-cyperus L.

Carex radiata (Wahlenb.) Small

Carex retrorsa Schwein.

Carex rosea Schk. ex Willd.

Carex sparganioides Muhlenb. ex Willd.

Carex stipata Muhlenb. ex Willd.

Carex tenera Dewey

Carex tribuloides Wahlenb.

Table 2.6. Check list of surveyed species by family (alphabetical order).

Carex vulpinoidea Michaux

Carex woodii Dewey

Carex specimen D719

Carex specimen D858

Carex specimen D868

Carex specimen D870

Carex specimen D879

Carex Section Ovales

Carex species

Scirpus atrovirens Willd.

DENNSTAEDTIACEAE

Pteridium aquilinum (L.) Kuhn

DRYOPTERIDACEAE

Athyrium filix-femina (L.) ssp. *angustum* (Willd.) Clausen

Athyrium thelypterioides (Michaux) Desv.

Cystopteris bulbifera (L.) Bernh.

Cystopteris fragilis (L.) Bernh.

Cystopteris tenuis (Michaux) Desv.

Dryopteris carthusiana (Villars) H.P. Fuchs

Dryopteris cristata (L.) Gray

Dryopteris intermedia (Muhlenb. ex Willd.) A. Gray

Dryopteris marginalis (L.) A. Gray

Gymnocarpium dryopteris (L.) Newman ssp. *dryopteris*

Matteuccia struthiopteris (L.) Tod.

Onoclea sensibilis L.

Polystichum acrostichoides (Michaux.) Schott

EQUISETACEAE

Equisetum arvense L.

Equisetum hyemale L. ssp. *affine* (Engelm.)Stone

Equisetum laevigatum A. Braun

Equisetum scirpoides Michaux

ERICACEAE

Vaccinium angustifolium Aiton

FABACEAE

Amphicarpaea bracteata (L.) Fern.

Desmodium glutinosum (Muhlenb. ex Willd.) DC ex Loudon

Medicago lupulina L.

Melilotus alba Medikus

Melilotus officinalis (L.) Pallas

Robinia pseudoacacia L.

Trifolium repens L.

Vicia cracca L.

FAGACEAE

Fagus grandifolia Ehrh.

Quercus alba L.

Quercus macrocarpa Michaux

Quercus rubra L.

Quercus species

FUMARIACEAE

Dicentra canadensis (Goldie) Walp.

Dicentra cucullaria (L.) Bernh.

GENTIANACEAE

Gentiana andrewsii Griseb.

GERIANIACEAE

Geranium maculatum L.

Table 2.6. Check list of surveyed species by family (alphabetical order).

Geranium robertianum L.

GROSSULARIACEAE

Ribes americanum Miller

Ribes cynosbati L.

Ribes glandulosum Grauer

Ribes lacustre (Pers.) Poiret

Ribes rubrum L.

Ribes triste Pall.

Ribes specimen D827

HYDROPHYLLACEAE

Hydrophyllum virginianum L.

IRIDACEAE

Iris versicolor L.

Iris species

JUGLANDACEAE

Carya cordiformis (Wangenh.) K. Koch

JUNCACEAE

Juncus tenuis Willd.

LAMIACEAE

Galeopsis tetrahit L.

Leonurus cardiaca L. ssp. *cardiaca*

Lycopus americanus Muhlenb. ex Bartram

Lycopus uniflorus Michaux

Mentha arvensis L.

Prunella vulgaris L.

Scutellaria lateriflora L.

LILIACEAE

Allium tricoccum Aiton

Clintonia borealis (Aiton) Raf.

Erythronium americanum Ker Gawler ssp. *americanum*

Maianthemum canadense Desf.

Maianthemum racemosum (L.) Link ssp. *racemosum*

Maianthemum stellatum (L.) Link

Polygonatum pubescens (Willd.) Pursh

Streptopus roseus Michaux

Trillium erectum L.

Trillium grandiflorum (Michaux) Salisb.

Uvularia grandiflora Smith

LYCOPODIACEAE

Lycopodium annotinum L.

Lycopodium dendroideum Michaux

Lycopodium obscurum L.var. *obscurum*

Lycopodium tristachyum Pursh

MENISPERMACEAE

Menispermum canadense L.

MONOTROPACEAE

Monotropa hypopithys L.

Monotropa uniflora L.

OLEACEAE

Fraxinus americana L.

Fraxinus nigra Marshall

Fraxinus pennsylvanica Marshall

ONAGRACEAE

Circea alpina L.

Circea lutetiana L. ssp. *canadensis* (L.) Aschers. & Magnus

Epilobium ciliatum Raf.

Table 2.6. Check list of surveyed species by family (alphabetical order).

Epilobium coloratum Biehler

Epilobium leptophyllum Raf.

Epilobium parviflorum Schreber

OPHIOGLOSSACEAE

Botrychium matricariaefolium A. Braun ex Koch

Botrychium multifidum (S. Gmelin) Rupr.

Botrychium virginianum (L.) Sw.

ORBANCHACEAE

Epifagus virginiana (L.) Barton

ORCHIDACEAE

Cypripedium calceolus L.

Liparis loeselii (L.) Rich. ex Lindley

OSMUNDACEAE

Osmunda claytoniana L.

Osmunda regalis L.

OXALIDACEAE

Oxalis stricta L.

Oxalis species

PAPAVERACEAE

Sanguinaria canadensis L.

PINACEAE

Abies balsamea (L.) Miller

Picea glauca (Moench) Voss

Pinus strobus L.

Tsuga canadensis (L.) Carriere

PLANTAGINACEAE

Plantago lanceolata L.

Plantago major L.

Plantago rugelii Decne.

POACEAE

Agrostis gigantea Roth

Agrostis stolonifera L.

Brachyelytrum erectum (Schreber in Roth ex Sprengel) P. Beauv.

Bromus inermis Leysser

Cinna latifolia (Trevir.ex Goeppinger) Griseb. in Ledeb.

Dactylis glomerata L.

Danthonia spicata (L.) P. Beauv. ex Roemer & Schultes

Elymus repens (L.) Gould

Elymus virginicus L.

Festuca arundinacea Schreber

Festuca pratensis Hudson

Festuca rubra L.

Festuca subverticillata (Pers.) E. Alexeev.

Glyceria striata (Lam.) A. Hitch.

Hystrix patula Moench

Leersia oryzoides (L.) Sw.

Leersia virginica Willd.

Milium effusum L.

Muhlenbergia frondosa (Poiret in Lam.) Fern.

Muhlenbergia mexicana (L.) Trin.

Oryzopsis asperifolia Michaux

Panicum acuminatum Sw.

Panicum capillare L.

Phalaris arundinacea L.

Phleum pratense L.

Poa alsodes A. Gray

Table 2.6. Check list of surveyed species by family (alphabetical order).

Poa compressa L.

Poa palustris L.

Poa pratensis L. ssp. *pratensis*

Poa saltuensis Fern. & Wieg.

Poa species

Schizachne purpurascens (Torrey) Swallen ssp. *purpurascens*

Sphenopholis intermedia (Rydb.) Rydb.

POLEMONIACEAE

Phlox species

POLYGALACEAE

Polygala paucifolia Willd.

POLYGONACEAE

Polygonum persicaria L.

Rumex orbiculatus A. Gray

PORTULACACEAE

Claytonia caroliniana Michaux

PRIMULACEAE

Lysimachia ciliata L.

Lysimachia nummularia L.

Lysimachia terrestris (L.) Britton, Sterns & Pogg.

Trientalis borealis Raf. ssp. *borealis*

PTERIDACEAE

Adiantum pedatum L. ssp. *pedatum*

PYROLACEAE

Chimaphila umbellata (L.) Barton

Pyrola elliptica Nutt.

RANUNCULACEAE

Anemone canadensis L.

Anemone quinqefolia L.

Anemone virginiana L.

Aquilegia canadensis L.

Caltha palustris L. ssp. *palustris*

Clematis virginiana L.

Hepatica acutiloba DC.

Ranunculus abortivus L.

Ranunculus acris L.

Ranunculus hispidus Michaux

Ranunculus recurvatus Poiret ex Lam.

Thalictrum dioicum L.

Thalictrum pubescens Pursh

RHAMNACEAE

Ceanothus americanus L.

Rhamnus alnifolia L'Her.

Rhamnus cathartica L.

ROSACEAE

Agrimonia gryposepala Wallr.

Amelanchier arborea (Michaux f.) Fern.

Amelanchier interior Nielson

Amelanchier species

Crataegus species #1

Crataegus species #2

Crataegus species #3

Crataegus species

Fragaria vesca L. ssp. *americana* (Porter) Staudt

Fragaria virginiana Miller

Geum allepicum Jacq.

Geum laciniatum Murray

Table 2.6. Check list of surveyed species by family (alphabetical order).

Geum rivale L.
Geum urbanum L.
Geum species
Potentilla norvegica L.
Potentilla recta L.
Prunus serotina Ehrh.
Prunus virginiana L. spp. *virginiana*
Rosa blanda Aiton
Rosa palustris Marshall
Rubus allegheniensis Porter
Rubus idaeus L.
Rubus occidentalis L.
Rubus odoratus L.
Rubus pubescens Raf.
Rubus specimen D840

RUBIACEAE

Galium aparine L.
Galium asprellum Michaux
Galium circaezans Michaux
Galium lanceolatum Torrey
Galium obtusum Bigelow
Galium palustre L.
Galium triflorum Michaux
Galium species
Mitchella repens L.

SALICACEAE

Populus balsamifera L.
Populus grandidentata Michaux
Populus tremuloides Michaux
Salix bebbiana Sarg.
Salix discolor Muhlenb.
Salix eriocephala Michaux
Salix petiolaris Smith

SAXIFRAGACEAE

Mitella diphylla L.
Tiarella cordifolia L.

SCROPHULARIACEAE

Verbascum thapsus L.
Veronica officinalis L.
Veronica serpyllifolia L.

SMILACACEAE

Smilax herbacea L.
Smilax hispida Muhlenb.

SOLANACEAE

Solanum dulcamera L.

TAXACEAE

Taxus canadensis Marshall

THELYPTERIDACEAE

Phegopteris connectilis (Michaux) Watt
Thelypteris noveboracensis (L.) Nieuwl.
Thelypteris palustris (Salisb.) Schott

THYMELAEACEAE

Dirca palustris L.

TYPHACEAE

Typha latifolia L.

TILIACEAE

Tilia americana L.

ULMACEAE

Table 2.6. Check list of surveyed species by family (alphabetical order).

Ulmus americana L.

URTICACEAE

Boehmeria cylindrica (L.) Sw.

Laportea canadensis (L.) Wedd.

Pilea pumila (L.) A. Gray

Urtica dioica L. ssp. *gracilis*

Urtica dioica L. ssp. *dioica*

VERBENACEAE

Phryma leptostachya L.

Verbena hastata L.

Verbena urticifolia L.

VIOLACEAE

Viola affinis Le Conte

Viola blanda Willd

Viola canadensis L.

Viola cucullata Aiton

Viola labradorica Schrank

Viola pubescens Aiton

Viola rostrata Pursh

Viola sororia Willd.

VITACEAE

Parthenocissus inserta (A. Kerner) Fritsch

Vita riparia Michaux

2.3.2 Relationships Among Environmental Variables

Relationships among the principal environmental variables are summarized in Tables 2.7-2.12. The edaphic and stand structure variables included in this summary were found to strongly influence the dispersion of species in CCA and DCA ordination space (see Sections 2.3.3 and 2.3.4). The patterns of association reported in this section provide general context for analyses reported in this, and later, chapters. A summary of environmental variables by quadrat is presented in Appendices 8-10.

The distribution of influential variables in relation to soil parent material is presented in Table 2.7. The frequency of edaphic variables varied by parent material. Seasonally dry depressions were more frequent than expected on glacio-fluvial materials, whereas, seasonally moist depressions were more frequent on lacustrine materials and less frequent on glacio-fluvial materials, respectively.Seasonally wet depressions were over-represented on calcareous outwash materials. Soil pH, available calcium, and percent soil organic matter, achieved their highest values on lacustrine parent materials.

In contrast, the frequency of forest cover types rarely differed on soil parent materials. The exceptions were oak - sugar maple stands which were over-represented on glacio-fluvial parent materials. Forest stands on calcareous outwash had the highest mean number of tree saplings 0-4 cm dbh. The latter pattern is more strongly correlated with moist and wet soils than with disturbance (see Table 4.3, Chapter 4).

The distribution of influential variables in relation to soil order is presented in Table 2.8. Seasonally dry depressions were more frequent than expected on Brunisolic soils and less frequent than expected on gleyed Brunisolic and gleyed Luvisolic soils. Seasonally wet depressions were over-represented on gleyed Luvisolic soils. Soil pH was highest on gleyed Brunisolic soils whereas available calcium and percent soil organic matter reached their highest mean values on Gleysolic soils.

Brunisolic soils were over-represented on glacio-fluvial parent materials, whereas Luvisolic soils were over-represented on calcareous outwash and under-represented on glacio-fluvial materials.

Table 2.7. Distribution of selected environmental variables by soil parent material. Cell values: number of quadrats with specified attribute (mean value of attribute for continuous variables). Chi-square tests of homogeneity, by row (categorical variables); Wilcoxon rank sum tests, independent samples, by row (continuous variables). Cell values in bold when differences among parent materials significant at $p<0.05$ after Bonferroni correction for number of cell or row tests in category. GF=glacio-fluvial, CT=calcareous till; L=lacustrine; CO=calcareous outwash. n = number of quadrats in category. Note: oak cover type excluded from analysis.

	Soil Parent Material							
Variable	GF (n=40)		CT (n=104)		L (n=8)		CO (n=40)	
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
SOIL ATTRIBUTES								
seasonally dry depressions	**40**	**24.6**	57	63.9	0	4.9	21	24.6
seasonally moist depressions	**0**	**8.8**	32	22.8	**8**	**1.8**	2	8.8
seasonally wet depressions	0	6.7	15	17.3	0	1.3	**17**	**6.7**
soil pH	5.9		6.8		**6.9**		6.7	
available calcium (cmol/kg)	5.1		14.1		**58.5**		8.1	
% soil organic matter	5.5		14.5		**69.2**		10.1	
SOIL ORDER								
brunisol	**40**	**14.6**	26	37.9	0	2.9	4	14.6
gleyed brunisol	0	5.4	22	14.1	0	1.1	4	5.4
luvisol	**0**	**11.9**	32	30.9	0	2.4	**25**	**11.8**
gleyed luvisol	0	6.5	16	16.8	**8**	**1.3**	7	6.5
gleysol	0	1.7	8	4.3	0	0.3	0	2.9
FOREST COVER TYPE								
oak	0		0		0		1	
oak + sugar maple	**30**	**11.3**	20	29.3	0	2.3	0	2.9
sugar maple	10	15.4	44	40.1	1	3.1	0	2.9
sugar maple + wet mesic/wet	0	10.4	35	27.1	6	2.1	0	2.9
wet mesic /wet	0	2.7	5	7.0	1	0.5	0	2.9
STAND STRUCTURE								
% canopy closure	87.7		86.5		85.8		82.1	
# live stems 0-4cm dbh	28.8		42.1		59.0		**60.0**	

Table 2.8. Distribution of selected environmental variables by soil order. Cell values: number of quadrats with specified attribute (mean value of attribute for continuous variables). Chi-square tests of homogeneity, by row (categorical variables); Wilcoxon rank sum tests, independent samples, by row (continuous variables). Cell values in bold when differences among soil orders significant at $p<0.05$ after Bonferroni correction for number of cell or row tests in category. B=brunisol; gB=gleyed brunisol; L=luvisol; gL=gleyed luvisol; G=gleysol. n = number of quadrats in category. Note: oak cover type excluded from analysis.

	Soil Order									
Variable	B (n=70)		gB (n=26)		L (n=57)		gL (n=31)		G (n=8)	
SOIL ATTRIBUTES										
seasonally dry depressions	**67**	**43.0**	**1**	**16.0**	50	35.0	**0**	**19.1**	0	4.9
seasonally moist depressions	0	15.3	19	5.7	1	12.5	18	6.8	4	1.8
seasonally wet depressions	3	11.7	6	4.3	6	9.5	**13**	**5.2**	4	1.3
soil pH	6.4		**7.6**		6.4		6.7		7.2	
available calcium (cmol/kg)	6.8		16.5		6.5		28.1		**37.4**	
% soil organic matter	6.3		14.0		8.9		33.6		**41.0**	
SOIL PARENT MATERIAL										
glacial-fluvial	**40**	**14.6**	0	5.4	**0**	**11.9**	0	6.5	0	1.7
calcareous till	26	37.9	22	14.1	32	30.9	16	16.8	8	4.3
lacustrine	0	2.9	0	1.1	0	2.4	**8**	**1.3**	0	0.3
calcareous outwash	4	14.6	4	5.4	**25**	**11.9**	7	6.5	0	1.7
FOREST COVER TYPE										
oak	0		0		1		0		0	
oak + sugar maple	**45**	**19.9**	0	7.4	9	15.8	0	8.8	0	2.3
sugar maple	19	27.1	4	10.1	**43**	**21.7**	8	12.0	0	3.1
sugar maple + wet mesic/wet	2	18.3	18	6.8	4	14.7	**22**	**8.1**	4	2.1
wet mesic /wet	4	4.8	4	1.8	0	3.8	1	2.1	**4**	**0.5**
STAND STRUCTURE										
% canopy closure	85.4		83.6		87.6		84.0		90.1	
# live stems 0-4cm dbh	39.7		**70.8**		42.6		40.9		13.5	

Table 2.9. Distribution of selected environmental variables by soil moisture class. Cell values: number of quadrats with specified attribute (mean value of attribute for continuous variables). Chi-square tests of homogeneity, by row (categorical variables); Wilcoxon rank sum tests, independent samples, by row (continuous variables). Cell values in bold when differences among moisture classes significant at $p<0.05$ after Bonferroni correction for number of cell or row tests in category. Dry=quadrat with seasonally dry depressions; Moist=quadrat with seasonally moist depressions; Wet=quadrat with seasonally wet depressions. n = number of quadrats in category. Note: oak cover type excluded from analysis.

	Soil Moisture Class					
Variable	Dry (n=117)		Moist (n=42)		Wet (n=33)	
	obs.	exp.	obs.	exp.	obs.	exp.
SOIL ATTRIBUTES						
soil pH	6.4		**7.1**		6.7	
available calcium (cmol/kg)	6.6		**31.4**		16.6	
% soil organic matter	7.3		**27.7**		20.8	
SOIL PARENT MATERIAL						
glacial-fluvial	**40**	**24.6**	**0**	**8.8**	0	6.7
calcareous till	57	63.9	32	22.8	15	17.3
lacustrine	0	4.9	**8**	**1.8**	0	1.3
calcareous outwash	21	24.6	2	8.8	**17**	**6.7**
SOIL ORDER						
brunisol	**67**	**43.0**	**0**	**15.3**	3	11.7
gleyed brunisol	**1**	**16.0**	**19**	**5.7**	6	4.3
luvisol	50	35.0	1	12.5	6	9.5
gleyed luvisol	**0**	**19.1**	**18**	**6.8**	**13**	**5.2**
gleysol	0	4.9	4	1.8	4	1.3
FOREST COVER TYPE						
oak	1		0		0	
oak + sugar maple	**54**	**33.1**	**0**	**16.3**	0	9.0
sugar maple	59	45.3	10	11.0	5	12.4
sugar maple + wet mesic/wet	**3**	**30.6**	**29**	**11.0**	**18**	**8.4**
wet mesic /wet	1	8.0	3	2.6	**9**	**2.2**
CANOPY CLOSURE						
% canopy closure	87.7		86.0		80.7	
# live stems 0-4cm dbh	39.9		50.3		49.6	

Table 2.10. Distribution of selected environmental variables by forest cover type. Cell values: number of quadrats with specified attribute (mean value of attribute for continuous variables). Chi-square tests of homogeneity, by row (categorical variables); Wilcoxon rank sum tests, independent samples, by row (continuous variables). Cell values in bold when differences among cover types significant at $p<0.05$ after Bonferroni correction for number of cell or row tests in category. Cover Type: 1 = red or white oak, no sugar maple; 2 = red, white oak + sugar maple; 3 = sugar maple, no red, white oak, no wet mesic or wet tree species; 4 = sugar maple + black ash, silver maple or American elm; 5 = black ash, silver maple, American elm, no sugar maple, no red, white oak. Cover Type 1 excluded from analysis. n = number of quadrats in category

	Forest Cover Type									
Variable	1 (n=1)		2 (n=54)		3 (n=75)		4 (n=49)		5 (n=13)	
	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.	exp.
SOIL ATTRIBUTES										
seasonally dry depressions	1		**54**	**33.1**	59	45.3	3	8.4	1	2.2
seasonally moist depressions	0		**0**	**11.9**	10	16.3	**29**	**11.0**	3	2.9
seasonally wet depressions	0		0	9.0	5	12.4	**18**	**8.4**	**9**	**2.2**
soil pH	6.2		6.1		6.6		6.9		**7.4**	
available calcium (cmol/kg)	2.1		4.6		10.3		23.0		**29.8**	
% soil organic matter	3.1		6.1		11.1		22.9		**29.9**	
SOIL PARENT MATERIAL										
glacial-fluvial	0		**30**	**11.3**	10	15.5	0	10.5	0	2.7
calcareous till	0		20	29.4	44	40.3	35	27.2	5	7.1
lacustrine	0		0	2.3	1	3.1	6	2.1	1	0.5
calcareous outwash	1		4	11.0	19	15.1	9	10.2	7	2.7
SOIL ORDER										
brunisol	0		**45**	**19.8**	19	27.1	**2**	**18.3**	4	4.8
gleyed brunisol	0		0	7.4	4	10.1	**18**	**6.8**	4	1.8
luvisol	1		9	15.8	**43**	**21.7**	4	14.6	0	3.8
gleyed luvisol	0		0	8.8	8	12.0	**22**	**8.1**	1	2.1
gleysol	0		0	2.3	0	3.1	4	2.1	**4**	**0.6**

Table 2.11. Attributes of forest stand structure by forest cover type. Cell values: mean percent of taxa in10m x 10m quadrats with specified attributes (mean number where noted); Wilcoxon rank sum tests, independent samples, by row (Cover Type 1 excluded from analysis); non-parametric median tests, by row (Cover Type 1 excluded from analysis). Highest value in bold when differences among cover types significant at $p<0.05$, after Bonferroni correction for number of tests in attribute group. Cover Type: 1 = red or white oak, no sugar maple; 2 = red, white oak + sugar maple; 3 = sugar maple, no red, white oak, no wet mesic or wet tree species; 4 = sugar maple + black ash, silver maple or American elm; 5 = black ash, silver maple, American elm, no sugar maple, no red, white oak. n = number of quadrats in category.

	Forest Cover Type				
Stand Attribute	1 (n=1)	2 (n=54)	3 (n=75)	4 (n=49)	5 (n=13)
# LIVE TREE STEMS > 1 m					
mean number	16	53.9	49.7	**68.0**	59.9
median number	-	46.0	42.0	65.0	47.0
range	0	9-121	9-168	9-152	9-181
DBH SIZE CLASS					
% stems 0-4 cm	75.0	68.4	71.0	76.1	83.5
% stems 4-10 cm	25.0	16.2	17.3	13.4	11.4
% stems 10-30 cm	0	**13.1**	9.3	8.5	2.9
% stems >30 cm	0	2.3	2.4	2.0	2.2
maximum DBH	8-10 cm Red Oak	88.0 cm White Oak	57.1 cm A. Beech	94.5 cm Silver Maple	46.4 Silver Maple
# LIVE TREE SPECIES > 1 m					
mean # species	8	6.7	4.5	**7.8**	5.6
median # species	-	6.5	4.0	**8.0**	5.0
range	0	2-12	1-10	2-12	1-12
% CANOPY CLOSURE					
mean % closure	88.5	86.5	**87.9**	85.9	70.4
median % closure	-	88.5	**90.5**	85.9	76.8
range	0	48.3-98.2	53.3-99.6	57.4-99.0	39.2-97.2

Table 2.12. Distribution of selected environmental variables by patch size. Cell values: number of quadrats with specified attribute (mean value of attribute for continuous variables). Chi-square tests of homogeneity, by row (categorical variables): Wilcoxon rank sum tests, independent samples, by row (continuous variables). Cell values in bold when differences among size classes significant at $p<0.05$, after Bonferroni correction for number of cell or row tests in category. Large=≥122 ha, Intermediate=43-121ha, Small=≤42 ha. n = number of quadrats in category. Note: oak cover type excluded from analysis.

	Patch Size Class					
Variable	Large (n=48)		Intermediate (n=95)		Small (n=49)	
	obs.	exp.	obs.	exp.	obs.	exp.
SOIL MOISTURE						
seasonally dry depressions	32	29.5	65	54.1	21	34.4
seasonally moist depressions	16	10.5	15	19.3	11	12.3
seasonally wet depressions	**0**	**8.0**	8	14.7	**24**	**9.3**
SOIL PARENT MATERIAL						
glacial-fluvial	16	10.0	24	18.3	**0**	**11.7**
calcareous till	16	26.0	56	47.7	32	30.3
lacustrine	**8**	**2.0**	0	3.7	0	2.3
calcareous outwash	8	10.0	8	18.3	**24**	**11.7**
SOIL ORDER						
brunisol	24	17.5	40	32.1	6	20.4
gleyed brunisol	0	6.5	16	11.9	10	7.6
luvisol	8	14.3	24	26.1	25	16.3
gleyed luvisol	16	7.8	**0**	**14.2**	15	9.0
gleysol	0	2.0	8	3.7	0	2.3
FOREST COVER TYPE						
oak	1		0		0	
oak + sugar maple	**24**	**13.3**	30	24.9	**0**	**15.8**
sugar maple	13	18.2	38	34.1	23	21.7
sugar maple + wet mesic/wet	9	12.3	16	23.0	25	14.7
wet mesic /wet	1	3.2	4	5.0	8	3.8

Gleyed Luvisolic soils were over-represented on lacustrine deposits. Forest stands composed of oak and sugar maple were over-represented on Brunisolic soils, whereas sugar maple stands, *sensu stricto*, were over-represented on Luvisolic soils. Stands composed of sugar maple and wet mesic or wet trees were over-represented on gleyed Luvisolic soils, whereas stands composed of wet mesic and wet species were over-represented on Gleysolic soils. Forests on gleyed Brunisolic soils had the highest mean number of live tree stems 0-4 cm dbh. The latter pattern was more strongly correlated with soil moisture than with disturbance.

The distribution of influential variables in relation to soil moisture is summarized in Table 2.9. Soil pH, available calcium, and percent soil organic matter, achieved their highest mean values in quadrats with seasonally moist depressions Stands composed of oak and sugar maple were over-represented in quadrats with dry depressions and were absent from quadrats with seasonally moist or seasonally wet depressions. Stands composed of sugar maple with wet mesic and wet species were over-represented in quadrats with seasonally moist, or seasonally wet, depressions. Stands composed of wet mesic and wet tree species were over-represented in quadrats with seasonally wet depressions.

The distribution of influential variables in relation to forest cover type is summarized in Tables 2.10 and 2.11. Soil pH, available calcium, and percent soil organic matter, achieved their highest mean values in stands dominated by wet mesic and wet trees. Patterns related to soil moisture, soil parent material and soil order were discussed previously. Stand structure variables also varied by forest cover type. Stands composed of sugar maple with oak had the highest mean percentage of stems in 10-30 cm dbh class, whereas stands composed of sugar maple, *sensu stricto*, had the highest mean, and median , percent canopy closure. Stands composed of sugar maple with wet mesic or wet species had the highest mean number of live stems, and, the highest mean, and median, number of tree species.

The distribution of influential variables in relation to patch size is summarized in Table 2.12. The greatest contrast was between large and small patches. Small patches were over-represented on

calcareous outwash materials and under-represented on glacio-fluvial materials. In keeping with this pattern, seasonally wet depressions were more frequent in small patches than in patches of intermediate or large size. Sugar maple stands with red or white oak were over-represented in large patches where soils were consistently drier than in patches of small or intermediate size.

2.3.3 Species Response to Environmental Gradients

The distribution of quadrats and patches in ordination space (DCA) is presented in Figure 2.1. In general, the species composition of quadrats tended to be more similar within, than among, forest patches. This tendency is revealed by the clustering of quadrats in patches 15, 18, and 22, lower right portion of the diagram, and by the clustering of quadrats in patches 10, 14 and 12, middle portion of the diagram. Canopy closure and moisture conditions within these patches are more uniform than in patches with quadrats that are broadly dispersed (patches 1, 3, 4, 6).

The species composition of quadrats with moist or wet depressions, seeps, and moist or wet forest floors, was typically more similar than the species composition of quadrats in upland settings. This pattern is revealed by tight quadrat clusters from dissimilar patches (e.g. quadrats from patches 4 and 20, 20 and 24, 19 and 24, 6 and 24, 6 and 19, 2 and 12, 4 and 12, 12 and 16, 2 and 6, 3 and 21, lower left portion of the diagram). A similar tendency was also observed in selected quadrats with closed forest floors or canopy gaps on dry soils (see tight clusters formed by quadrats from patches 1and 7, 9 and 18, 15 and 18, 15 and 23, 15 and 22, and, 8 and 23, lower right portion of the diagram). Several of these clusters had similar parent materials and soil orders.

Taken together, these trends suggest that the primary influence on species composition has been similarity in site conditions. However, when edaphic conditions within patches are similar, other factors such as within-patch dispersal and disturbance history may intensify the similarity in species composition within patches. The similarity in species composition in moist and wet habitats suggests that species have had an opportunity to sample most habitats within the regional landscape during the post-glacial period. Pattern in the distribution of species in the present-day landscape, therefore, may primarily reflect historic opportunities for germination and persistence. The

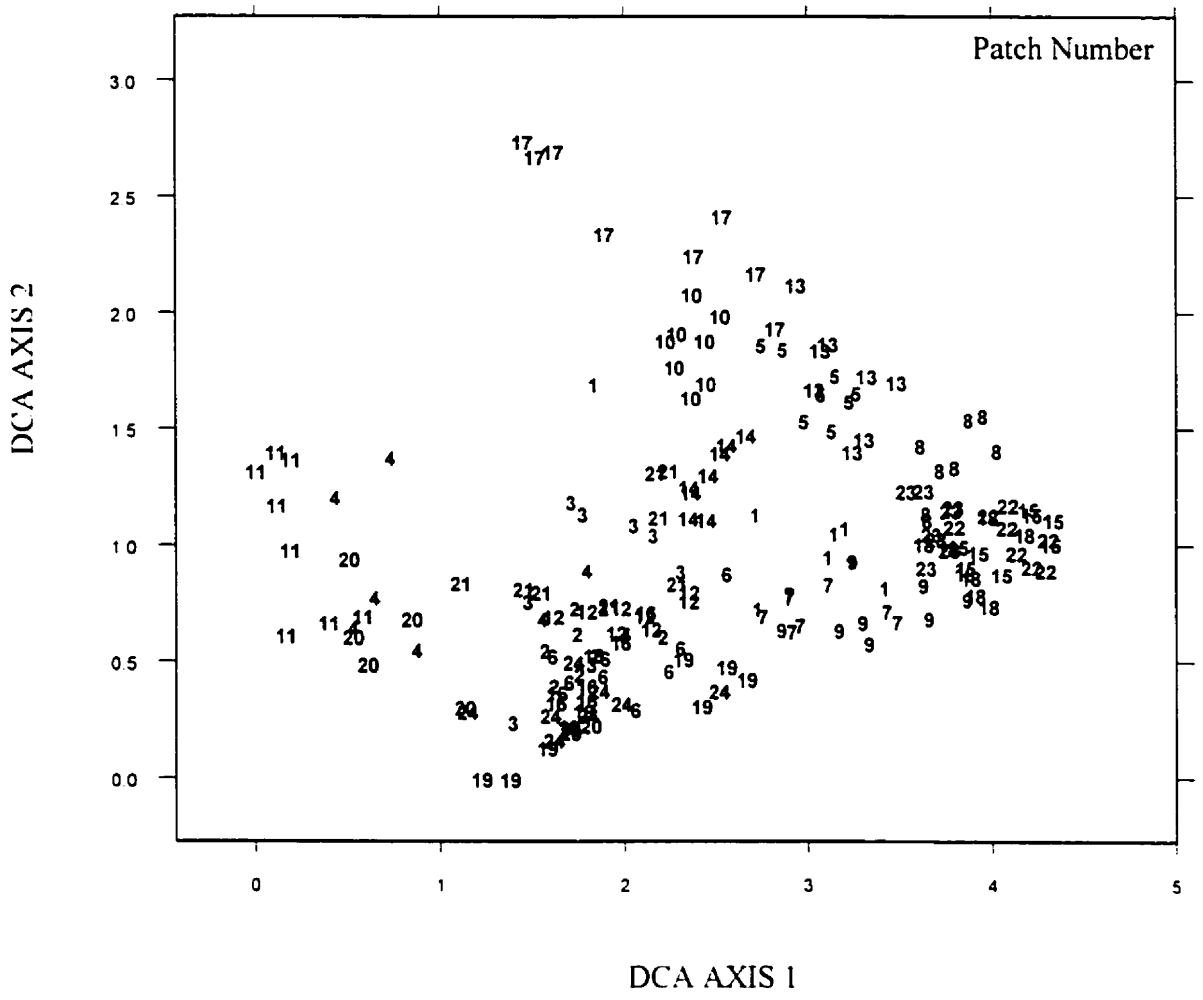

Figure 2.1. Distribution of forest patches (N=24) in relation to DCA axes 1 and 2. Note the degree to which quadrats in each patch (N=8) cluster in ordination space.

availability of propagules appears not to have been a constraint, when viewed on long time scales.

The distribution of species in CCA ordination space (Figure 2.2) was strongly influenced by gradients in soil moisture, soil order, forest cover type, percent canopy closure, and soil parent material (see inter-set correlations, Table 2.13). The ordination explains 25.6% of the total inertia in species scores ($F=3.748$, $p<0.001$, Monte Carlo permutation test, $n=9,999$ permutations), after fitting patch membership as a co-variable; the first and second axis of the ordination collectively explain 42.8% of the variance explained by submitted environmental variables.

The first axis is a complex gradient dominated by soil moisture, cover type, and soil parent material (see inter-set correlations, Table 2.13). The second axis is a complex gradient dominated by soil order and percent canopy closure. Species on the upper left side of the diagram achieved their maximum fitted abundance in closed, dry, maple-oak stands, on Brunisolic soils overlying glacio-fluvial and calcareous till parent materials. In contrast, species on the upper right side of the diagram achieved their maximum fitted abundance in open, wet forest stands dominated by wet-mesic and wet tree species, on gleyed Brunisolic soils overlying calcareous outwash. Species on the lower right side of the diagram achieved their maximum fitted abundance in closed and open, wet forest stands dominated by sugar maple and wet-mesic or wet tree species, on Gleysolic or gleyed Luvisolic soils overlying calcareous till. Species in the left-of-centre region of the ordination diagram achieved their maximum fitted abundance in closed, dry, sugar maple stands on Luvisolic and gleyed Brunisolic soils overlying calcareous till and calcareous outwash parent materials. Species in the right-of-centre region of the ordination diagram achieved their maximum fitted abundance in closed, moist and wet stands dominated by sugar maple with wet-mesic or wet species, on gleyed Luvisolic and Luvisolic soils overlying calcareous till and lacustrine parent materials.

All but four of the sixteen environmental variables had a significant influence on the dispersion of fitted species scores, after fitting all remaining variables as co-variables, and, after Bonferroni correction for $n=16$ Monte Carlo permutation tests ($n=1,000$ permutations) (Table 2.13). The non-significant variables were: # trees 0-4 cm dbh, # trees 4-10cm dbh, # microhabitats, and disturbed

Legend Figure 2.2

Annotation	Environmental Variable	Arrow Points To:
MOIST	moisture class	seasonally dry depressions
PATCHarea	patch area	largest patches
10-30cm	live tree stems 10-30 cm dbh	quadrats with highest # stems
CANCLOS	% canopy closure	high % closure (low light)
PI	patch isolation	high patch isolation
SO	soil order	gleysols
#MH	# microhabitats	quadrats with highest # microhabitats
SOM	% soil organic matter	high % soil organic matter
SPM	soil parent material	calcareous outwash
OMH	open microhabitats *s.l.*	open microhabitats
CT	cover type	wet mesic-wet trees (no sugar maple)
pH	soil pH	high soil pH
DIST	disturbance *s.l.*	quadrats with trails, regenerating fields, canopy gaps
#TS	# tree species	quadrats with highest # species
0-4cm	live tree stems 0-4cm dbh	quadrats with highest # stems

Ordination Details

1. Species in ordination space are located at the centroid of quadrats (not shown) that have the highest fitted mean abundance for the species (Scaling Mode 2).
2. The co-ordinates for the heads of arrows are the bi-plot scores for Axis 1 and Axis 2.
3. Patch membership was designated a co-variable: the effect of replicated samples within forest patches has therefore been removed from the ordination.
4. The submitted environmental variables explain 25.6% of the variance in species composition in the ordination (100 x Σ canonical eigenvalues $\div$ Σ unconstrained eigenvalues). The first and second axis collectively explain 42.8% of the variance explained by the submitted variables. The model and first axis are highly significant: F-ratio (overall test) = 3.748, $p < 0.001$; F-ratio (Axis I) = 12.074, $p < 0.001$; Monte Carlo permutation tests (n=9,999).

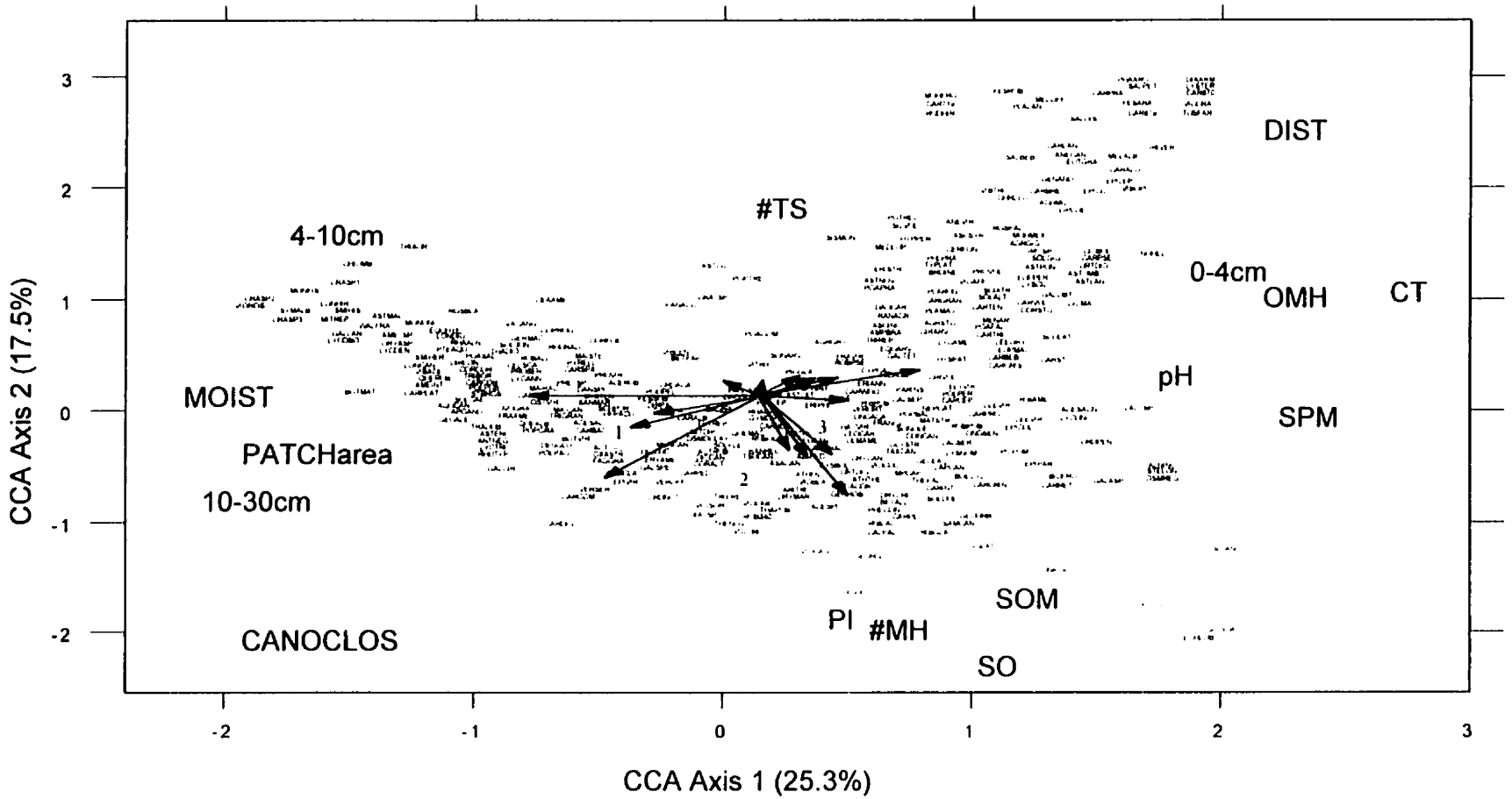

Figure 2.2. Species ordination (CCA) constrained by environmental variables. See legend for description of annotated variables. See Table 2.2 for environmental states at ends of arrows; see Appendix 3 for names of species. Species positions approximate. 1. ASTECORD, CARDDIPH, CAREARCT, CAREDEWE, CARELAXI, CAREROSE, CARPCARO, CLAYCARO, CLINBORE, EQUISCIR, HYDRVIRG, LACT-CANA, PANAQUIN, RANUABOR, RIBECYNO, SANGCANA, TILEAME, THUJOCC, VIOLPUBE; 2. ABIEBALS, ACERNEGU, ALLITRIC, CAREPLAN, CAULTHAL, CIRCLUTE, DRYOCART, DRYOINTE, FRAGVESC, MIILIEFU, POLYACRO, RUBUODOR, VERBTHAP; 3. AMBRARTE, ARCTMINU, CARERADI, CARE_868, EQUIARVE, FESTPRAT, FRAXPENN, JUNCTENU, LOBE SP, POA ALSO, POTENORV, RUMEORBI, SOLICANA, SOLIRUGO, TARAOFFI, VERBHAST.

Table 2.13. Relative importance of environmental variables in species ordination (CCA). % Total Variance = (Σ canonical eigenvalues for variable ÷ Σ unconstrained eigenvalues in the ordination) x 100, after fitting the co-variable Patch; % Unique =(Σ canonical eigenvalues for variable ÷ Σunconstrained eigenvalues in the ordination) x 100, after fitting all remaining variables as co-variables. Partial F-statistics and P-values derived from Monte Carlo permutation tests for model (n=1000 permutations) after fitting remaining variables as co-variables.

Environmental Variable	Inter-set Correlation		% Variance in Species Composition Explained			
	CCA Axis 1	CCA Axis 2	% Total Variance	% Unique	F-statistic	P-value
soil moisture	-0.721	0.164	4.7	1.8	3.10	0.001
cover type	0.709	0.248	4.5	1.3	2.30	0.001
soil parent material	0.510	0.110	3.1	1.9	3.35	0.001
% canopy closure	-0.457	-0.464	3.4	0.9	1.65	0.001
open microhabitats	0.447	0.206	2.6	1.0	1.66	0.001
soil order	0.387	0.248	4.5	1.8	3.18	0.001
trees 10-30 cm dbh	0.329	-0.080	1.9	0.8	1.44	0.001
% soil organic matter	0.326	-0.438	3.0	1.3	2.21	0.001
# microhabitats	0.292	-0.389	2.0	0.7	1.22	0.090
disturbed microhabitats	0.284	0.219	1.8	0.8	1.33	0.030
patch area	-0.274	-0.072	1.6	1.4	2.51	0.001
patch isolation	0.214	-0.370	2.9	2.2	3.85	0.001
trees 0-4 cm dbh	0.202	0.214	1.2	0.4	0.70	0.800
soil pH	-0.080	-0.005	2.6	1.4	2.48	0.001
# live tree species	0.065	0.267	2.0	1.7	3.04	0.001
trees 4-10 cm dbh	0.041	0.146	1.1	0.6	1.12	0.210

microhabitats. The stand structure variables were strongly correlated with sugar maple abundance and soil moisture (see Table 4.3, Chapter 4), whereas, the composition of disturbed microhabitats was dominated by species with an affinity for closed forest conditions (see Figure 2.4 and related discussion). The non-significance of microhabitat number simply reflects the composite nature of this variable. The contribution of patch membership to the dispersion of species scores was significant ($F=2.776$, $p<0.001$), however, and accounted for 4.3% of the explained variance, and 1.2% of the total variance, in species scores. Patch membership was therefore designated a co-variable, when testing for a treatment effect of environmental variables, to minimize the effects of replicated samples within patches.

The degree to which species were restricted to a particular edaphic condition, forest cover type, or disturbance state is summarized in Table 2.14. In general, the distribution of species was restricted more by differences in soil parent material and soil order than by differences in forest cover type and soil moisture. Comparatively few species were restricted by differences in canopy closure. Only 10.4 % and 12.8 % of species were present on every soil parent material, and soil order, respectively, whereas, 19.4 % and 23.0 % of species were present in every forest cover type, and soil moisture class, respectively. In contrast, 69.2% of species were recorded in both open and closed canopy conditions.

Inspection of the percentage of taxa restricted to a given environmental state reveals that proportionally fewer species were restricted to seasonally moist (5.4%) and seasonally wet microhabitats (5.0%) than to seasonally dry microhabitats (40.1%). This suggests that species of seasonally moist and wet habitats were more tolerant of dry conditions than species of dry habitats were of seasonally moist or wet conditions. A greater tolerance of excess moisture may account for the small percentage of species restricted to lacustrine parent materials (1.9%), and gleyed Brunisolic soils (4.7%), since the number of quadrats with seasonally moist depressions was significantly higher on these substrates (Table 2.9).

Species in this data set also showed a pronounced tolerance of gradients in canopy closure. In

Table 2.14. Number of species with a restricted and unrestricted spatial distribution in relation to soil parent material, soil order, soil moisture, cover type, canopy closure. Note: "oak" cover type (N=1 quadrat) included in "oak+sugar maple" for this analysis.

Environmental Variable	# Species	Species Restricted to Environmental State		Species Present in Every State	
		#	%	#	%
SOIL PARENT MATERIAL (total)	413	145	35.1	43	10.4
glacio-fluvial	116	13	11.2	-	
calcareous till	334	70	21.0	-	
lacustrine	104	2	1.9	-	
calcareous outwash	307	60	19.5	-	
SOIL ORDER	413	110	26.6	53	12.8
brunsisol	280	42	15.0	-	
gleyed brunisol	253	12	4.7	-	
luvisol	258	31	12.1	-	
gleyed luvisol	198	17	8.6	-	
gleysol	92	8	8.7	-	
SOIL MOISTURE (total)	413	156	37.8	95	23.0
seasonally dry microhabitats	337	135	40.1	-	
seasonally moist microhabitats	241	13	5.4	-	
seasonally wet microhabitats	159	8	5.0	-	
FOREST COVER TYPE (total)	413	107	25.9	80	19.4
oak, and, oak + sugar maple	199	18	9.0	-	
sugar maple	305	30	9.8	-	
sugar maple + wet-mesic, wet	287	30	10.5	-	
wet mesic + wet	333	29	8.7	-	
CANOPY CLOSURE (total)	413	127	30.8	286	69.2
open microhabitats	341	55	16.1	-	
closed microhabitats	358	72	20.1	-	

contrast to other variables, there were more, rather than fewer, species present in every state. This suggests that shade tolerant species are rarely displaced by taxa with an affinity for open habitats during disturbance events.

The relative contribution of patch variables, edaphic variables and matrix variables to the dispersion of species in ordination space is summarized in Figure 2.3. Overall, patch variables, *sensu stricto*, explained more of the variance in composition (36.1%) than did edaphic variables (28.1%) or matrix variables (10.2%). Edaphic variables explained 34.6% of the variance explained by patch variables, *sensu lato* {(19.2 + 1.4) ÷ (36.1 +19.2 + 1.4 + 2.8) = 34.6}, and, 21.7% of the variance explained by matrix variables, *sensu lato* {(1.4 +2.2) ÷ (10.2 + 2.8 +1.4 + 2.2) = 21.7}. Matrix variables, on the other hand, explained only 7.1% of the variance explained by edaphic variables, *sensu lato*, and patch variables, *sensu lato*. The implications for the relative contribution of local versus regional processes are discussed in Section 2.4.

2.3.4 Species Response to Microhabitats

Species were responsive to the pragmatic classification of microhabitats used in this study (Figure 2.4). With few exceptions, the microhabitats were well separated in ordination space and were dispersed in relation to the moisture and disturbance gradients that defined them. The similarity in species composition (marked by the proximity of habitats in ordination space) varied among habitats but even the most widely separated habitats had at least some species in common since the length of the first axis was less than 4.0 standard deviation units long (ter Braak 1987). This result is consistent with the broad moisture tolerance of many of the taxa occurring in more than 25 microhabitats (Table 2.15). As expected, the composition of species in microhabitats was more uniform than in the ordination of quadrats (total inertia for the ordination of microhabitats was 2.737 versus 7.100 for the ordination of quadrats). Taken together, these patterns provide indirect evidence of the role of environmental heterogeneity in structuring the composition of forest patches.

The strongest overlap in species composition occurred in open stumps and closed moist depressions (overlapping annotation in Figure 2.4). This was due to the capacity of species of moist forest floors

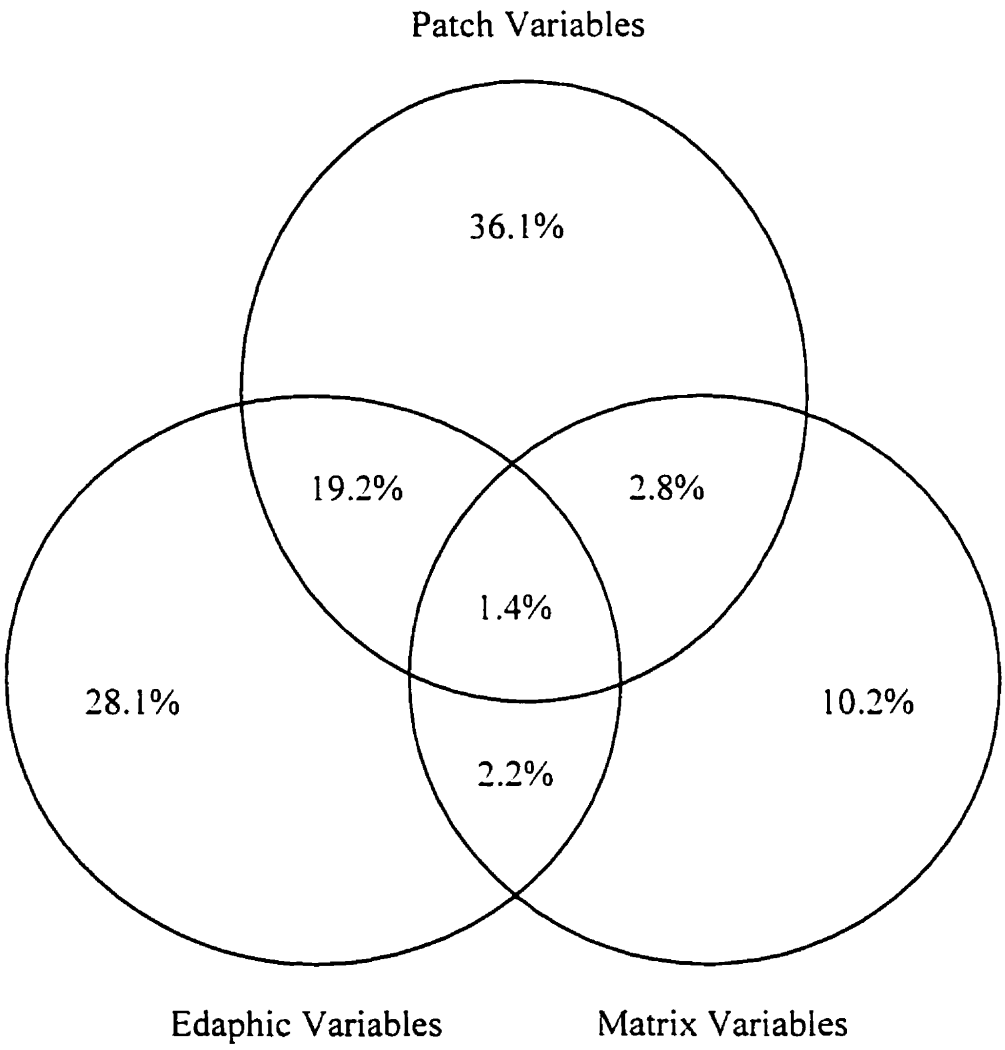

Figure 2.3. Partial decomposition of variance in CCA species ordination: local versus regional processes Patch variables (cover type, % canopy closure, stem diameter class, # tree species, # tree stems, # microhabitats, open microhabitats, disturbed microhabitats, patch membership), *sensu stricto*, explain 59.5% of the variance explained by patch variables, edaphic variables (soil parent material, soil order, soil moisture, % soil organic matter), and matrix variables (patch area, patch isolation). Edaphic variables explain 34.6% of the variance in species composition explained by patch variables, *sensu lato*, and 21.7% of the variance explained by matrix variables, *sensu lato*. Patch variables explain 25.2% of the variance in species composition explained by matrix variables, *sensu lato*; matrix variables, in turn, explain 7.1% of the variance explained by patch variables, *sensu lato*. The variables in this model explain 100% of the explained variance, and 27.4% of the total variance, in the original species ordination.

Legend Figure 2.4

Annotation	Microhabitat
floorD	seasonally dry forest floors-closed canopy (cc)
floorM	seasonally moist forest floors-cc
depM	seasonally moist forest depressions-cc
floorW	seasonally wet forest floors-cc
depW	seasonally wet forest depressions-cc
seep	seep-cc
gapD	seasonally dry gap-cc
gapM	seasonally moist gap-cc
mound	mound-cc
pitD	seasonally dry pit-cc
pitM	seasonally moist pit-cc
pitW	seasonally wet pit-cc
log	log-cc
stump	stump-cc
rrm	raised root mat-cc
stone	stone-cc
lane	lane/road-cc
ditch	ditch-cc
regfield	regenerating field-cc
FLOORd	seasonally dry forest floors-open canopy (oc)
FLOORm	seasonally moist floor-oc
DEPm	seasonally moist forest depressions-oc
DEPw	seasonally wet forest depressions-oc
SEEP	seep-oc
GAPd	sasonally dry gap-oc
GAPm	seasonally moist gap-oc
GAPw	seasonally wet gap-oc
MOUND	mound-oc
PITd	seasonally dry pit-oc
PITw	seasonally wet pit-oc
LOG	log-oc
STUMP	stump-oc
RRM	raised root mat-oc
LANE	lane/road-oc
DITCH	ditch-oc
REGFIELD	regenerating field-oc
RIPMEADOW	riparian meadow-oc
RIPMARSH	riparian marsh-oc
RIPTHICKET	riparian thicket-oc

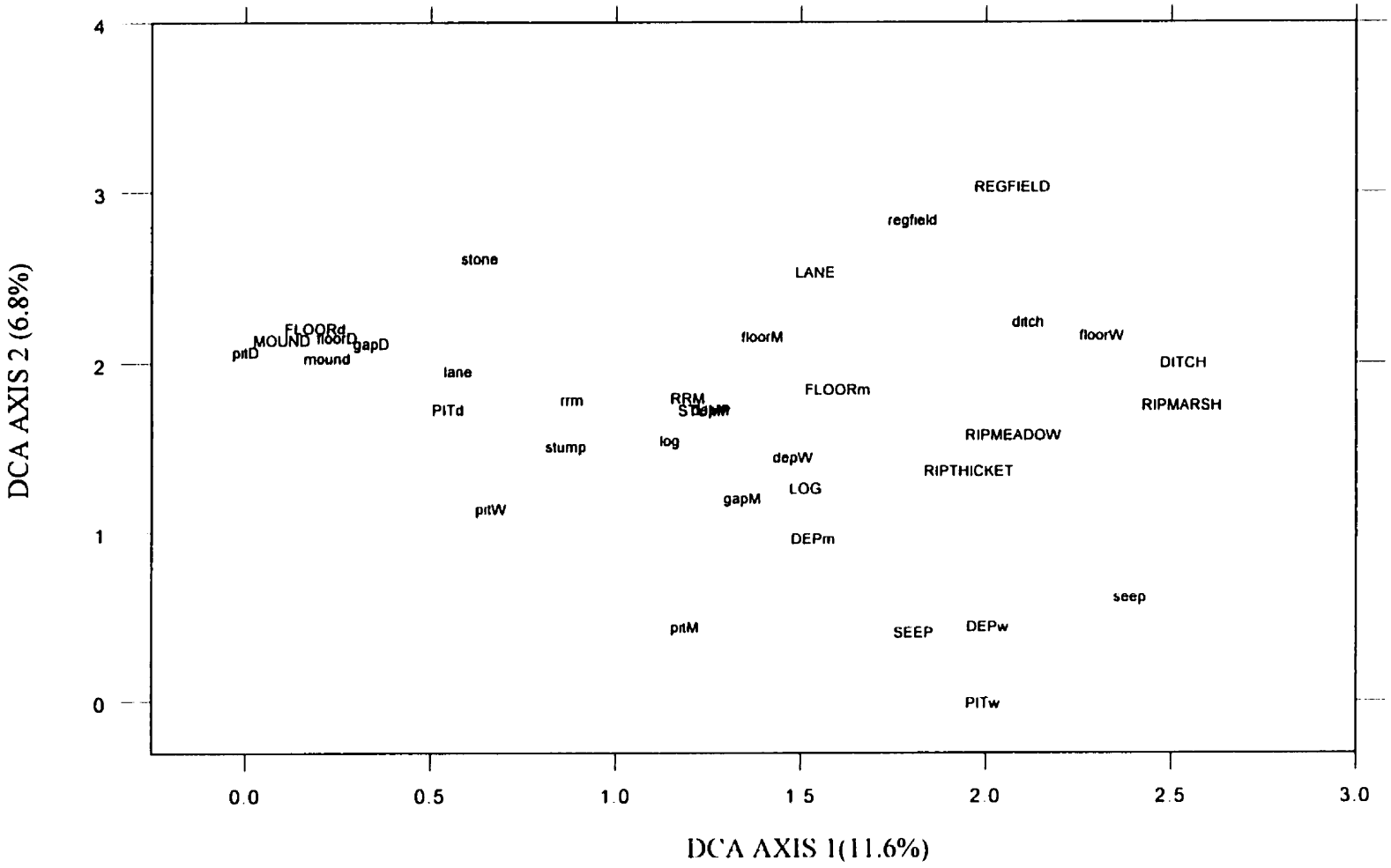

Figure 2.4. Distribution of microhabitats in relation to DCA axes 1 and 2. See legend for description of annotated variables. Note: FLOORd = dry open canopy gaps; FLOORm = moist open canopy gaps. Overlapping annotation = STUMP, depM.

Table 2.15. Number of microhabitats occupied by surveyed taxa. See Notes for list of taxa present in more than 25 microhabitats.

# Microhabitats	# Taxa	% of N=413 taxa
1	58	14.0
2-5	138	33.4
6-10	85	20.6
11-15	52	12.6
16-20	35	8.5
21-25	32	7.7
26-30	11	2.7
31-35	1	0.2
36-39	1	0.2

Notes:
Taxa present in more than 25 microhabitats: *Arisaema triphyllum, Aster lateriflorus, Carex gracillima, Circea lutetiana, Epipactis helleborine, Galium triflorum, Glyceria striata, Impatiens capensis, Parthenocissus inserta, Pilea pumila, Prunus virginiana, Solidago canadensis, Taraxacum officinale.*

to colonize open stumps. Approximately 80% of species on open stumps occurred in closed moist depressions whereas only 20% of species in closed moist depressions occurred on open stumps (Appendix 6, 7). The near overlap with species of open raised root mats is due primarily to the capacity of species of moist forest floors to colonize both stumps and raised root mats since open stumps rarely occurred in quadrats with open raised root mats.

The cluster of microhabitats on the extreme left of the ordination diagram reveals that the species composition of canopy gaps, tip-up mounds and dry tree pits in this data set was very similar to the species composition of closed, dry, forest floors. This suggests that species of the forest floor persist in canopy gaps and readily colonize dry mounds and pits created by wind-thrown trees. In keeping with this interpretation, 85% of the species recorded in the latter habitats (n=246 species) also occurred on closed, dry forest floors. The 36 species which did not occur on closed dry forest floors were found in open dry canopy gaps (30 species), closed mounds (4 species), open mounds (1 species), or closed canopy gaps (1 species). The majority of these taxa (80.6%) were species with affinity for "open" or "open + forest" habitats.

In general, the dispersion of microhabitats in ordination space appears to be influenced by differences in soil moisture, canopy closure and human disturbance. Moisture exerts the strongest influence over the composition of species, based on the tendency for habitats with similar moisture conditions to occur in the same sector of ordination space (seasonally dry habitats typically to the left, seasonally moist and seasonally wet habitats typically to the right). Open and closed habitats of the same type tend to occur together, and, in the sector of ordination space that reflects their moisture status. The tendency for open habitats to occur to the right of closed habitats reflects the shift in species composition arising from the germination requirements of light-demanding species.

The analysis of microhabitats was extended to clarify the influence of gap size on the composition canopy gaps on mesic soils. If colonization events during the gap phase were a significant influence on species composition, then one would expect to see an increasing departure from closed forest floors with increasing gap size, since species of open habitats should increasingly be favored under

conditions of increased light. Gaps in ordination space should therefore cluster in relation to gap size, and, larger gaps should be more remote from the ordination position of "closed dry forest floors" than small gaps. If other factors are more important determinants of the species composition of forest floors, then neither pattern should arise.

The results of this analysis are shown in Figure 2.5. The dispersion of gaps in DCA ordination space is only weakly patterned at best. The smallest gaps ("1", "2") are as likely to be close to the reference condition as distant from it, and, some of the largest gaps ("9", "10") are closer to the reference condition than many of the smaller gaps. If there is a general trend in the ordination, it is for gaps of larger size to be closer to the reference condition, and, for gaps of smaller size to be more distant. Gap size, *per se*, therefore, does not appear to be a significant contributor to the species composition of forest floors.

The factors responsible for this "pattern" are not readily apparent. Gaps in closest proximity to the reference condition tend to occur on calcareous till and outwash parent materials, whereas gaps remote from the reference condition tend to occur on glacial-fluvial parent materials and on calcareous till. Remote gaps on calcareous till occur exclusively on gleyed Luvisolic soils whereas proximate gaps on calcareous till occur on soils that are not gleyed. Differences in the species composition of gaps, therefore, may largely be due to differences in edaphic conditions.

The largest gaps in this analysis (labeled "10") differed sharply in the number of taxa with the capacity to persist in soil seed banks. The proportion of taxa with the capacity for prolonged dormancy in the gap nearest to the reference condition was <6% whereas the proportion of taxa in the gaps in the lower right portion of the diagram was >21%. The former gap was situated within an otherwise closed forest whereas the latter gaps were situated at the edge of a recently clear-cut forest stand. Differences in the species composition of these gaps , therefore, may be due in part to differences in seed bank size or in the degree of seed bank germination. If the latter, then large gaps (>>100m^2) may be a significant contributor to the transient composition of species on forest floors.

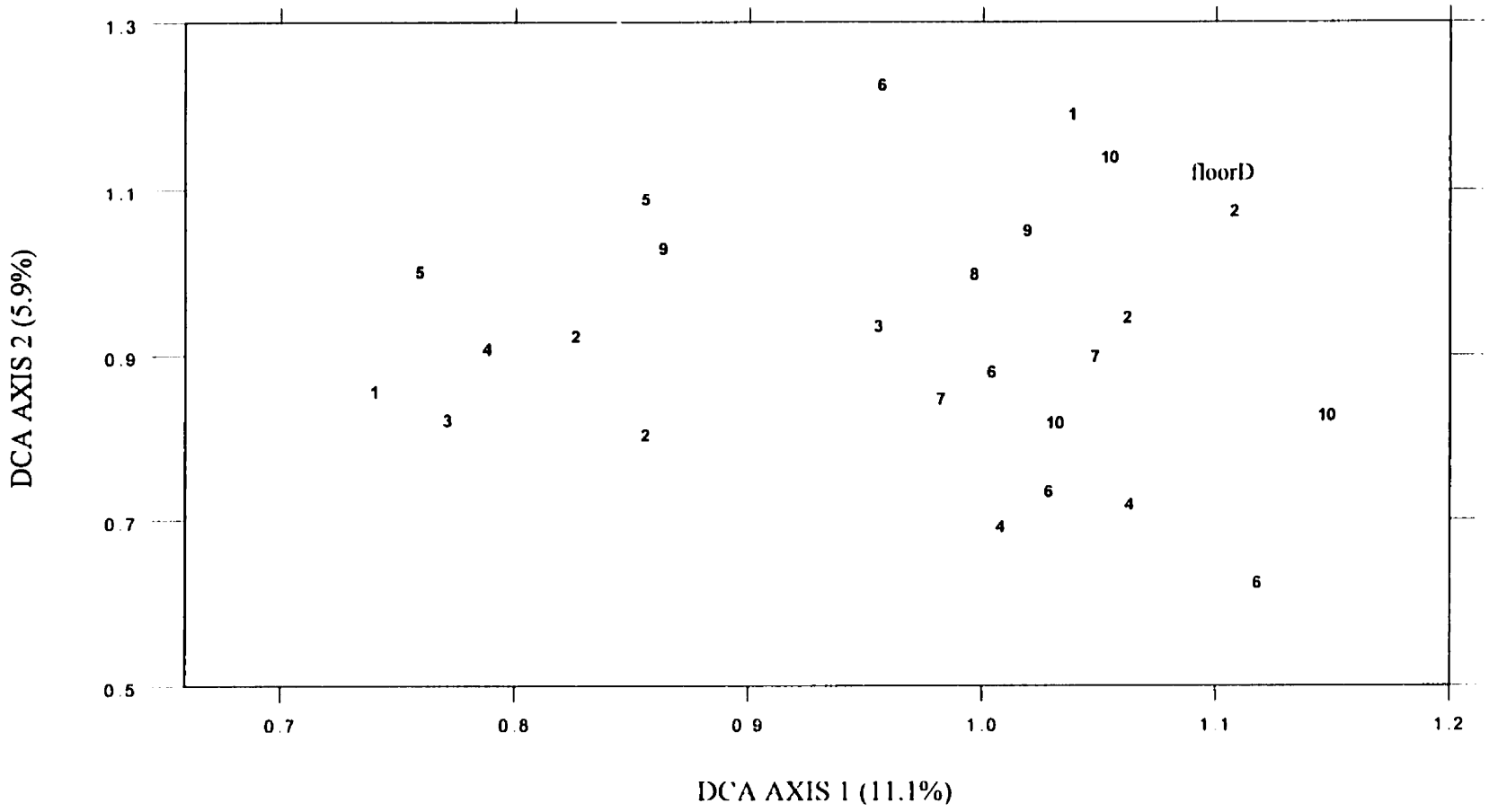

Figure 2.5. DCA ordination of open, seasonally dry, canopy gaps. Legend: gap size class in $10m^2$ increments (numbered 1 to 10); the microhabitat "closed, seasonally dry, forest floors" (floorD) has been included in the ordination for reference purposes.

The degree to which species were restricted to a given type of microhabitat is summarized in Figure 2.6. Four broad habitat categories were used for this analysis: closed, seasonally dry, forest floors *sensu stricto*; natural disturbance features (canopy gaps, tree-pits, tip-up mounds, stumps, logs); features created by human disturbance (regenerating fields, lanes, ditches); and, moist or wet habitats (forest floors, depressions, seeps, riparian meadow, riparian marsh, riparian thicket). Most species (79.2%) were recorded in more than one habitat category and approximately one-third of species (33.2%) were found in every category.

Species in this study were particularly tolerant of conditions created by the death or removal of a canopy tree (canopy gaps, tree pits, tip-up mounds, stumps, logs). Such features were colonized by 86.0% of the species on closed, dry, forest floors, 82.0% of the species in moist or wet habitats, and, 78.0% of the species in habitats created by human disturbance. However, the capacity of species to colonize or persist on features created by natural disturbance were not uniform. More species were recorded in canopy gaps (282) than on tip-up mounds (180), logs (120), pits (97), or stumps (64) (Appendix 5). This suggests that most species in these forests have access to alternative habitats where their competitors may do poorly or not survive, and, where populations of their own kind may expand.

Approximately 20% of the sampled flora (90 species) were restricted to features of one category. In keeping with the dispersion of microhabitats in Figure 2.4, restricted species were more constrained by moisture (42 species) than by human or natural disturbance (32 and 16 species, respectively).

2.3.5 Response of Sugar Maple and Understory Herbs to Available Calcium

The response of sugar maple to the availability of calcium cations in the upper 15 cm of the soil profile was examined to determine if there was evidence of increased survivorship of sugar maple saplings on calcium rich soils. The stand structure of undisturbed maple stands was evaluated in relation to increasing calcium availability on mesic soils overlying calcareous till. Preliminary analysis had revealed that soils of the Luvisolic order were typically more calcium rich than soils

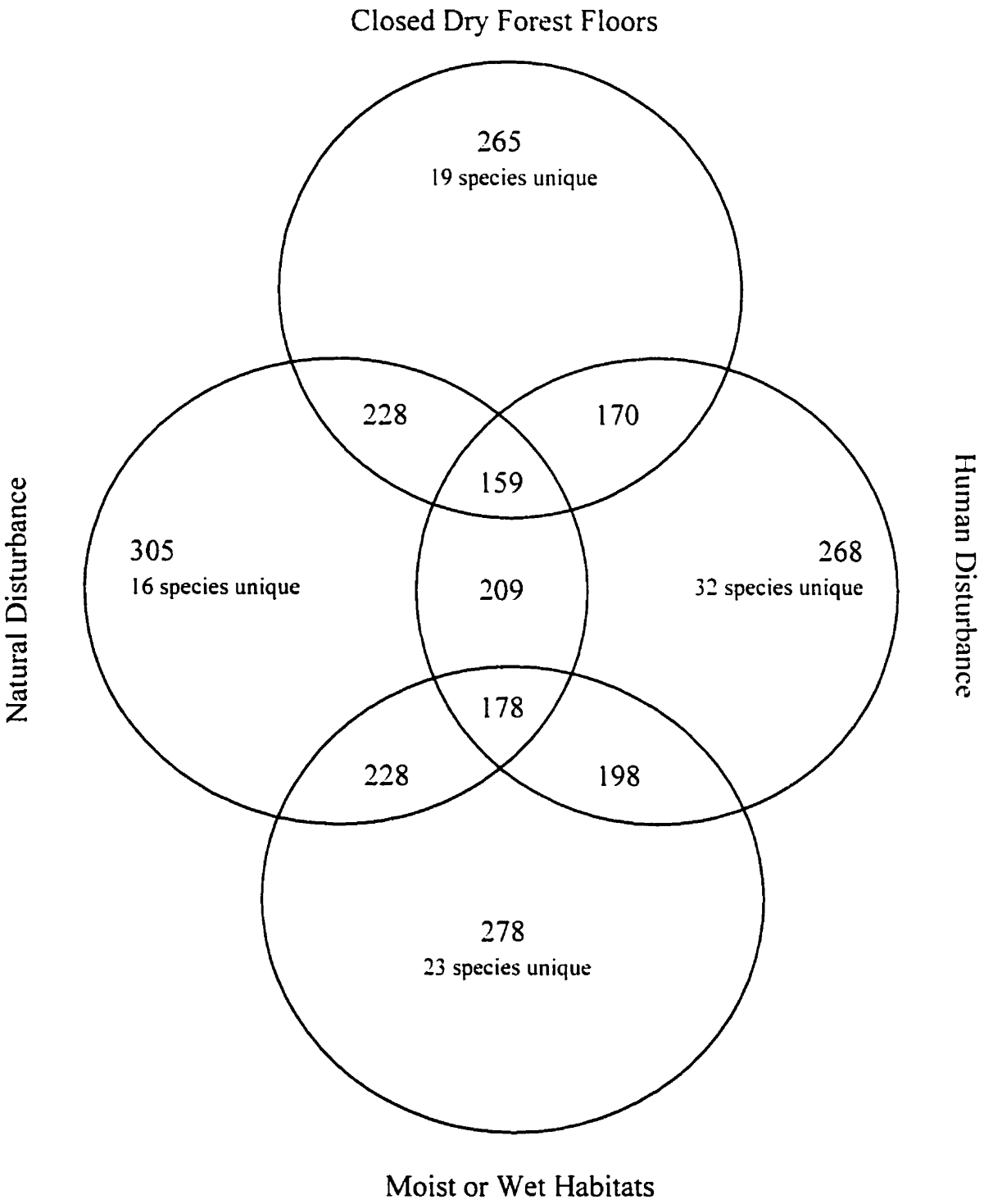

Figure 2.6. Distribution of species among microhabitats. Annotation: number of species recorded in habitat category. Natural Disturbance = canopy gaps, tree pits, tip-up mounds, stumps, logs (in dry, moist or wet conditions); Human Disturbance = regenerating fields, lanes, ditches; Moist or Wet Habitats: floors, depressions, seeps, riparian meadow, riparian marsh, or riparian thicket. Unique Species: species restricted to features in habitat category.

of the Brunisolic order, and, that the latter soils often contained free calcium carbonate in the upper 15 cm of the soil profile. Sugar maple response was therefore evaluated in relation to non-reactive soils when the analysis contained more than one soil order.

The relative abundance of sugar maple on non-reactive soils is presented in Figure 2.7. The percentage of sugar maple stems increased with increasing calcium availability in all size classes. The response was significant in the 0-4 cm, 4-10 cm, and 10-30 cm size class. Calcium availability explained 13 % to 19 % of variance in sugar maple abundance in these size classes. The trends in absolute abundance (not shown) were similar in direction but weaker (only the response for the 10-30 size class was statistically significant).

The relative abundance of sugar maple on Brunisolic soils is presented in Figure 2.8. The samples in this analysis were from the same soil order and soil series, and, thus were the most uniform with respect to the degree of soil weathering and soil development. Forest stands were typically younger than in the preceding analysis and did not contain any stems in the >30 cm size class. The calcium gradient was approximately 50 % longer owing to the inclusion of reactive soils. As before, the percentage of sugar maple stems increased with increasing calcium availability in the 0-4 cm, 4-10 cm, and 10-30 cm size classes. The percent variance in sugar maple abundance explained by available calcium was much higher, however, and ranged from 54 % in the 0-4 cm size class to 35 % in the 10-30 cm size class. The trends in absolute abundance (not shown) were strongest in the 4-10 cm size class, where differences in calcium availability explained 70.9 % of the variance in the number of sugar maple stems in 10m x 10m quadrats. In contrast to previous results, available calcium did not explain differences in the number of sugar maple stems in the 0-4 cm size class.

Taken together, these results provide indirect evidence of increased survivorship of sugar maple stems in undisturbed second-growth stands on calcium rich, mesic, soils overlying calcareous till. Caution is required, however, since the sample size in each analysis was small. The contribution of quadrats without stems to the significance of the relationship is strong. In many analyses, this would be cause for concern. In this analysis, however, the absence of stems means that maturing sugar

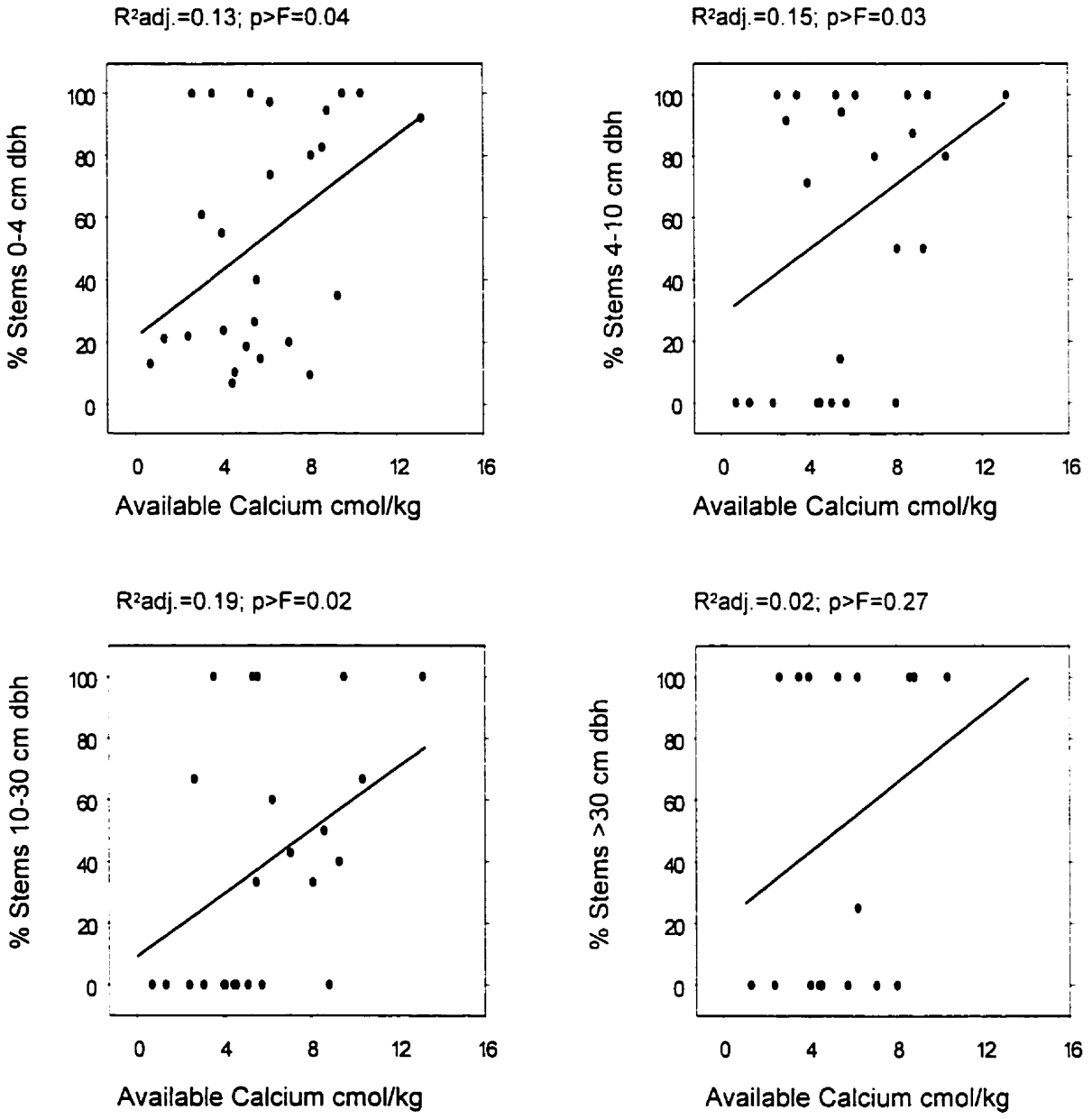

Figure 2.7. Sugar maple abundance versus available calcium in upper 15 cm of soil profile on Brunisolic and Luvisolic soils overlying calcareous till. Response variable is the percentage of live tree stems (>1m) in specified size class that are *Acer saccharum*. N=29 10m x 10m quadrats in 7 forest patches. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis (see text). Quadrats with apparent human disturbance excluded from analysis. Forest cover = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, species).

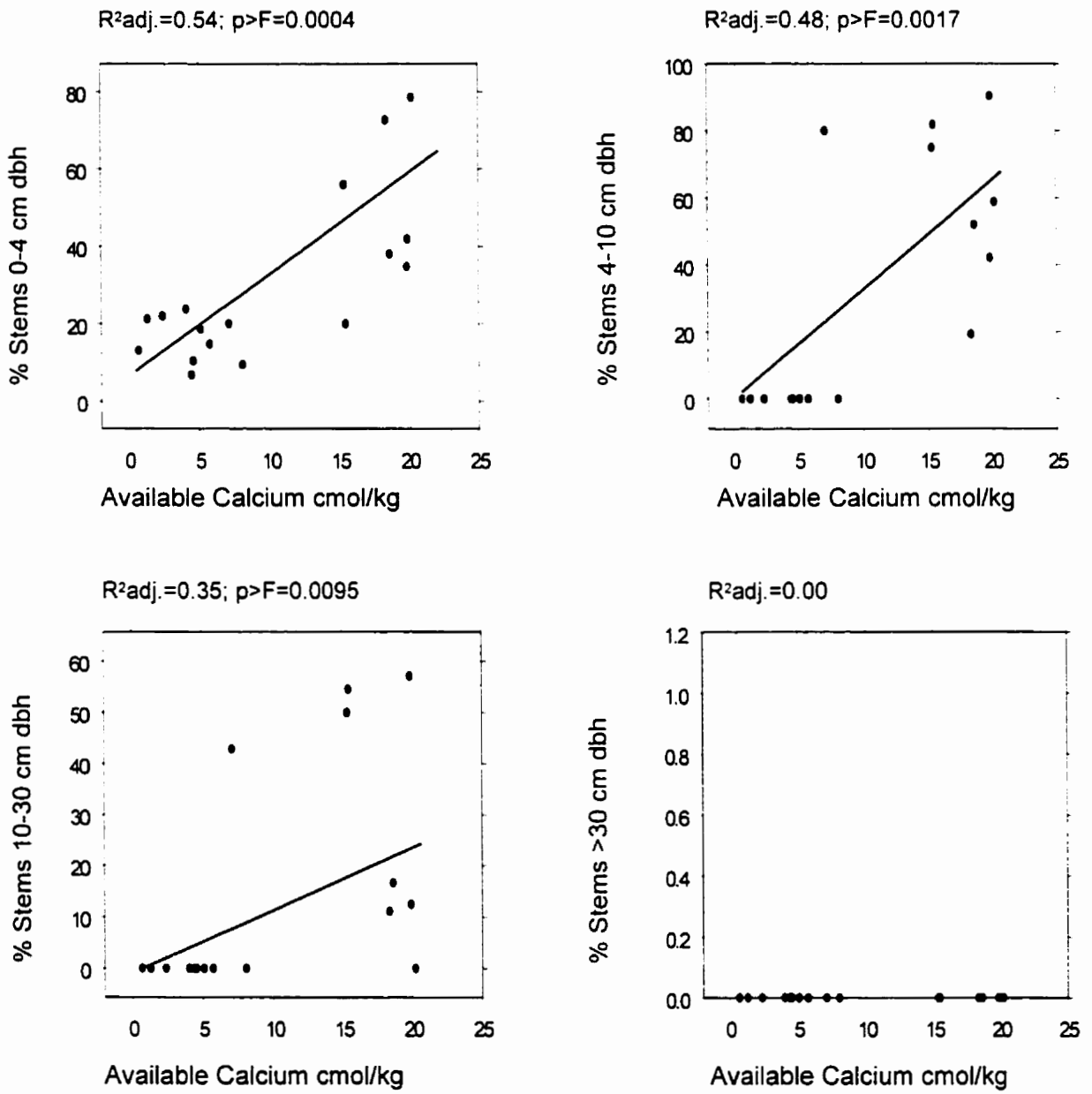

Figure 2.8. Sugar maple abundance versus available calcium in upper 15 cm of soil profile on Brunisolic soils overlying calcareous till. Response variable is the percentage of live tree stems (>1m) in specified size class that are *Acer saccharum*. N=17 quadrats in 3 forest patches. Soils with free calcium carbonate in upper 15 cm of soil profile included in analysis. Quadrats with apparent human disturbance excluded from analysis. Forest cover type = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic or wet species).

maple stems did not survive. This interpretation is supported by the absence of "zero percent" quadrats in the 0-4 cm size class, and, the marked tendency for "zero percent" quadrats to increase with size class and to occur on low calcium soils. The justification for including them in this analysis, therefore, is that they are inherent to the hypothesis being tested.

The modest explanation of variance in the first analysis (Figure 2.7) is due in part to the inclusion of quadrats from stands on Luvisolic and Brunisolic soils. For a given concentration of calcium, the percentage of stems that were sugar maple was consistently greater on Luvisolic than Brunisolic soils. This suggests that factors other than calcium have contributed to this result. One apparent factor is antagonism in the uptake of potassium and magnesium (see Chapter 5). Other factors that may have contributed to observed differences in sugar maple abundance are examined in Chapter 4.

The response of shade tolerant and intolerant herbs to increasing sugar maple abundance and calcium availability is presented in Figure 2.9. The response was evaluated in undisturbed stands on Brunisolic and Luvisolic soils overlying calcareous till. The analysis was undertaken to test the presumption of declining light levels on calcium rich soils. In keeping with expectations, the percentage of shade tolerant herbs in 10m x 10m quadrats increased with increasing sugar maple abundance and calcium availability. In contrast, the number of shade intolerant herbs declined. The variance in response explained by increasing sugar maple abundance, and by increasing calcium availability, was similar.

The calcium affinity of plants that flower prior to, or after, canopy closure is presented in Figure 2.10. As in the preceding case, the analysis was restricted to undisturbed forest stands on Brunisolic and Luvisolic soils overlying calcareous till. Ephemeral spring herbs were typically found on more calcium-rich soils than plants with persistent shoots that flowered prior to, or after, canopy closure. Early spring flowering plants with persistent shoots occurred on more calcium rich soils than mid to late season flowering plants, but not significantly so. The apparent affinity of ephemeral spring herbs for calcium-rich soils is consistent with their distribution elsewhere in the Great Lakes region.

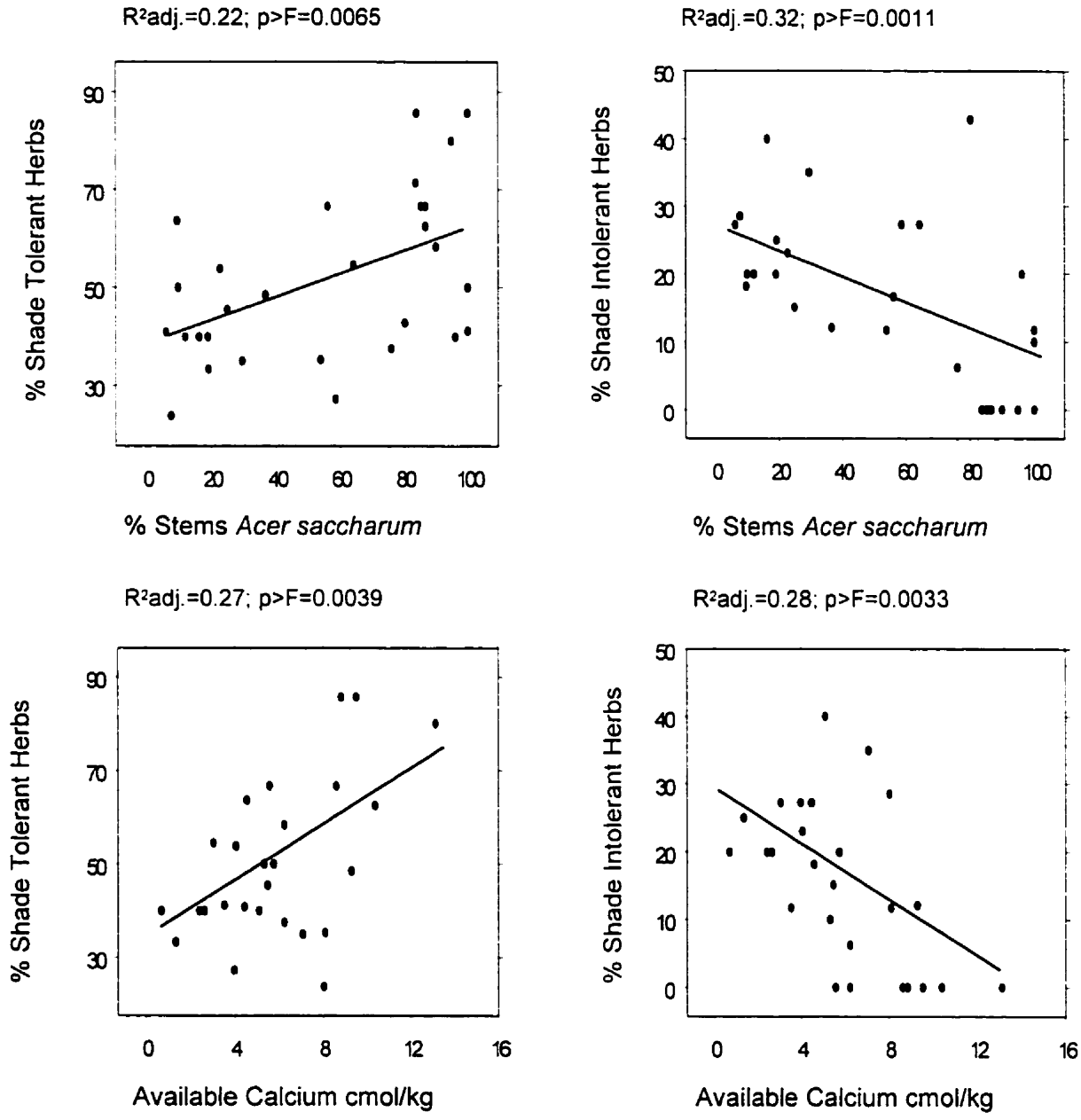

Figure 2.9. Herb response to increasing sugar maple abundance and available calcium on Brunisolic and Luvisolic soils overlying calcareous till. N=29 10m x 10m quadrats in 7 forest patches. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis (see text). Quadrats with apparent human disturbance excluded from analysis. Forest cover type = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet mesic or wet tree species.

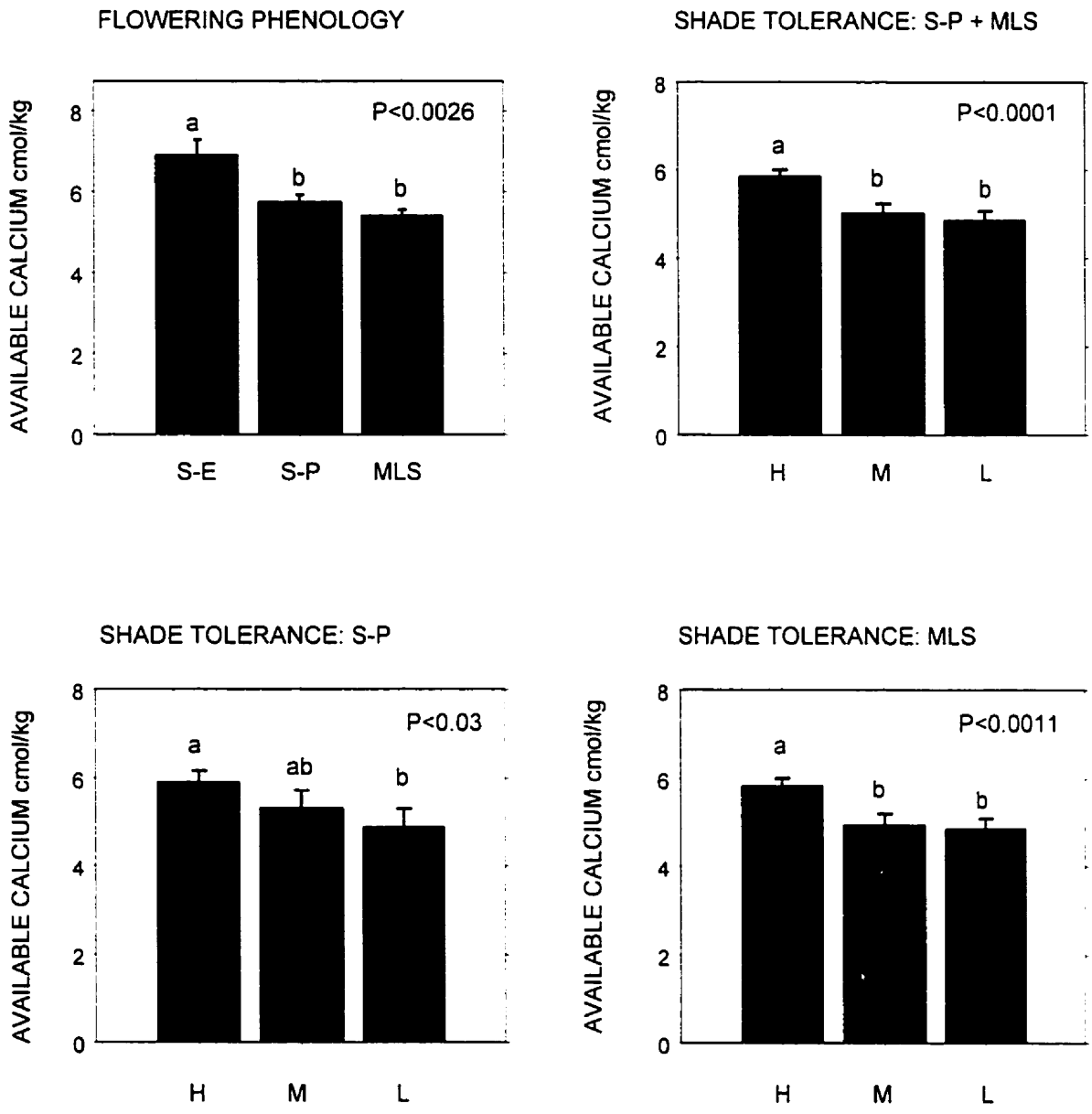

Figure 2.10. Mean calcium affinity and shade tolerance of understory plants in relation to flowering phenology on Brunisolic and Luvisolic soils overlying calcareous till. Legend: S-E=spring ephemeral herbs, S-P = early spring flowering plants with persistent shoots, MLS = mid to late season flowering plants with persistent shoots, H = high shade tolerance, M = moderate shade tolerance, L = low shade tolerance. N=29 10m x 10 quadrats in 7 forest patches. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis. Quadrats with apparent human disturbance excluded from analysis. Forest cover type = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic ro wet tree species. Error bars: one standard error mean.

where they are typically confined to fertile, glaciated soils (Rogers 1982, Curtis 1959).

The calcium affinity of plants with persistent shoots was examined further to determine if the more shade tolerant plants of this functional group were restricted to the more calcium rich soils. In keeping with the initial analysis of shade tolerance (Figure 2.9), plants that possessed a high shade tolerance were found on soils that were more calcium rich than plants of intermediate or low shade tolerance. This pattern was present in taxa that flowered before, or after, canopy closure.

Taken together, these results suggest that plants in these forests have partitioned the calcium availability gradient in relation to the degree of shade stress to which they were exposed. An ephemeral habitat was more strongly associated with calcium-rich soils than early or mid to late season flowering.

2.3.6 Plant Attributes

The preceding analyses have shown that the distribution of species in sampled patches has been determined in part by differences in environmental conditions. The following analysis summarizes the degree to which the functional attributes of plants explain the distribution of species in the forest understory. The attributes included in the ordination analysis were life history, provenance, life form, habitat affinity, shade tolerance and moisture affinity.

The variance in species composition explained by these attributes is summarized in Table 2.16. Habitat affinity and life form, respectively, explained 10.5% and 9.7% of the dispersion of species scores in CCA, whereas, provenance and life history explained 5.4% and 2.4%, respectively. Habitat affinity and life form, collectively, explained 17.3% of the dispersion of species scores. By comparison, the comprehensive set of environmental variables examined in this study explained 25.6% of the dispersion in species scores in a related ordination (Figure 2.3). A large fraction of the variation in the composition of plants in the forest understory, therefore, can be explained by the habitat affinity and life form of species in the regional species pool.

Table 2.16. Proportion of total inertia in the dispersion of species scores (CCA) explained by functional attributes of sampled plants. Overall test of ordination models by Monte Carlo permutation tests, n=1000 permutations.

Attribute	Σ Constrained Eigenvalues	Σ Unconstrained Eigenvalues	% Total Inertia Explained	F statistic	p>F
Habitat Affinity[1]	0.745	7.100	10.5	7.35	0.001
Life Form[2]	0.689	7.100	9.7	3.31	0.001
Provenance[3]	0.363	7.100	5.1	10.25	0.001
Life History[4]	0.169	7.100	2.4	2.30	0.001
Habitat Affinity + Life Form[5]	1.225	7.100	17.3	4.22	0.001

Notes:
1. Forest affinity class excluded from analysis due to high collinearity with other variables.
2. Fern life form excluded from analysis due to high collinearity with other variables.
3. Native provenance class excluded from analysis due to high collinearity with other variables.
4. Biennial life history excluded from analysis due to high collinearity with other variables.
5. Forest affinity class and fern life form excluded from analysis due to high collinearity with other variables.

The tolerance of life forms to shade, and to excess moisture, are summarized in Tables 2.17 and 2.18, respectively. The most shade tolerant life forms were the fern allies, ferns and trees. The vines, shrubs, and herbs were intermediate in shade tolerance, whereas, the grasses were the least shade tolerant. The shade tolerance of taxa within life forms was not uniform, however, and often ranged across the gradient. Nevertheless, the difference in shade tolerance among life forms was highly significant ($p>\chi^2=0.0001$, Likelihood ratio test).

The moisture tolerance of taxa also varied by life form. Shrubs, trees, herbs and grasses were more frequent on the drier soils, whereas, vines, ferns, and fern allies were more frequent on mesic and moist soils. The life forms most tolerant of wet soils were the grasses, herbs, shrubs and ferns. When trees are removed from the analysis, the difference in moisture tolerance among life forms is not significant ($p>\chi^2=0.0987$, Likelihood ratio test). Trees were highly over-represented in tolerance class 2 (facultative upland), and absent from tolerance classes 1 (obligate upland) and 5 (obligate wetland).

The distribution of selected attributes within examined microhabitats is presented in Table 2.19. As expected, non-native species achieved their highest proportional abundance on open farm lanes and access roads, open and closed regenerating farm fields, and, in seasonally dry tree pits. With the exception of the latter habitat, these habitats were also rich in taxa with an affinity for open habitats. Species with an affinity for wet habitats were most abundant in open seasonally wet tree pits, closed and open seeps, and open riparian marshes. The widespread occurrence of species with a facultative or obligate affinity for wetland habitats was not expected. This pattern is in keeping with previous results (Table 2.14) and suggests that in these forests, at least, such taxa have a much broader moisture tolerance than their classification would indicate. The widespread but modest presence in closed habitats of taxa with an affinity for open habitats suggests that conditions for germination and establishment are more limiting than conditions for persistence.

Table 2.17. Shade tolerance of sampled flora by life form. Legend: Class 1=highest shade tolerance, Class 5=lowest shade tolerance. High ST = shade tolerance classes 1,2; Low ST = shade tolerance classes 4,5. Differences in shade class significant (χ^2=66.44, p<0.0001, Likelihood ratio test). Shade tolerance classification derived from Nimerfro and Brand (1993) and Ellenberg (1988).

	Shade Tolerance Class (% Classified Taxa)					Summary		
Life Form	1	2	3	4	5	Mean	% High ST	% Low ST
Tree	26.9	23.0	30.8	15.4	3.8	2.46	50.0	19.2
Shrub	14.9	17.0	21.3	31.9	14.5	3.15	31.9	46.4
Vine	0	11.1	44.4	33.3	11.1	3.44	11.1	44.4
Fern	47.4	31.6	15.8	5.3	0	1.79	78.9	5.3
Fern Ally	40.0	40.0	0	0	20.0	2.20	80.0	20.0
Grass	0	0	17.6	47.1	35.3	4.18	0	82.4
Herb	18.2	11.9	13.3	33.6	23.1	3.31	30.1	56.7

Table 2.18. Moisture tolerance of sampled flora by life form. Legend: Class 1=lowest tolerance to excess moisture (obligate upland), Class 5=highest tolerance to excess moisture (obligate wetland). High MT = moisture tolerance classes 4,5; Low MT = moisture tolerance classes 1,2. Differences in moisture class among life forms significant only when trees are included in the analysis (χ^2=57.11, p<0.0002, Likelihood ratio test). Moisture tolerance classification derived from Oldham *et al.* (1995).

	Moisture Tolerance Class (% Classified Taxa)					Summary		
Life Form	1	2	3	4	5	Mean	% Low MT	% High MT
Tree	0	51.72	20.7	27.6	0	2.76	51.7	27.6
Shrub	34.0	22.6	11.3	24.5	7.5	2.49	56.6	32.1
Vine	0	33.3	55.5	11.1	0	2.78	38.3	11.1
Fern	13.0	26.1	30.4	21.7	8.7	2.87	39.1	30.4
Fern Ally	12.5	12.5	50.0	25.0	0	2.88	25.0	25.0
Grass	18.8	28.1	18.8	25.0	9.4	2.78	46.9	34.4
Herb	28.3	21.5	18.0	18.9	13.3	2.67	49.8	32.2

Table 2.19. Percentage of classified taxa (all life forms) in surveyed microhabitats by provenance, habitat affinity and moisture affinity. Legend: **Provenance** (N=407 species; all life forms): N=native, A=alien; **Habitat Affinity** (N=358 species; trees excluded from analysis): F=taxa found only in forested habitats, FO=taxa found primarily in forested habitats but also found in open habitats, OF=taxa found primarily in open habitats but has capacity to invade closed habitats, O=taxa found only in open habitats; **Moisture Affinity** (N=387 species; all life forms): OFU=obligate or facultative upland taxa, F=facultative taxa (found in both upland and wetland habitats), OFW=obligate or facultative wetland taxa. %SA = percent study area (19,200m2).

Microhabitat			Plant Attribute								
Variable	% SA	# Taxa	Provenance		Habitat Affinity				Moisture Affinity		
			N n=349	A n=58	F n=76	FO n=92	OF n=126	O n=64	OFU n=190	F n=76	OFW n=121
seasonally dry forest floors/rises-cc	54.3	265	90.9	8.7	28.7	26.0	24.2	7.5	55.5	19.2	21.9
seasonally dry forest floors/rises-oc	6.8	205	86.8	13.2	26.3	24.4	24.9	11.2	57.6	21.4	18.0
seasonally moist forest floors/rises-cc	5.4	197	88.8	10.2	17.3	25.9	35.0	7.6	38.6	19.3	40.6
seasonally moist forest floors/rises-oc	2.2	153	84.3	13.7	18.3	26.1	34.0	8.5	35.9	19.6	42.5
seasonally moist forest depressions-cc	4.1	137	89.8	9.5	21.1	32.1	27.7	5.1	36.5	17.5	43.1
seasonally moist forest depressions-oc	0.2	42	85.7	14.3	21.4	35.7	21.4	9.5	26.2	11.9	61.9
seasonally wet forest floors/rises-cc	0.6	83	83.1	14.5	6.0	24.1	51.8	7.2	19.3	20.5	57.8
seasonally wet forest depressions-cc	4.0	115	90.4	8.7	22.6	29.6	31.3	4.3	34.5	13.9	49.6
seasonally wet forest depressions-oc	1.0	38	86.8	13.2	10.5	42.1	28.9	5.3	26.3	10.5	63.2
seep-cc	0.9	33	90.9	6.1	9.1	39.4	27.3	6.1	0	12.1	78.8
seep-oc	0.3	25	96.0	4.0	20.0	44.0	28.0	0	8.0	24.0	68.0

Table 4._. Percentage of classified taxa (all life forms) in surveyed microhabitats by provenance, habitat affinity and moisture affinity.

Microhabitat			Plant Attribute								
			Provenance		Habitat Affinity				Moisture Affinity		
Variable	% SA	# Taxa	N n=349	A n=58	F n=76	FO n=92	OF n=126	O n=64	OFU n=190	F n=76	OFW n=121
seasonally dry gap-cc	2.2	115	90.4	8.7	28.7	25.2	28.7	2.6	63.4	19.1	14.8
seasonally dry gap-oc	6.8	205	86.8	13.2	26.3	24.4	24.9	11.2	57.6	21.4	18.0
seasonally moist gap-cc	0.5	68	86.8	11.8	25.0	30.9	29.4	0	38.2	14.7	45.6
seasonally moist gap-oc	3.0	153	84.3	13.7	18.3	26.1	34.0	8.5	35.9	19.6	42.5
seasonally wet gap-oc	1.0	82	87.8	11.0	12.2	30.5	39.0	9.8	26.8	13.4	58.5
mound-cc	3.6	165	93.3	6.7	30.9	26.7	20.6	6.1	64.2	14.5	18.8
mound-oc	0.4	76	84.2	15.8	31.6	28.9	19.7	9.2	68.4	18.4	11.8
seasonally dry pit -cc	0.4	81	95.1	4.9	34.6	28.4	18.5	0	71.6	17.2	11.1
seasonally dry pit-oc	0.1	26	80.8	19.2	26.9	30.8	26.9	3.8	61.5	15.4	23.1
seasonally moist pit-cc	0.3	5	100.0	0	40.0	40.0	20.0	0	40.0	0	60.0
seasonally wet pit-cc	0.2	18	94.4	5.6	38.9	22.2	27.8	0	38.9	22.2	38.9
seasonally wet pit-oc	0.1	1	100.0	0	0	0	100.0	0	0	0	100.0
log-cc	0.5	102	92.2	7.8	22.5	31.4	26.5	2.9	39.2	17.6	41.2
log-oc	0.2	64	90.6	7.8	21.9	26.6	29.7	3.1	34.4	15.6	45.3

Table 4._. Percentage of classified taxa (all life forms) in surveyed microhabitats by provenance, habitat affinity and moisture affinity.

Microhabitat			Plant Attrrbute								
			Provenance		Habitat Affinity				Moisture Affinity		
Variable	% SA	# Taxa	N n=349	A n=58	F n=76	FO n=92	OF n=126	O n=64	OFU n=190	F n=76	OFW n=121
stump-cc	0.2	51	90.2	9.8	19.6	35.3	17.6	2.0	47.1	19.6	31.4
stump-oc	0.1	34	88.2	11.8	26.5	32.4	32.4	2.9	44.1	20.6	35.3
raised root base-cc	1.3	138	91.3	7.2	24.6	27.5	25.4	4.3	42.8	20.3	33.3
raised root base-oc	0.6	96	86.5	12.5	17.7	28.1	31.3	8.3	36.5	22.9	36.5
stone-cc	0.1	20	95.0	5.0	10.0	50.0	25.0	10.0	55.0	25.0	20.0
lane/road-cc	2.3	89	93.3	6.7	25.8	30.3	25.8	1.1	52.8	22.5	23.6
lane/road-oc	1.3	181	76.8	21.5	13.3	22.1	35.4	18.2	40.9	19.3	34.8
ditch-cc	0.3	68	88.2	11.8	10.3	22.1	42.6	11.8	27.9	14.7	55.9
ditch-oc	0.1	33	90.1	9.9	3.0	30.0	39.4	18.2	27.3	9.1	63.6
regenerating field-cc	1.3	125	80.8	18.4	4.8	16.8	45.6	16.8	44.8	16.8	36.0
regenerating field-oc	1.3	147	77.6	21.8	4.1	15.6	44.2	23.1	44.2	16.3	38.1
riparian meadow-oc	0.7	75	85.3	13.3	13.3	29.3	38.7	13.3	22.7	14.7	60.0
riparian marsh-oc	0.4	46	87.0	10.9	10.9	26.1	45.7	15.2	15.2	15.2	67.4
riparian thicket-oc	0.1	37	86.5	10.8	10.8	37.8	32.4	8.1	16.2	21.6	59.5

2.4. Discussion

i) Environmental Heterogeneity

On a regional spatial scale, environmental heterogeneity was an important contributor to the number of recorded taxa. Approximately two-thirds (64.2%) of the sampled flora was recorded on closed, seasonally dry, forest floors, *sensu stricto*. Differences in edaphic conditions, and the presence of disturbance features, therefore provided additional habitat for approximately one-third of the species recorded in this study.

In this study, the contribution of environmental heterogeneity to species richness was strongly scale dependent. Whereas 21 microhabitats contributed to a significant difference in species richness at the quadrat scale (10m x 10m), only 9 microhabitats did so at the patch scale. In keeping with this pattern, 38 of 39 microhabitats contained at least one unique species when evaluated at the quadrat scale, whereas, 33 and 13 microhabitats did so when evaluated at the patch scale and landscape scale, respectively (see Tables 4.4, 4.5 and 4.6, Chapter 4).

One apparent reason for this pattern is that heterogeneity provides alternative habitat for species of broad environmental tolerance. In these forests, most species (79.2%) were found to occur in more than one habitat category (*sensu* Figure 2.6), and several species (33.2%) were present in every category. Comparatively few species (21.8%) were confined to one habitat type. Of these, 32 species were confined to features created by human disturbance, 23 species were confined to moist or wet conditions, 19 species were confined to closed dry forest floors, and 16 species were confined to features created by natural disturbance. Of the species that did not occur on closed, dry, forest floors, 77 (52.0%) occurred in at least one other habitat category and 41 (27.7%) occurred in every other category. Taken together, these results suggest that most species were able to germinate or persist in a variety of settings and that only rarely were they confined to one type of habitat on the forest floor. Which habitats were occupied by which species depended on the scale of the analysis, the local configuration of habitats, and the environmental tolerance of the species involved. In general, the smaller the spatial scale, the greater the contribution of heterogeneity to species diversity.

In this study, species were particularly tolerant of conditions created by the death or removal of a canopy tree (canopy gaps, tree pits, tip-up mounds, stumps, logs). Such features were colonized by 86.0% of the species on closed, dry, forest floors, 82.0% of the species in moist or wet habitats, and, 78.0% of the species in habitats created by human disturbance. However, the capacity of species to colonize or persist on features created by natural disturbance was not uniform. More species were recorded in canopy gaps (282) than on tip-up mounds (180), logs (120), pits (97), or stumps (64). Only 20% of the species on these features were not found elsewhere on the forest floor.

Taken together, these results provide broad support for the hypothesis that environmental heterogeneity facilitates the coexistence of species through the spatial and temporal segregation of competing species (Hutchinson 1961, Levin 1974). By virtue of their capacity to colonize at least one other type of habitat, most species in these forests have access to alternative environments where competitors may do poorly or not survive, and, where populations of their own kind may expand (Pickett 1980, Comins and Noble 1985, Chesson 1986, Bazzaz 1991).

ii) Contribution of Canopy Disturbance to Species Composition

The species composition of canopy gaps was similar to the species composition of the adjacent forest floor. In general, the species composition of dry open canopy gaps was not responsive to differences in gap size (1-100 m^2). This suggests that the composition of plant assemblages is dominated by persistent taxa and that colonization or extinction events during the gap phase rarely alter the composition of the understory flora in a significant way. Nevertheless, the marked change in species composition of quadrats adjacent to a large, recent, clear-cut suggests that larger canopy openings may stimulate the germination of buried seeds and cause significant transient change in species composition (Metzger and Schultz 1984).

These findings are consistent with the results of studies of specific features in forests of the U.S. northeast. Studies of forest gaps that examined compositional differences have reported little difference between species in gaps and the adjacent forest floor (Ehrenfield 1980, Moore and Vankat 1986, Pickett 1987, 1988a, 1988b, Mladenoff 1990, and Goldblum 1997. Gaps in these studies were

created by tree fall, gypsy moth defoliation, standing dead trees, or experimental treatments; gap size ranged from 5-214 m^2 and from 1-30 years of age.

Similarities have also been reported in the species composition of forest floors, logs, and tree pits. Thompson (1980), for example, reported that logs and tree pits were readily colonized by herbs from the forest floor and that approximately 90% of the species on logs, and 85% of the species in pits, were recorded within 1 metre of these features. These findings are consistent with the results of this study. All species recorded in tree pits, and 94% of species recorded on logs, were recorded on closed forest floors.

Studies of tip-up mounds and tree pits, in contrast, have reported distinctive species assemblages associated with these features (Beatty 1984, Peterson and Pickett 1990, Peterson *et al.* 1990, Peterson and Campbell 1993). In keeping with the results of this study, mounds were typically more species rich than pits, although the reverse pattern has been reported for fresh pits and mounds in a large area of catastrophic windthrow (Peterson and Pickett 1990). Studies of environmental conditions reveal that the soil in tree pits is typically wetter, more alkaline, has a thicker litter layer, soil organic matter content, and, experiences less extreme temperature fluctuations, than the soil on adjacent mounds (Dwyer and Merriam 1981, Beatty and Stone 1986, Peterson and Campbell 1993). Leaf litter depth may be a limiting factor in these habitats since differences in species composition were non-significant when leaf litter was experimentally removed from pits in deciduous forests in central New York (Beatty and Sholes 1988). Excess moisture is also expected to be limiting in pits with seasonally saturated soils (Beatty 1984). In keeping with these expectations, low species richness was associated with both leaf litter and seasonally saturated soils in this study.

iii) Response of Sugar Maple to Available Calcium

Sugar maple was more abundant, in relative and absolute terms, in undisturbed second-growth stands on mesic soils that were rich in calcium cations. Stems that were subject to shade stress and self thinning were more responsive to differences in available calcium than were stems in the upper canopy. When differences among stands were standardized with respect to soil parent material, soil

order, and soil series, available calcium explained 70.9 % of the variance in the number of sugar maple stems in the 4-10 cm size class, and, 54.0 % to 35.0% of the variance in the proportion of stems in the 0-4 cm, 4-10 cm, and 10-30 cm size class.

These results are consistent with the sharp reduction in mortality of juvenile sugar maple trees observed on calcium rich soils in oak transition-northern hardwood forests in northwestern Connecticut (Kobe *et al.* 1995, Kobe 1996). Juvenile trees in these studies were defined as any individual > 25 cm tall that did not have foliage reaching the canopy of the stand. The upper limit varied from site to site but did not exceed 10 cm dbh (diameter breast height). In deep shade (less than 5% full sun), the probability of mortality in sugar maple stems declined from 99.8 % on acid schist/gneiss uplands to 14.8 % on base rich soils overlying calcareous bedrock. Differences in sapling mortality and growth rates successfully predicted the composition of regional forests when incorporated in a model of forest dynamics (SORTIE).

The mechanisms by which trees benefit from calcium rich soils are presently unresolved. Recent studies of cold temperate trees have found an association between foliar calcium levels and dark respiration rates in red spruce (McLaughlin *et al.* 1991, McLaughlin and Kohut 1992). In these studies, dark respiration rates declined in the presence of increasing foliar calcium and contributed to net carbon assimilation in young saplings (1.2 - 2.0 m tall). Foliar calcium levels were positively correlated with calcium levels in the soil, a finding broadly supported by fertilization studies in both hardwood and conifer trees (Dr. V. Timmer, Department of Forestry, University of Toronto, *pers. com.*). In keeping with the widespread expectation that plants adapted to low light should have lower carbon losses via dark respiration, Lusk and Reich (2000) recently confirmed that juveniles (0.4 -1.5 m tall) of shade tolerant angiosperm trees typically have lower dark respiration rates than associated less-tolerant species.

An alternative mechanism by which calcium rich soils may contribute to sapling survivorship is increased nitrogen availability mediated by a calcium-based rise in soil pH. Dancer *et al.* (1973) have shown that nitrification rates are strongly and positively correlated with increasing soil pH over

the pH range 4.7 to 6.6. On calcium rich soils, soil pH is enhanced when calcium cations are taken up by tree roots and returned to the soil surface by litter feedback dynamics (Boerner 1984, Khanna and Ulrich 1991, Wilmot *et al.* 1995). In keeping with this mechanism, leaves of sugar maple seedlings on deeply shaded sites (<5% canopy openness) had higher nitrogen levels, and higher growth rates, on soils with higher nitrification rates in northern Wisconsin(Walters and Reich 1997). Soil moisture also varied on these soils, however, and the relative contribution of nitrogen and soil moisture could not be determined.

Studies have recently been initiated in the U.S. northeast to clarify which of these calcium-based explanations best explains tree growth and mortality relations in upland settings (Dr. A. Finzi, Department of Biology, Boston University, *pers. com.*; Dr. R. K. Kobe, Department of Forestry, Michigan State University, *pers. com.*). At present, the collective findings of these studies suggests that calcium nutrition has important consequences in the dynamics and distribution of north temperate trees. Local differences in soil chemistry may therefore lead to spatial patterning in the distribution of canopy trees that has heretofore been associated with regional differences in mineral substrate (Braun 1950, Curtis 1959, Pastor *et al.* 1984, Host and Pregitzer 1992, Reich *et al.* 1997, van Breemen *et al.* 1997).

iv) Response of Herbs to Understory Shade

The response of shade tolerant and intolerant herbs to increasing sugar maple abundance (Figure 2.9) is consistent with declining light at the forest floor. This was not unexpected. After beech and hemlock, sugar maple casts the deepest shade in forests in the Great Lakes region (Pacala *et al.* 1996), and, has the lowest percent transmission of photosynthetically active radiation (Canham *et al.* 1994).

Curtis (1959) has argued that the forest floor is a demanding environment that requires specialized traits for success and that it is the limited set of species that possess those traits that has led to the striking uniformity in species composition in the mesic hardwood forests of eastern North America. In keeping with this hypothesis, 92.5% of the species that were prevalent in the understory of forests

in the Maple-Basswood forest region in Wisconsin were present in maple dominated forests in this study (Appendix 14).

Early spring flowering is one of several plant traits that has been associated with deep shade in the forest understory. In herbs with low shade tolerance, early flowering is associated with an ephemeral (Sparling 1967), or winter annual (Rogers 1982), life history. Each facilitates net carbon gain by restricting the growth phase to periods when the canopy is leaf free. More commonly, however, the early flowering habit is associated with varying degrees of shade tolerance that enables shoots and leaves to persist until mid to late summer (Sparling 1967, Rogers 1982). The latter combination of characters was more common in the Peterborough area where only six of sixty-two early flowering species were spring ephemerals (*Allium tricoccum, Caulophyllum thalictroides, Claytonia caroliniana, Dicentra canadensis, Dicentra cucullaria, Erythronium americanum*); only one species (*Galium aparine*) was a known winter annual.

Related plant traits that may facilitate survival in deeply shaded habitats include winter-green leaves (Bierzychudek 1982) and the initiation of shoot growth (Taylor and Pearcy 1976) or flower initials (Bierzychudek 1982) in early autumn. The former trait greatly extends the period of carbon gain in species such as *Carex plantaginea, Hepatica acutiloba, Maianthemum canadense, Tiarella cordifolia, Trientalis borealis, Viola blanda,* and *Viola rostrata,* whereas the latter traits facilitate early spring growth and flowering in species such as *Allium tricoccum, Trillium grandiflorum, Arisaema triphyllum,* and *Geranium maculatum.*

The capacity of plants to tolerate deep shade has been attributed to a suite of traits that facilitate the capture and processing of light energy at the lowest net cost. Morphological characters associated with shade plants include: thin leaves with a large surface area (Grime 1965); a higher proportion of chlorophyll *b* relative to chlorophyll *a* (Boardman 1977); a chloroplast with large grana stacks oriented in more than one plane (Boardman 1977); a higher proportion of leaf nitrogen allocated to chlorophyll than to carboxylating enzymes and other proteins (Seeman *et al.* 1987, Niinemets 1997, Lusk and Reich 2000); a rapid stomatal response to changes in light intensity (Hicks and Cabot

1985); and leaves deployed in horizontal, non-overlapping layers (Grime 1965, Horn 1971). These traits facilitate the capture of energy in low light environments while minimizing the energetic cost to construct and maintain plant tissue. The latter is perceived to be especially important since it results in a lower leaf dark respiration rate and lowers the compensation point for net carbon gain (Grime 1965, Loach 1967, Lambers *et al.* 1983, Lusk and Reich 2000). These characters were not scored directly in this study owing to the lack of a suitable data set.

v) Response of Herbs to Available Calcium

Data from this study suggests that many plants of the forest understory may be responsive to differences in available calcium. Ephemeral spring herbs, for example, typically occurred on more calcium rich soils (mean concentration = 6.9 cmol/kg) than plants with persistent shoots that flowered prior to, or after, canopy closure. Early spring flowering plants with persistent shoots typically occurred on more calcium rich soils than plants which flowered mid to late season and completed most or all of their life cycle under a closed canopy (mean concentration = 5.7 and 5.4 cmol/kg, respectively), but not significantly so. The shade tolerant members of the latter functional groups, however, occurred on more calcium rich soils than species with moderate and low shade tolerance. This pattern suggests that plants in these forests have partitioned the calcium availability gradient in relation to the degree of shade stress to which they were exposed.

The mechanism(s) by which plants benefit from calcium rich soils have not been resolved. However, the greater availability of nitrogen arising from a calcium-mediated rise in soil pH may be particularly important for ephemeral spring herbs, since they typically complete their life cycle before the canopy closes (*Allium tricoccum*, the apparent exception, flowers mid to late summer). These species typically have a high light compensation point and a high saturation light intensity (Sparling 1967, Taylor and Pearcy 1976) and may therefore have a greater physiological requirement for nitrogen than more shade tolerant species. The reported affinity of ephemeral spring herbs for base rich, and particularly calcium rich, soils (Curtis 1959, Rogers 1982) may therefore be due in part to the greater availability of nitrogen on these soils.

For shade tolerant herbs, however, the principal mechanism may be a calcium-mediated reduction in dark respiration rate. The morphology and physiology of these species typically emphasizes the conservation of reserves rather than photosynthetic performance (Went 1957, Grime 1965, Loach 1967) and thus may benefit more from a reduction in dark respiration rate than from a greater availability in nitrogen. Efficient use of high irradiance requires a high nitrogen investment in carboxylating enzymes and proteins responsible for photosynthetic electron transport (Niinemets 1997). Shade tolerant species, however, typically allocate proportionally more leaf nitrogen to chlorophyll than to carboxylation capacity (Seeman *et al.* 1987). This investment pattern is thought to be the primary reason why shade tolerant species have a lower respiration rate per unit of leaf N (Lusk and Reich 2000) and an intrinsically low photosynthetic plasticity (Niinemets 1997). In keeping with the latter finding, experimental transfers of plants between high and low light environments have shown that dark respiration rates can change much more rapidly than photosynthetic capacity (Azcon-Bieto and Osmond 1983, Sims and Pearcy 1991). Taken together, these findings suggest that shade tolerant plants on calcareous soils may benefit more from a reduction in dark respiration rate than from a greater availability in nitrogen.

vi) Contribution of Patch, Edaphic and Matrix Variables to Species Composition

Patch variables explained more variance in the distribution of species in the forest understory than did edaphic or matrix variables (36.1%, 28.1% and 10.2%, respectively). Patch variables in this analysis were measures of stand structure (forest cover type, stem diameter class, # tree species), stand disturbance (% canopy closure, regenerating fields, lanes, canopy gaps), and overall plant response to local site conditions and biotic interactions (patch membership). Edaphic variables were measures of inherent moisture retention capacity and soil fertility (soil parent material, soil order, soil moisture class, and percent soil organic matter). Matrix variables were measures of the degree of forest fragmentation in the local landscape (patch area and patch isolation).

For the purpose of this analysis, patch variables were viewed as indicators of processes operating on ecological time scales and at small spatial scales, whereas, edaphic and matrix variables were viewed as indicators of processes operating on long time scales and at larger spatial scales. Within

this framework, the results of this analysis suggest that both local and regional processes have influenced the composition of sampled plant assemblages. In particular, the strong contribution of edaphic variables provides support for the view that the diversity of species in a given setting cannot be explained solely by processes operating on short time scales at the local spatial scale (Ricklefs 1987, Ricklefs and Schluter 1993).

The principal contribution of this analysis, however, is that it reveals the inherent difficulty in selecting appropriate indicators for such a test and in characterizing processes at the appropriate spatial and temporal scale.

In its present form, this analysis clearly overstates the regional contribution of edaphic processes by failing to acknowledge that ecological consequences of regional differences in soil moisture and soil fertility are expressed at the scale of the germinating seed and the competing plant assemblage. The contributions of recruitment limitation and success to species diversity are thus regional, in the sense that they are a consequence of glaciation and pedogenesis, and local, in the sense that operate at the scale of the forest patch and influence the strength of competitive interactions. The former reaffirms the importance of viewing local processes in broader context whereas the latter affirms the primacy of processes operating at the local scale.

In its present form, this analysis may also overstate the contribution of forest fragmentation, since large patches in this study were situated primarily on dry sandy soils, and, small patches were situated primarily on loam soils that were often seasonally moist or wet. Differences in species composition, therefore, may be due primarily to differences in edaphic conditions rather than to post-settlement colonization and extinction events. The degree to which the composition of present-day assemblages is the legacy of past migration events in a continuous forest environment is unknown. However, the modest percentage of alien taxa in vegetation samples (typically < 5%, Appendix 9), the similarity in composition of canopy openings and the adjacent forest floor (Figure 2.4), and the predominance of short-distance dispersal (see Chapter 3), suggests that the composition of the understory flora has been little modified by forest fragmentation.

The larger issue raised by Ricklefs (1987) remains, however. Periodic and chance events such as hurricanes, pathogens, fire, differential rates of migration, and past land use, when discerned, have all been shown to have a marked influence on the composition of present-day assemblages. While it is clear that a comprehensive explanation of community requires an integration of physical and biological factors, over space and time, the practical challenge of how to achieve that explanation has not been met.

vii) Percent Variance in Species Composition Explained by CCA Ordination

The percentage of the variance in species composition explained by environmental variables in CCA ($\sum$canonical eigenvalues ÷ $\sum$unconstrained eigenvalues) was a modest 25.6%. A subset of these same variables, in contrast, explained 58.3 % of the variance in species richness in multiple linear regression (see Chapter 4.0). Reports of modest explanations of variance in CCA are widespread in the ecological literature (e.g. ter Braak 1987, Borcard *et al.* 1992, Okland and Eilertsen 1994, Aude and Lawesson 1998, Ohmann and Spies 1998, ter Braak 1999). In forest studies, the percent of total variance explained (%TVE) has ranged from 10% (Ohmann and Spies 1998) to 48% (Aude and Lawesson 1998) despite comprehensive environmental data.

In my study, four properties of the data may contribute to the modest percent of variance explained by environmental variables. First, the median species frequency was 7 quadrats. This property will generate a higher turnover in species composition for a given richness and thus reduce the percent of variance explained in CCA. This phenomenon has been characterized as a rare species effect by Ohmann and Spies (1998) but it applies more generally since most species are "rare" in most data sets.

Second, the median number of microhabitats per 10m x 10m quadrat was 3 (range 1-10). In principle, environmental heterogeneity should lead to differences in composition for a given value of species richness, since species vary in the type and range of habitats occupied. This in turn should lead to greater variability in species composition and reduce the percent of variance explained in CCA. In keeping with this expectation, habitat diversity explained more variance in species

richness (F=11.5, r^2adj.=0.052, simple linear regression) than in the dispersion of species in CCA ordination space (F=3.83, Monte Carlo permutation test, %TVE=1.97%) (follow-up analyses, not shown).

Third, the spatial resolution of the environmental data is large relative to the conditions experienced by a given seed, seedling, or maturing plant. This should lead to a lower explained variance in species composition since recorded data will fail to account for variability in conditions that lead to differential germination, growth, and persistence. Soil conditions that contribute to differential germination success and to the availability of essential nutrients, for example, typically occur on the scale of centimetres (Harper *et al.* 1965, Harper 1977, Pacala and Silander 1990, Kosola *et al.* 1999) whereas soil properties in this study were measured on the scale of metres or taken from published regional soil surveys. The maximum correlation between vegetation and environment should be achieved when differences in plant-environment and plant-plant interactions reflect the average variation in the physical and biotic environment (Reed *et al.* 1993). The scale at which this occurs has been shown to be attribute dependent (Palmer 1990, Reed *et al.* 1993, Ohmann and Spies 1998).

In keeping with this pattern, attributes of the environment that varied at larger spatial scales (such as soil parent material, soil order, cover type) typically explained more variance in composition and richness than attributes that varied at smaller spatial scales (such as stand structure variables, disturbance features). Differences in soil parent material, for example, explained 4.5% of the variance in species scores in CCA, and 20.9% of the variance in species richness, whereas the presence/absence of disturbance features explained only 1.8% of the variance in species scores in CCA and 5.5% of the variance in species richness (Table 2.13 and follow-up analyses, not shown).

Fourth, the temporal resolution of the environmental data often fails to account for past events that are known contributors to differences in composition and richness, such as post-glacial plant migration (Davis 1981a), major storm events (Henry and Swan 1974), extreme values for temperature and moisture (Okland 1996, Ohmann and Spies 1998), and land use (Pettit *et al.* 1995, Motzin *et al.* 1996). While aspects of these events may be captured by analyses of pollen profiles

(Davis 1983), stand structure (Lorimer 1985), soil properties (Bormann *et al.* 1995), soil profiles (Beke and McKeague 1984), fire scars (Lorimer 1985), etc., the contribution of stand history is likely to remain largely undefined.

Additional sources of unexplained variation reside in certain technical properties of CCA. The goal of CCA is to select the linear combination of environmental variables that maximizes the dispersion of species scores in ordination space (ter Braak 1987). Unlike principal components analysis (PCA), CCA is not a maximal variance extraction technique and thus the fraction of inertia explained by CCA can be quite modest (ter Braak 1999). In strict terms, the "percentage variance" reported in CANOCO is not a true variance. Rather it is the portion of the total inertia that is explained by the extracted axes (ter Braak 1999). This proportion is an analogue to r^2 in linear regression but is not a true coefficient of determination. One consequence of this is that when the number of variables is less than the number of extracted axes, the fraction of inertia explained by the submitted variables will always be less than 100%. Moreover, as in CA, site scores on the second axis may form a quadratic relation with those on the first axis. This fault, known as the "arch effect", is typically less of a problem in CCA, but when present, will contribute to the inertia of the ordination and reduce (or enhance!) the amount of variance that can be explained (ter Braak 1999). As a consequence, ter Braak (1999) has cautioned users not to interpret a low (high) "variance explained" as a poor (good) fit of the ordination model.

The modest percentage variance in species composition explained by traditional data sets in CCA, therefore, may not be unreasonable. While the contribution of certain technical aspects of the method may not be readily quantified, there are several properties of traditional data sets that may account for the modest explanation of variance in species composition in CCA, and, for a modest explanation of variance in composition compared to species richness.

viii) Pattern of Functional Attributes in Relation to Environmental Gradients

The functional attributes of plants examined in this study individually explained more variance in the dispersion of species scores in CCA than did most attributes of the environment (Tables 2.16 and

2.13). Habitat affinity and life form individually explained more variance in the distribution of species than did provenance or life history, and, collectively explained 67.4% of the variance explained by environmental variables (Figure 2.2). The capacity of life form to explain variance in the distribution of species is the more interesting case, in this study, since habitat affinity was defined in relation to canopy closure.

The capacity of life form to explain variance in the distribution of sampled species is due in part to the difference among life forms in shade tolerance (Table 2.17). Grasses, herbs, shrubs and vines in these forests were relatively shade intolerant and were significantly more frequent in quadrats with low canopy closure (high light) ($p<0.0003$, Wilcoxon rank sum tests, not shown). In keeping with this outcome, the number of species of the most shade tolerant life forms (fern allies, ferns, trees) did not vary with canopy closure.

The moisture tolerance of species varied within, but typically not among, life forms (Table 2.18). With the exception of the fern allies, the species associated with each life form were more tolerant of upland conditions (moisture classes 1,2) than of lowland conditions (moisture classes 4,5). In apparent contrast to this pattern, the ferns, grasses and herbs were proportionally more species rich in quadrats with gleyed soil horizons and seasonally wet depressions . The contradiction is more apparent than real, however, since a majority of ferns, grasses and herbs were tolerant of moist to wet conditions when the taxa of intermediate tolerance (moisture class 3) are taken into account. The moisture regime of quadrats with seasonally wet depressions typically ranged from mesic to wet and thus provided micro-sites for taxa across the moisture continuum. In keeping with this perspective, the mean moisture tolerance rating of species in 10m x 10m quadrats did not vary among moisture classes ($p>\chi^2=0.98$, Wilcoxon rank sum test, not shown).

Life forms in these forests, therefore, appear to be more diversified with respect to moisture than to light. This pattern is not unexpected given that differences in moisture availability are less transient than differences in the availability of light. In keeping with this line of reasoning, the difference in shade tolerance among life forms was not significant when only "F" and "F+O" species were

considered. Species with an affinity for open habitats were also diversified with respect to moisture ($p>\chi^2=0.28$, Likelihood ratio test, not shown) and were as likely to be found in natural canopy openings associated with large seeps as in upland habitats beneath canopy gaps created by human disturbance or by wind-throw. As in the previous case, the difference in shade tolerance among life forms is not significant when only "O" and "O+F" species are considered.

A sharp contrast in shade tolerance does arise, however, in life forms that are predominately shade tolerant, such as the ferns, fern allies, and trees, or, that are predominately shade intolerant, such as the vines and grasses ($p>\chi^2=0.0001$, Likelihood ratio test, not shown). These life forms may be found in both open and closed habitats, but not with equal frequency. In contrast, the herbs and shrubs were more diversified across the light gradient and species were equally as likely to be found in closed as in open habitats. Differences in shade tolerance among these life forms are not significant ($p>\chi^2=0.48$, Likelihood ratio test, not shown). These patterns persist when non-native species (which are predominately shade intolerant) are removed from the analysis.

Life form, therefore, is a significant contributor to differences in the composition and distribution of species in these forests. Based on the patterns of shade and moisture tolerance summarized above, the distribution of most life forms should be markedly non-random. Ferns and fern allies should occur primarily on moist soils under a closed canopy; vines should occur primarily on moist soils under a thin or broken canopy; and, grasses should occur on a variety of soils but primarily under broken or open canopy conditions. Herbs and shrubs, on the other hand, should be found throughout the forest. And, not surprisingly, this is typically what was found.

2.5 Principal Findings

1. Traditional environmental factors explained 25.6% of the variation in composition of plant assemblages in the understory of twenty-four, second-growth, northern hardwood, forests near Peterborough, Ontario. The distribution of species was most strongly influenced by gradients in soil moisture, soil order, forest cover type, percent canopy closure, and soil parent material.

The patterns in plant response to differences in soil moisture, soil fertility, and available light are consistent with the results of previous studies of hardwood forests in the Great Lakes region and northeast United States.

2. The distribution of species within forest patches was strongly influenced by microhabitat features created by glacial history, landscape position, the death of canopy trees, and human disturbance: moist or wet forest floors, seeps, tip-up mounds, tree pits, stumps, logs, canopy gaps, raised root mats, lanes, ditches and regenerating fields. These features created habitat opportunities for 35.8% of the recorded flora that did not occur on closed, seasonally dry, forest floors, *sensu stricto*.

   These results provide support for the hypothesis that environmental heterogeneity contributes to species diversity through the provision of novel resources.

3. Environmental heterogeneity at the patch scale provided alternative habitat for species of broad environmental tolerance. When the distribution of species was examined in relation to four generalized habitat categories (closed dry forest floors; moist or wet habitats; features created by human disturbance; features created by natural disturbance), most species (79.2%) were present in more than one habitat category, and several species (33.2%) were present in every category. Comparatively few species (21.8%) were confined to only one habitat type.

   In these forests, species were particularly tolerant of conditions created by the death or removal of a canopy tree (canopy gaps, tree pits, tip-up mounds, stumps, logs). Such features were colonized by 86.0% of the species on closed dry forest floors, 82.0% of the species in moist or wet habitats, and 78.0% of the species in habitats created by human disturbance. However, the capacity of species to colonize or persist on these features was not uniform. More species were recorded in canopy gaps (282) than on tip-up mounds (180), logs (120), pits (97) or stumps (64).

These results provide support for the hypothesis that heterogeneity facilitates the coexistence of species through spatial and temporal segregation of competing species. By virtue of their capacity to colonize at least one other habitat in the local environment, most species in these forests have access to alternative environments where their competitors may do poorly or not survive and where populations of their own kind may expand.

4. The species composition of canopy gaps was similar to the species composition of the adjacent forest floor. The species composition of dry open canopy gaps was typically not responsive to differences in gap size (1-100 m^2). This suggests that the composition of plant assemblages is dominated by persistent taxa, and, that colonization or extinction events during the gap phase rarely alter the composition of understory plants in a significant way. A marked change in the species composition of quadrats adjacent to a recent clear-cut stand suggests that larger canopy openings may stimulate germination of buried seeds and cause significant transient change in the composition of understory plants.

5. Marked differences in the survivorship of juvenile sugar maple stems was observed on a gradient of increasing calcium availability in undisturbed forest stands on mesic soils overlying calcareous till. Stems that were subject to shade stress and self-thinning were more responsive to differences in available calcium than were stems in the upper canopy. When differences among stands were standardized with respect to soil parent material, soil order and soil series, available calcium explained 70.9% of the variance in the number of stems in the 4-10 cm dbh size class, and, 54.0% to 35.0% of the variance in the proportion of stems in the 0-4 cm, 4-10 cm, and 10-30 cm dbh size class.

The data are consistent with the sharp reduction in mortality of juvenile sugar maple stems observed on calcium rich soils in oak transition-northern hardwood forests in northwestern Connecticut (Kobe *et al.* 1995, Kobe 1996) and suggest that on mesic soils the distribution and abundance of sugar maple may be secondarily constrained by the availability, and ratio, of base cations.

6. Data from this study suggests that plants of the forest understory may also be responsive to differences in available calcium. Spring ephemeral herbs, and shade tolerant plants generally, typically occurred on more calcium-rich soils than plants of moderate or low shade tolerance. Plants with persistent shoots that flowered prior to canopy closure typically occurred on more calcium rich soils than plants with persistent shoots that flowered mid to late season, but not significantly so. Traits that extend the period of carbon gain in deeply shaded habitats, such as a winter annual life history, winter-green leaves, and, the initiation of shoot growth or flower initials in the early autumn, were strongly associated with sugar maple stands on calcium-rich soils.

The mechanisms by which plants benefit from calcium rich soils have not been resolved. The greater availability of nitrogen arising from a calcium-mediated rise in soil pH may be particularly important for ephemeral spring herbs since they typically complete their life cycle prior to canopy closure. Shade tolerant herbs, however, may benefit more from a calcium-mediated reduction in dark respiration rate since the morphology and physiology of these species typically emphasizes the conservation of resources rather than photosynthetic performance.

7. Patch variables explained more variance in the distribution of species in the forest understory than did edaphic or matrix variables (36.1%, 28.1% and 10.2%, respectively). Patch variables were viewed as indicators of processes that operate at small temporal and spatial scales, such as competitive interactions, short-distance dispersal, and heterogeneity created by the death or removal of canopy trees. Edaphic variables were viewed as indicators of processes that operate at larger temporal and spatial scales an such as glaciation and pedogenesis. Matrix variables were viewed as indicators of dispersal and migration constraint within the present-day landscape.

Within this framework, the results of this analysis suggest that both local and regional processes have influenced the composition of sampled plant assemblages. The strong

contribution of edaphic variables provides support for the view that the diversity of species in a given setting cannot be explained solely by processes operating on short time scales at the local spatial scale.

8. Habitat affinity and life form explained 67.6% of the variance in species composition explained by environmental variables. The explanatory power of these variables was largely due to their capacity to account for differences in the availability of light. Ferns and fern allies occurred primarily on moist soils under a closed canopy: vines occurred primarily on moist soils under a thin or broken canopy: grasses occurred on a variety of soils but primarily under broken or open canopy conditions. Herbs and shrubs were found throughout the forest understory.

3.0 DISPERSAL PATTERNS

3.1 Introduction

Dispersal is the stage in a plant's life cycle in which the spore, seed, fruit, or vegetative propagule, detaches from the mother plant, travels through space, and comes to rest on a nearby or distant surface (Ridley1930, Berg1983, Little and Jones1980). Dispersal may be achieved in one or more episodes and involve one or more agents (Matlack 1989, Beattie and Lyons 1975, Venable and Levin 1985, Greene and Johnson 1997). The sequence of events may differ somewhat for vegetative propagules but must result in a detached, independently-rooted, ramet to be considered dispersal in this study. In spatially structured populations, dispersal is expected to serve three population-dynamic functions: i) reduction in the risk of low demographic success; ii) escape from the negative consequences of crowding; and, iii) escape from the negative consequences of interactions with siblings (Venable and Brown 1988, 1993).

Pattern in dispersal events is predicted to have profound consequences for populations and communities since dispersal governs variance in the size and composition of the seed rain (Clark and Yi 1995), affects the probability that a diaspore will land in a site suitable for germination (Harper1977, Sorensen 1978, Venable and Levin1985), determines the initial conditions that seeds and seedlings confront (Schupp and Fuentes 1995), affects the initial spatial array of individuals in a population (Thiede and Augspurger1996), determines who interacts with whom and with what intensity (Shmida and Ellner 1984, Pacala 1986, Silander and Pacala 1990, Rees 1996, Rees *et al.* 1996), influences local extinction rates by affecting the probability that declining or extirpated populations are rescued (Brown and Kodric-Brown 1977, Holt 1993), influences the rate at which plants colonize new habitat (Halpern *et al.* 1990, Matlack 1994, Kotanen 1997, Brunet and von Oheimb 1998) and the sequences in which they arrive (Drake 1991, Fastie 1995),and, influences the level of gene flow within and between populations and thus the degree to which neighboring plants are related (Williams and Guries 1994) and genetic variation is structured spatially (Levin 1981, Hamrick and Godt 1997, Hamrick *et al.* 1993).

The diaspores of many species possess morphological features or chemical properties that facilitate dispersal by a particular agent or mechanism (Ridley 1930, Dansereau and Lems 1957, van der Pijl 1982, Thompson *et al.* 1997). Features considered important for dispersal in temperate forest habitats, and their associated dispersal syndrome, include the following: a fleshy pulp or aril that is eaten by frugivores and the seeds are regurgitated or excreted unharmed (endozoochory); hooks, barbs, awns or scabrous hairs that cling to fur or feathers (epizoochory); an oil body (elaiosome) that is attractive to ants and the seed or fruit is moved before the body is eaten and the seed discarded unharmed (synzoochory *s.l.*, myrmecochory *s.s.*); wings, plumes, hairs, flattened or inflated structures that increase air resistance and slow the rate of aerial descent of seeds and fruits (anemochory); a splash-cup or ballistic mechanism that forcefully expels the seed from the plant (ballochory); a hard seed coat or antifungal agent that facilitates the persistence of seeds in buried seed pools (chronochory); a detachable vegetative propagule or disintegrating rhizome, stolon or runner that permits the establishment of an independent ramet (various syndromes, autochory *s.l.*) (Ridley 1930, van der Pijl 1982, Sorensen 1986, Warr *et al.* 1992, Thompson *et al.* 1997. The terminology for dispersal syndromes follows van der Pijl (1982) and Little and Jones (1980); suffix "-chory" from *chorein* = to wander.

The spatial arrangement of established plants is governed initially by the distance diaspores travel in space or time, the nature of the dispersing agent, and the character of the receiving environment. The distance diaspores travel in space is influenced by a variety of factors including propagule morphology (Baker and O'Dowd 1982, Sacchi 1987, Willson 1993), the agent of dispersal (Hughes *et al.* 1994), plant height (Sheldon and Burrows 1973), inflorescence position (Trapp 1988), proximity and character of the surrounding vegetation (Thiede and Augspurger 1996), weather variables (Campbell 1983), seed processing method of animal vectors (Levey 1986), retention time in the digestive tract of animal vectors (Proctor 1968), retention time on the exterior of animal vectors (Bullock and Primack 1977), ferrying time by insects (Berg 1975, Jules 1996), and related factors. In general, diaspores with facilitating features travel farther than those without special devices (Willson 1993), smaller and lighter diaspores travel farther than larger and heavier diaspores of similar mode (Hoppes 1988, Matlack 1989), diaspores dispersed by animals travel farther than

those dispersed on the wind or by ballistic mechanisms (Appendix 11), diaspores dispersed from taller plants and elevated positions travel farther than those dispersed from shorter plants and lower positions (Sheldon and Burrows 1973). For most plants, the proportion of diaspores dispersed declines sharply with distance creating seed dispersal curves with long tails (Portnoy and Willson 1993). The small fraction of diaspores that disperse beyond their immediate surroundings is considered critical for species of transient habitats (Harper *et al.* 1970, Meyer and Schmid 1999), and for metapopulations (Husband and Barrett 1996, Valverde and Silvertown 1997), and may be essential for plant fitness in general (Stebbins 1971, 1974).

The manner in which distance contributes to the population-dynamic functions of dispersal is presently being re-evaluated as studies reveal that many species lack features that may facilitate dispersal (Willson 1993, Hughes *et al.* 1994), that most diaspores travel only metres or tens of metres from the parent plant (Levin 1981, Willson 1993, Hughes *et al.* 1994, Cain *et al.* 1998, Appendix 11), that most dispersal events in spatially variable environments place diaspores in less favorable environments (Cohen and Levin 1991, Holt and McPeek 1996), and, that short distance dispersal may promote coexistence among species (Atkinson and Shorrocks 1981, Shmida and Ellner 1984, Pacala 1986, Silander and Pacala 1990, Hurtt and Pacala 1995, Rees *et al.* 1996). These and related studies suggest that for many plants the most important dispersal outcome is achieved at a distance of 1-2 canopy diameters from parent plant and that any further advantage to be gained at greater distances is not greatly affected by the dispersal mode adopted (Hughes *et al.* 1994, Portnoy and Willson 1993).

Nevertheless, that some propagules must achieve longer dispersal distances for overall plant fitness appears certain in view of the evolution of polychorous (multimodal) species and their investment in structures such as elaiosomes, and dimorphic seeds, which greatly extend the dispersal reach of diaspores (Berg 1969, Westoby 1981, Venable and Levins 1985); the continuous variation in morphology of dispersal structures of individual plants that extends the dispersal reach of unimodal species and monomorphic seeds (Sacchi 1987, Michaels *et al.* 1988); and, the skewed frequency distributions of dispersal distances achieved by all plants, no matter what the mode of dispersal

(Portnoy and Willson 1993). Distance matters, therefore, though not perhaps to the degree once thought (Ridley 1930).

The environment in which a diaspore lands is often a matter of chance alone. However, for some modes, and for propagules that travel only a short distance, the probability of landing in a particular type of environment is better than chance. The directed quality of such dispersal creates the basis for pattern in the spatial arrangement of plants. Direct analysis of the seed rain provides the strongest evidence for directed dispersal (*sensu* Howe and Smallwood 1982, Hanzawa *et al.* 1988) since the spatial arrangement of established plants can be influenced by differential germination success, competitive interactions, and other factors.

For plants dispersed by animal ingestion, the character of the seed rain, and where it lands, may be influenced by a variety of mechanisms, including the behavior and habitat preference(s) of the dispersing agent, the size and composition of the fruit consumed, the manner in which the fruit is eaten and seeds are processed, the degree to which seeds are voided alone or in the company of others, and the type of habitat in which post-foraging behavior occurs (Proctor 1968, Thompson and Willson 1978, McDonnell and Stiles 1983, Johnson *et al.* 1985, Levy 1986, Piper 1986, Stiles and White 1986, Hoppes 1988, Malmborg and Willson 1988, White and Stiles 1990, Stiles 1992, Schupp 1993, Kollmann 1995). Spatial pattern arising from these mechanisms has been detected in the seed-fall of bird dispersed plants in an Illinois woodland (Hoppes 1988, Malmborg and Willson 1988) where 53% of the seeds of fleshy fruits from artificial displays (seven species, representing four life forms) fell in tree-fall gaps, 33% fell within 9 metres of the gap edge, and 14% fell in undisturbed forest. Pattern in the receiving environment has also been reported for species of oak, beech, and pine arising from the seed caching behavior of blue jays (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985) and Clark's nutcracker (Vander Wall and Balda 1977, Tomback and Linhart 1990). Pattern in the consumption of seeds by small mammals has rarely been detected owing to complex interactions among contributing factors (Willson and Whelan 1990, Whelan *et al.* 1991, Willson 1993b, Boman and Caspar 1995), although a tendency for scat to be deposited at the base of trees and on logs has often been observed.

For plants dispersed on the exterior of animals, the character of the seed rain and the receiving environment are expected to be less predictable, owing to differences in the "set" of individual barbs, the rate of uptake and retention of diaspores in different vegetation types, the rate of detection and removal of diaspores by animal vectors, and, the adhesive properties of diaspores and animal hides (Agnew and Flux 1970, Bullock and Primack 1977, Sorensen 1986, Williams and Guries 1994, Kiviniemi 1996). Unlike dispersal by ingestion, dispersal by adhesion is often a random process in which diaspores attach and detach as the animal moves. Depending on local circumstances and the vector involved, some diaspores may travel only a short distance, while others may travel farther than fruits dispersed by animal ingestion or the wind (Sorensen 1986, Matlack 1994, Brunet and von Oheimb 1998). Nevertheless, pattern has been detected in the spatial distribution of established plants. In an intercontinental survey of ten regional floras, plants with adhesive fruits were more likely than other plants to occur in disturbed, meadow, lakeshore, and desert habitats, and, were significantly more common in woodlands than in other habitats examined (Sorensen 1986).

For plants dispersed by ants, the destination of the diaspore is the nest and associated disposal sites which are often located within metres to tens of metres of the parent plant (Berg 1975, Handel 1976, Culver and Beattie 1978). The character of the surrounding environment in which the seedling emerges, however, has rarely been assessed. In habitats where myrmecochory is common (dry sclerophyll vegetation in Australia; meadows and forest understories in North Temperate regions Rice and Westoby 1981,1993; Sernander 1906, as cited in Rice and Westoby 1986; Beattie and Culver 1981), ant-dispersed species are commonly found in a variety of microsites. The environment in which a seedling establishes, therefore, may have more to do with the degree of heterogeneity in the local environment than with the presence or absence of particular conditions. The relative importance of benefits arising from the escape from predators (O'Dowd and Hay 1980, Heithaus 1981), the distance diaspores move (Westoby and Rice 1981), or the placement of seeds in suitable microsites (Hanzawa *et al.* 1988), is still open to debate (Rice and Westoby 1986, Andersen 1988).

For plants dispersed by wind and by ballistic mechanisms, the character of the receiving environment is expected to be highly variable. For most diaspores, however, the receiving environment will be

the immediate surroundings of the parent plant since most diaspores travel only a short distance (Appendix 11). Pattern in the spatial array of these species, therefore, is expected to arise from differential germination success, and competitive interactions, rather than from the effects of dispersal *per se*.

For plants dispersed in persistent seed pools (*sensu* Thompson *et al.* 1997), the character of the receiving environment will be governed primarily by environmental heterogeneity since the seeds of these plants are typically dispersed by the wind, ballistic mechanism, or adhesive fruits. The environment in which germination takes place, however, will typically be disturbed habitats since dormancy is favored to evolve in small-seeded plants in variable environments (Venable and Brown 1988). The seeds of these plants typically lack the metabolic reserves to establish under a closed canopy (Saverimuttu and Westoby 1996, Westoby *et al.* 1996).

From information presented thus far, one may conclude that: i) dispersal has consequences for population and community structure; ii) dispersal may be a non-limiting process within habitat patches owing to the predominance of short-distance dispersal; iii) the environment in which a diaspore lands is governed by its mode of dispersal; iv) dispersal is primarily a deterministic process for diaspores that remain close to the parent plant; v) dispersal is primarily a stochastic process for those that travel more than a few metres from the parent plant; vi) both short and long-distance dispersal contribute to plant fitness; vii) pattern in the seed rain may arise from dispersal but may prove difficult to discern in established vegetation owing to the number of mechanisms involved.

The contribution of dispersal to pattern in plant communities may be affected by interactions with other plant traits that contribute to reproductive success. Interactions among traits that represent different ways of escaping unfavorable conditions have attracted particular attention since selection pressure that favors one trait may indirectly select against another (Levin *et al.* 1984, Venable and Brown 1988, Rees 1993). Reported interactions and apparent trade-offs of interest to this study include: seed size and habitat (Salisbury 1942, 1974, Baker 1972, Mazer 1989, 1990); seed size and seed number (Harper 1977); seed size and dispersal mode (Westoby *et al.* 1992, Hughes *et al.* 1994,

Rees 1996); seed size and dormancy (Rees 1996); dormancy and dispersal (Bulmer 1984, Rees 1996); seed size, dormancy and dispersal (Venable and Brown 1988); longevity and dormancy (Rees 1993, 1994); growth form and mode of dispersal (Harper *et al.* 1970, Hughes *et al.* 1994, Leishman *et al.* 1995); dispersal, dormancy, perenniality and iteroparity (Silvertown 1984); and, seedling success and dispersal (Morse and Schmitt 1985).

The relations between seed size and mode of dispersal have important implications for pattern since related trade-offs between seed size and germination success, and between seed size and dispersal distance, may restrict the range of habitats occupied by a particular dispersal mode. The finding by Westoby *et al.* (1992) that dispersal mode is rarely constrained by seed size is highly significant, therefore, since it implies that the habitats in which plants establish will rarely be constrained by the way in which they disperse. This greatly increases the range of solutions (to ecological problems) available to plants. Observed trends in the frequency of modes in relation to increasing seed mass (unassisted - wind - adhesion - ant - ballistic - vertebrate) (Hughes *et al.* 1994) suggest that some modes of dispersal may confer greater fitness benefits (Westoby *et al.* 1995), or be more constrained phylogenetically (Harvey and Pagel 1991, Harvey *et al.* 1995), than others for a given seed mass and habitat. These trends suggest that pattern may arise within and between habitats in the proportion of species dispersed by a given mode. Differences in dispersal spectra derived from published floras (Willson *et al.* 1990, Jurado *et al.* 1991, Westoby *et al.* 1992, Leishman *et al.* 1995), and from original studies (Dansereau and Lems 1957, Frenkel 1970, Pojar 1974, Luftensteiner 1979, Ellner and Schmida 1981, Hoehne 1981, Westoby *et al.* 1990), are consistent with this expectation.

The relations between dispersal and germination biology have been studied rarely. That such relations occur are not in question since plants in which dispersal attributes fail to harmonize with germination requirements cannot replace themselves (consider, for example, the rapid loss of dispersal capacity among species of open inland habitats germinating on ocean beaches reported by Cody and Overton 1996). One may also conclude from first principles that the direction in which natural selection typically acts is from germination biology to dispersal attributes, since it is primarily the alleles (for dispersal) that are compatible with germination requirements that are passed

along in a colonization event. To date, the impact of germination biology on dispersal attributes has been examined in relation to three phenomena: seed dormancy, seed heteromorphism, and, polymorphism in germination requirements.

The impact of germination biology on dispersal processes is most clearly resolved in the case of spatial dispersal and seed dormancy (treated in this study as dispersal in time, after Willson *et al.* 1990, but arguably, and perhaps more appropriately, classified as a germination strategy, after Baskin and Baskin 1998). Modeling by several researchers reveals that the capacity for dormancy should rarely evolve in species with efficient spatial dispersal since dispersal reduces the likelihood that all seeds will be exposed to unfavorable conditions in any one year (e.g. Venable and Lawlor 1980, Cohen and Levin1987, Venable and Brown 1988). Similarly, dormancy is not expected to evolve in species with large seeds, since the attendant store of provisions significantly improves the chance that a seedling may establish under a closed canopy or other unfavorable conditions (Venable and Brown 1988, Rees 1996, Saverimutto and Westoby 1996). Dormancy may select for higher dispersal, however, when the probability is high that diaspores will find a suitable patch, and, when the amplitude of environmental variation is large (Cohen and Levin 1987, 1991). High dormancy and high dispersal, therefore, are most likely to arise in disturbed habitats in species that have small, wind-dispersed, seeds. The impact of germination biology on dispersal for species with perennial life histories has not been modeled, but is not expected to differ with respect to the trends reported here (Venable and Brown 1993).

The impact of germination biology on dispersal attributes has been examined more thoroughly in species with dimorphic (heteromorphic) seeds than in other functional groups (Harper 1965, 1977; Sorensen 1978; Flint and Palmblad 1978; Venable and Lawlor 1980; Baker and O'Dowd 1982; Olivieri and Berger 1985; Venable 1985; Venable and Levin 1985, Venable *et al.* 1995, and references therein). Seed heteromorphism is the production of seeds of different morphologies or behaviors by single individuals (Venable 1985). It is more common in annuals, plants of arid and semi-arid regions, and weeds, but it is not restricted to these plants (Venable *et al.* 1995). Heteromorphic seeds often display a polymorphism for both germination and dispersal (Harper 1965,

Silvertown 1984) thereby enabling individual plants to "hedge their bets" with respect to the timing and general location of germination events (Sorensen 1978, Seger and Brockmann 1985).

In general, the seed morph that has the more precise germination requirement, and the capacity for dormancy, remains in the immediate vicinity of the parent plant whereas the morph that can establish under a wider range of conditions, and lacks dormancy, disperses beyond the local patch (Venable and Lawlor 1980, Olivieri and Berger 1985). The former combination provides some measure of reproductive assurance (Pannell and Barrett 1998), as well as, a mechanism for reducing competition with siblings (Olivieri and Berger 1985) and non-related species. The latter combination, on the other hand, enables seeds to reach a wider range of habitats and to germinate rapidly in settings that provide suitable conditions for establishment. In the summer annual, Heterosperma pinnatum (Asteraceae), the relations between germination attributes and dispersal reach have been shown to be heritable and correlated with differences in habitat (Venable *et al.* 1995). In keeping with recent theory (Venable and Brown 1993), achenes that germinated rapidly and were capable of longer-distance dispersal were selected against at sites where early germination was hazardous. In those environments, flower heads contained a significantly lower proportion of rapidly germinating achenes than flowering heads in habitats where the risk of germination was less hazardous.

The degree to which monomorphic seeds possess germination polymorphisms has been examined rarely. According to Harper (1977) and Silvertown (1984), cryptic seed heteromorphism (variable seed behavior that is not accompanied by dramatic morphological differentiation) may be a widespread phenomenon affecting many plant species (Venable 1985). In a study of seedling performance and dispersal capacity in the common milkweed, Asclepias syriaca, Morse and Schmitt (1985) found that germination and seedling success were positively correlated with seed size and negatively correlated with dispersal reach. These results were interpreted as evidence of a conflict between seedling performance and dispersal capacity since the seeds that were most capable of reaching distant sites were the seeds least capable of establishment and growth. This conclusion may not reveal the true fitness of seeds dispersed over longer distances, however, since Asclepias syriaca has the capacity to form persistent seed banks (*sensu* Thompson *et al.* 1997, Burnside *et al.* 1996).

Given that approximately 50% of the seeds in this study failed to germinate, and that the seeds which failed to germinate were significantly lighter than those which did, it is possible that the smaller and more vagile diaspores of this species have the capacity for prolonged dormancy. If true, then the case for conflict between seedling performance and dispersal has not been demonstrated. However, if the smaller seeds in Asclepias syriaca were to possess more capacity for dormancy than larger seeds, then a germination polymorphism may be present in the monomorphic seeds of this weedy perennial.

The larger issue raised by the Morse and Schmitt study remains unresolved, however, and points to a fitness limitation that is inherent in the dispersal curve of all species and that may account for the small fraction of diaspores that leave the immediate vicinity of most parents. Although the variety of mechanisms by which germination polymorphism may arise (Silvertown 1984), and the various forms and degrees of dormancy that have evolved (Baskin and Baskin 1998), may each reduce the risk of regeneration failure in vagile diaspores, it would appear that these mechanisms have not been sufficient to modify the seed shadow of most species (Portnoy and Willson 1993). They may, however, permit a larger fraction of diaspores to disperse over longer distances and to colonize suitable habitat in patchy and disturbed environments.

From the preceding discussion, additional conclusions regarding the contribution of dispersal to pattern in established vegetation may be drawn: i) the habitat in which a species germinates should rarely be constrained by its mode of dispersal, although a given mode may be more frequent in some habitats than others; ii) reproductive success in plants requires some measure of harmonization between dispersal attributes and germination biology; iii) the fraction of seeds that disperses beyond the immediate vicinity of the parent plant may depend more on the germination biology of the species than on the mechanical constraints imposed by the mode of dispersal; iv) dispersal attributes are heritable and subject to natural selection.

Study Objectives and General Approach: The contribution of dispersal to spatial structure and species diversity in the forest understory has rarely been examined. The objectives of this chapter,

therefore, are to further this understanding by: i) identifying patterns of association between modes of dispersal and plant traits that may independently contribute to pattern in the distribution of species; and, ii) identifying patterns in the distribution of modes of dispersal within the forest understory and in relation to gradients in limiting resources.

The basic approach was to characterize the sampled flora in relation to the traits of interest and then to search for pattern in the established vegetation. The dispersal attributes of 413 vascular plants from 24 forest stands were classified in relation to the agent of dispersal and then examined for pattern in relation to plant traits (life form, life history, provenance, fruit type, taxonomic rank, environmental states (environmental gradients, microhabitats, habitat affinity, moisture affinity, shade tolerance), plant abundance (frequency class, richness class, cover class), and landscape properties (patch size and patch isolation). Particular attention was given to the herbaceous flora since it represented the full range of dispersal modes recorded in these forests. Pattern was assessed with reference to descriptive statistics, non-parametric statistics, detrended correspondence analysis (DCA), and canonical correspondence analysis (CCA).

This thesis represents the first time that the dispersal spectrum has been characterized in relation to microhabitats within the forest understory.

The contribution of dispersal to differences in species richness in sampled forest stands is analyzed in Chapter 4.

3.2 Methods

3.2.1 Classification of Dispersal Modes

3.2.1.1. Overview

Mode of dispersal was inferred from the morphology or known properties of the diaspore. Species were assigned to one or more of the following syndromes based on the known or presumed function of the facilitating feature: dispersal by animals (zoochory), dispersal by wind (anemochory),

dispersal by mechanical expulsion (ballochory), dispersal by prolonged dormancy in the soil (chronochory), dispersal by vegetative expansion (autochory), dispersal by unassisted means (atelechory), and, dispersal by more than one mode (polychory). Animal dispersal was further classified in relation to the proximate mechanism, in view of differences in habitat preferences and foraging patterns of the animal vectors: dispersal by ingestion (endozoochory), dispersal by adhesion (epizoochory), and, dispersal by active conveyance or handling (synzoochory). Dispersal by animal conveyance was further classified for similar reasons: dispersal by seed caching, and, dispersal by ants (myrmecochory).

Dormancy is considered to be a dispersal character, in this study, in recognition of the contribution of persistent seed pools to community structure and species richness (Venable and Brown 1988, 1993; Kalisz *et al.* 1997). Other plant traits that contribute to dispersal in time, such as iteroparity, perenniality, and persistent life history stages, are considered alternatives to dispersal since they do not affect the morphology or physical attributes of the diaspore. Serotiny, if present, would have been a dispersal character since it affects the release of the diaspore. Despite their short dispersal reach, rhizomes, stolons, and runners are treated as dispersal characters since they satisfy the definition of dispersal when they result in the establishment of a detached, independently rooted, ramet.

The purpose of the classification is descriptive: to identify the agents, structures and attributes that facilitate the dispersal of recorded taxa. It is concerned solely with the capacity of the agent to transport a spore or seed unharmed, and is silent with respect to the capacity of the agent to deliver the propagule to a "safe site" (dispersal efficiency), and, to the proportion of seedlings in a population that may be attributed to a particular vector (dispersal effectiveness) (Harper 1977, Reid 1989, Bustamente *et al.* 1992, Schupp 1993).

The classification is also silent with respect to the status of facilitating structures and properties as adaptations for dispersal. Depending on the definition used, these features may be adaptations for dispersal or not (Reeve and Sherman1993). If the definition requires that the feature be built by

natural selection for its current role (e.g. Gould and Vrba 1982), then most features would not be adaptations for dispersal since their original function may have been to protect the developing ovule (Stebbins 1974) or to serve some other purpose. If the definition only requires that the feature or property results in higher fitness than alternative variants in the same environment (Reeve and Sherman 1993), then many features in this study would be considered adaptive in some habitats but not, perhaps, in all. In keeping with the requirements of many definitions of adaptation, dispersal characters have been shown to contribute to plant fitness, to be heritable, and to be subject to natural selection (e.g. Cody and Overton 1996,Venable *et al.* 1995).

The morphology and dispersal properties of diaspores were evaluated in the field and with reference to the published literature and the Montgomery Seed Collection, Royal Ontario Museum, Toronto, Ontario. Fruit terminology follows Gleason and Cronquist (1991). The classification of recorded taxa is presented in Appendix 2; a listing of species codes and corresponding scientific names is presented in Appendix 3.

3.2.1.2 Classification Criteria and Related Considerations

Dispersal by Animals (Zoochory): Dispersal by animals may be achieved by ingestion (endozoochory), adhesion (epizoochory) or active conveyance (synzoochory) (Sernander 1901, as cited in Fahn and Werker 1972). Facilitating properties and considerations are discussed below. The principal frugivores and myrmecochores in Eastern North America are presented in Appendices 12 and 13, respectively.

Animal Ingestion (Endozoochory): Dispersal by ingestion is achieved when the fleshy pulp of an aril or fruit is eaten by an animal and the seeds are regurgitated or excreted unharmed (Ridley 1930, van der Pijl 1982, Willson *et al.* 1990). Species were so classified if the seed possessed a fleshy aril; or, if the fruit was a berry, drupe, drupelet, pome; or, if an achene was embedded in a fleshy receptacle or enclosed by a fleshy hypanthium. Fleshy fruits that possessed an elaiosome were classified as ant dispersed. Trillium erectrum and Streptopus roseus were classified as ant dispersed but may be polychorous based on the analysis of Trillium by Berg (1958), as cited in Stebbins 1974.

and, on the classification of Streptopus by Willson 1986.

The criterion for dispersal by ingestion excludes seeds and fruits eaten by granivores since the hard seed coat, which is the facilitating property, cannot be discerned visually, and, since published tests of viability were not sufficient to classify the taxa in this study (e.g. McAtee 1947, Krefting and Roe 1949, Flaming and Proctor 1968). Non-fleshy diaspores consumed by animals were therefore classified as dispersed by "unassisted" means. While dispersal by granivores is generally discounted (Willson 1986), some fraction of consumed seeds invariably survives passage through the beak, gizzard, or stomach of the bird, mammal or insect, and contributes to the long-distance dispersal of species that lack fleshy diaspores (Krefting and Roe 1949, van der Pijl 1982, Morton and Hogg 1989, Stiles 1989, Schupp 1993). The surviving fraction varies with both the diaspore and the consuming agent. Collinge (1913) reports the germination of 281 species of herbaceous plants from 142 droppings of the house sparrow, bull finch and green finch, whereas Rossler (1936), in contrast, reports that only 7 of 40,000 seeds of various herbaceous plants germinated in the scat of California linnets.

The criterion for dispersal by ingestion also excludes nuts swallowed and regurgitated by jays and other seed caching animals. While satisfying the operational requirement that seeds be regurgitated or excreted unharmed, the swallowing of nuts for the purpose of later retrieval and consumption (Darley-Hill and Johnson 1981, Johnson and Adkisson 1985) implies intentionality that is lacking in dispersal by frugivores. Nut fruits were therefore classified as being dispersed by active conveyance or handling.

Fleshy fruits in the forests of Eastern North America are consumed by birds, mammals, and at least one reptile, the Eastern Box Turtle (Martin *et al.* 1951). Most fleshy fruits in these forests are consumed by both birds and mammals based on data summarized in Martin *et al.* (1951). In that study, 46 of 48 genera of fleshy-fruited plants east of the Mississippi River were consumed by each animal class. Overlaps with birds and mammals have also been reported for genera consumed by the Eastern Box Turtle (Hamilton 1941, Wilson 1986, Rust and Roth 1981). Further differentiation

among fleshy fruits arising from differences in foraging and processing within and among animal classes was not pursued, therefore, in view of the lack of capacity to discriminate among animal agents (based on the presence or absence of selected fruit characters).

Animal Adhesion (Epizoochory): Dispersal by animal adhesion is achieved when a diaspore becomes passively attached to the fur or feathers of an animal by means of barbed, hooked or scabrous awn, bristle, hair or spine, and the seed is subsequently removed or released unharmed (Sorensen 1986). The facilitating structure in this study may be present on the fruit (typically), hypanthium (Agrimonia), involucral bract (Arctium, Cirsium), lemma (Poaceae), stem or leaf (Galium, Leersia).

The criterion for dispersal by adhesion excludes fruits that become sticky when wet (viscid fruits) since this character is not readily observed and is rarely reported in technical manuals. Species that may be dispersed by mucilaginous seeds in this study are Plantago major and Prunella vulgaris (Ridley 1930, p.549). Kerner (1895, p.869) reports that the fruits of Solanum are sticky when over-ripe and adhere to the hair and bristles of animals.

The criterion for dispersal by adhesion also excludes diaspores that may be dispersed in mud adhering to the feet of birds or mammals (Ridley 1930) since facilitating structures are not required for this mode of dispersal. Species that are most likely to be dispersed by this mechanism are small-seeded plants of wet and wet-mesic habitats.

The adhesive status of diaspores with awns, bristles, hairs or spines that lack barbs, hooks or scabrous properties was selectively tested with fruits from the Montgomery Collection, Royal Ontario Museum, Toronto. Although diaspores lacking these structures were excluded by Sorensen (1986), their adhesive properties may be sufficient to facilitate short-distance dispersal, particularly when wet (Morton and Hogg 1989, personal observation). Diaspores that adhered to an inclined cotton shirt when dropped from an upraised hand were deemed to be "adhesive" and were included in the classification (cited as "Montgomery Collection Test" in Appendix 2).

Active Handling or Animal Conveyance (Synzoochory): Dispersal by animal conveyance is achieved when the diaspore is intentionally transported by an animal for some purpose and the seeds are regurgitated or discarded unharmed (Fahn and Werker 1972, van der Pijl 1982). When the diaspore is transported for the purpose of storing food, but is forgotten or not eaten, the dispersal syndrome is "seed caching" (Smith and Reichman 1984), "larder hoarding", or "scatter hoarding" (Stapanian and Smith 1978). When the diaspore bears an elaiosome (an outgrowth of a seed or fruit in which lipids are stored) that is eaten by ants, or by vespid wasps, and the seed is discarded unharmed, the syndrome is "myrmecochory" (Sernander 1906) and "vespichory" (Jules 1996), respectively. In this study, the elaiosome may be attached to the seed (typically), schizocarp (Galium), base of the style (Carduus, Cirsium), or, comprise the basal portion of the perigynium (Carex) (Sernander 1906). In this study, the acknowledged fruit type dispersed by seed caching is the nut, although other fruit types may be so dispersed.

The criterion for dispersal by animal conveyance leaves open the purpose for which the diaspore is conveyed. Diaspores passively conveyed on plant parts that are intentionally transported for nesting material (Ridley 1930, Morton and Hogg 1989) is not considered to be synzoochory in this study since the property of interest does not relate to the diaspore.

The traditional test for myrmecochory has been behavioral: transport by ants and disposal of the seed unharmed (Sernander 1906, Berg 1975, Hughes and Westoby 1992b). Chemical assays and morphological assessments are not sufficient owing to uncertainty regarding the nature of the attractant (Bresinsky 1963, Marshall *et al.* 1979, Howard *et al.* 1981, Gordon 1983, Skidmore and Heithaus 1988, Brew *et al.* 1989) and the status of arils, caruncles and strophioles as agents of myrmecochory (Fahn and Werker 1972, Roth 1977, Beattie 1985). Therefore, only species that have been tested and been shown to be dispersed by ants have been classified as myrmecochores. This requirement was waived for Carex pensylvanica, based on an analysis of lipid content conducted for this study by Dr. M. Kahn, Department of Botany, University of Toronto, and, for Claytonia caroliniana, Dicentra canadensis, Polygala pauciflora, Viola labradorica, Viola sp., based on the known status of conspecifics and the presence of prominent "elaiosomes". Additional genera not

classified as myrmecochores in this study, but reported to be ant-dispersed in Europe, are Ranunculus (Roth 1977), Juncus (Bresinsky 1963), Allium, Convovulus, Festuca, Geranium, Impatiens, Iris, Polygala, Polygonum, Potentilla,, Silene, Stellaria, Trientalis, and Waldsteinia (Sernander 1906).

Dispersal by Wind (Anemochory): Dispersal by wind is achieved when the rate of descent of the diaspore is slowed by an aerodynamic shape or by virtue of its small size and light weight (Ridley 1930, Fahn and Werker 1972, van der Pijl 1982, Burrows 1986). Structures that facilitate wind dispersal in this study are wings, accrescent tepals, an inflated perigynium, a detachable panicle, a coma of fine hairs, or, a pappus of plumose, capillary or barbellate bristles.

The criterion for wind dispersal makes provision for small, light diaspores that otherwise lack a facilitating morphology. This approach departs from Willson *et al.*(1990), who excluded such diaspores because of the problem in defining an appropriate threshold size. This argument has been accepted for seeds but not for spores. The former have been classified as "unassisted", whereas the latter have been classified as "wind dispersed". Orchid seeds, while dust-like in character (and thus classified as "unassisted" by Willson *et al.*1990), have a flattened wing-like region surrounding the germ (Summerhayes 1951, Montgomery 1977, personal observation), or an inflated and air-filled seed coat (Rasmussen 1951, Arditti 1992), that contributes to their capacity to remain aloft for long periods, and thus are classified as wind dispersed in this study.

Wind-push contributes to the short-distance dispersal of many fruits through the catapult effect of swaying stems or direct pressure on a flattened profile. In keeping with the conservative approach adopted in this study, most of these species have been classified as dispersed by "unassisted" means since they lack a distinctive facilitating morphology. Selected species that have been classified as "wind ballists" (van der Pijl 1982) are described in the section entitled "Dispersal by Mechanical Expulsion (Ballochory)".

"Aerodynamic" structures, such as plumose hairs, wings, accrescent tepals, and inflated perigynia,

may enhance the buoyancy of diaspores on water as well. This dimension has not been classified owing to the lack of flowing water in surveyed stands. Classified species that may be water dispersed in other settings include: Boehmeria cylindrica, Carex intumescens, Carex retrorsa, Rumex orbiculatus, Salix spp., and Typha latifolia.

Dispersal by Prolonged Dormancy (Chronochory): Dispersal by prolonged dormancy is achieved when a seed regenerates from a long-term persistent seed bank (Thompson *et al.* 1997). Species were classified as chronochores if their seeds have been reported to persist in the soil for at least five years, and, if the methodology for determining persistence satisfied the criteria of Thompson *et al.* (1997) for a Type 3 seed bank.

The threshold for defining long-term persistence was established pragmatically since five years represented the termination point for a significant proportion of burial experiments (Thompson *et al.* 1997). The ecological significance of this threshold is that it differentiates seeds with limited capacity to persist in the soil from those with greater capacity. Seeds that can persist at least five years in the soil often remain viable for much longer (Thompson *et al.* 1997) and thus represent an important source of propagules for the colonization of disturbed sites.

The term "chronochory" (khronos = time + chorein = to wander) originates with this study.

Dispersal by Mechanical Expulsion (Ballochory): Dispersal by mechanical expulsion is achieved when the seed is forcefully expelled from the plant by explosive dehiscence (Ridley 1930, Fahn and Werker 1972, Beer and Swain 1977, Stamp and Lucas 1983), a splash-cup or springboard mechanism activated by falling water droplets (Brodie 1951, 1955; Savile 1953, 1979; Savile and Hayhoe 1977), or, by a swaying stem activated by wind-push (Ridley 1930, van der Pijl 1982).

The criterion for mechanical expulsion by a swaying stem has been applied conservatively since the dispersal of most plants is enhanced by this mechanism. Only plants that are known for catapulting their seeds, or that possessed a specialized morphology (e.g. a censer mechanism, or an inflated

hypanthium) for controlling or enhancing the release of seeds from swaying capsule or follicle, were recognized as anemoballists in this study.

Dispersal by Vegetative Expansion (Autochory): Dispersal by vegetative expansion is achieved when a detachable propagule, or, a disintegrating rhizome, stolon or runner, gives rise to a detached, independently rooted, ramet (Bell 1991). Detachable propagules in this study are bulbils (Cicuta bulbifera, Cystopteris bulbifera), twigs and branchlets (Salix spp.).

Dispersal by vegetative expansion has been excluded as a dimension of polychory to facilitate comparisons between sexual and asexual modes of dispersal.

Dispersal by Unassisted Means (Atelechory): Dispersal by unassisted means is achieved by diaspores that lack an apparent feature or property to facilitate their movement through space or time. These species are presumably dispersed by animal ingestion since each has a sizable geographic range in Eastern North America (Gleason and Cronquist 1991).

Dispersal by Multiple Agents (Polychory): Dispersal by multiple agents is achieved when the diaspore is dispersed by two or more of the following modes: zoochory, anemochory, chronochory, or ballochory. Dispersal by vegetative expansion has been excluded as a dimension of polychory to facilitate comparison between sexual and asexual modes of dispersal.

The results of this classification are presented in Appendix 2.

3.2.2 Classification of Other Plant Traits

Additional plant traits evaluated in this study were life form (tree, shrub, vine, fern, fern ally, grass, herb), life history (annual, biennial, perennial), provenance (native, alien), and fruit type (achene, berry, caryopsis, capsule, drupe, follicle, legume, nut, nutlet, pome, samara, schizocarp, and silique). The spores of inventoried ferns and fern allies, and the arillate and winged seeds of inventoried gymnosperms, were classified as "fruit" for ease of use. The authority for provenance was Morton

and Venn (1990); the authority for life form, life history and fruit type was Gleason and Cronquist (1991). A summary of plant traits by species is presented in Appendix 2.

3.2.3 Identification of Pattern

In this study, a relationship between (among) variables was deemed to constitute a "pattern" when the relationship was significant statistically, or, when the variables of interest were aggregated in ordination space. Protocols and assumptions for testing patterns of association are described below.

3.2.3.1 Pattern in Relation to Plant Attributes

The relationship between modes of dispersal and other plant traits was examined with respect to life form, life history, provenance, modality, fruit type, and taxonomic rank. These traits are known, or have the potential, to vary with environmental conditions for independent reasons and thus may confound interpretations of the role of dispersal in structuring the composition and abundance of plant assemblages. Published data were not sufficient to characterize the germination traits of sampled species.

The relationship between modes of dispersal and examined traits was summarized by descriptive statistics and tested by chi-square tests of homogeneity by row or cell. In keeping with the subsequent focus on understory herbs, only the results for the herb life form are reported. The expected value for each test was the proportion of herbs in the sampled flora with the trait of interest. The defining equation was the following:

Expected value = (the number of herbs dispersed by mode in sampled patches÷ the total number of herbs in the data set) X (the number of herbs with the trait of interest).

The total number of herbs in sampled patches was 252; however, the total number of herbs in a given test varied, since taxa were not always classifiable in relation to the trait of interest. Given the large number of tests in each analysis, the status of tests after Bonferroni correction for the number of tests was reported.

The analyses were performed in JMP, Version 3.2.2. SAS Institute. The results of this analysis are reported in Tables 3.1 to 3.8.

3.2.3.2 Pattern in Relation to Environmental Variables

The tendency for the dispersal modes of herbs to be associated with particular environmental states was examined in relation to habitat affinity, moisture affinity, shade tolerance, environmental gradients, and microhabitats (see Chapter 2 for definitions and descriptions of variables).

The relationship between modes of dispersal and the habitat affinities of herbs was tested by chi-square tests of homogeneity, by row and cell. Chi-square tests of independence were not appropriate for this analysis since selected herbs were dispersed by more than one mode and thus were recorded in more than one dispersal category.

The relationship between modes of dispersal and selected environmental gradients was tested by Wilcoxon rank sum tests with independent samples. The response variable in each test was the proportion of taxa in 10 m x 10 m quadrats that were herbs dispersed by a given mode. Analysis of variance was not appropriate for this analysis since the response variable was based on count data and rarely satisfied the normality and equal variance assumptions of ANOVA. Only the major gradients (see Chapter 2) were included in this analysis.

Analyses were performed in JMP, Version 3.2.2., SAS Institute, Inc. The results of this analysis are reported in Tables 3.9 to 3.12.

Patterns of association were also examined in the ordination space of detrended correspondence analysis (DCA) in order that trends may be assessed in relation to compositional similarities among quadrats and to environmental affinities among species. DCA was preferred to CCA for this analysis, since the dispersion of quadrats in DCA is governed by species relations with the underlying environment rather than with the restricted set of variables chosen for study. Pattern analysis was conducted by visual inspection. In order to reveal the main trends in the data, only the quadrats in

which the mode was prominent were labeled (i.e. quadrats in which the proportion of taxa dispersed by the labeled mode was ≥the 75% quantile of proportions for that mode in the study area).

The distribution of dispersal modes in relation to environmental variables was evaluated with reference to canonical correspondence analysis (CCA). Here the pattern of interest was the degree to which modes of dispersal were associated with the set of environmental variables examined in Chapter 2. For this analysis, the species codes of species were replaced by modes of dispersal which then functioned as "pseudo-species" in the ordination. The abundance values for each mode were the proportions of taxa dispersed by the mode in each 10m x 10m quadrat in which it occurred.

The DCA and CCA ordinations were performed in CANOCO, Version 3.12; the ordination diagrams were produced in S-Plus, Version 4.5, and re-formatted for presentation purposes in Microsoft Publisher 98. The results of this analysis are presented in Figures 3.1 to 3.6.

The relationship between modes of dispersal and environmental states was re-examined at the microhabitat scale since environmental conditions within quadrats were rarely uniform. Pattern was investigated in relation to three analytical contexts: i) difference in the number of herbs recorded in each microhabitat; ii) difference in the proportion of herbs in contrasting microhabitats, paired samples; iii) difference in the proportion of herbs in contrasting microhabitats, independent samples.

Context (i) clarified the degree to which differences in the proportion of herbs in contrasting habitats were due to the number of herbs dispersed by the mode of interest; context (ii) clarified the degree to which differences in the proportion of herbs in contrasting habitats was due to factors other than dispersal; context (iii) revealed the degree to which the frequency of modes changed under contrasting habitat conditions but did not clarify the role of dispersal since the degree of dispersal limitation in sampled quadrats was not known.

The relationship between dispersal mode and microhabitat in context (i) was tested by chi-square tests of homogeneity by column, row, and cell. The relationship in context (ii) was tested by

Wilcoxon signed-ranks tests, using paired samples from each quadrat in which the contrasting habitats were present. The number of habitat contrasts that could be assessed by this method was constrained by the minimum sample size associated with this test (6 paired comparisons, all of like sign, are required for the test to be significant at the 5% level: Sokal and Rohlf 1995, p.444). The relationship in context (iii) was tested by Wilcoxon rank sum tests, using independent samples. Quadrats in which the mode was present in each habitat were excluded from the analysis.

Analyses were performed in JMP, Version 3.2.2., SAS Institute, Inc. The results of this analysis are reported in Tables 3.13 to 3.15.

3.2.3.3 Pattern in Relation to Abundance Variables

The relationship between mode of dispersal and plant abundance was examined in relation to species frequency, plant cover, and species richness.

The relationship between mode of dispersal and species frequency was tested by chi-square tests of homogeneity by row and cell. Three frequency classes were established for the analysis: "high" ($\geq$25 quadrats), "intermediate" (3-24 quadrats), and "low" ($\leq$2 quadrats). The thresholds for the "high" and "low" classes were taken, arbitrarily, to be the 75% and 25% quantiles of species frequency, respectively.

The relationship between mode of dispersal and plant cover was tested by chi-square tests of homogeneity by column (*df* 8), row (*df* 6), and cell (*df* 1). Eight cover classes were established for the analysis: trace (1-5 individuals or small clumps), <1%, 1-5%, 5-15%, 15-25%, 25-50%, 50-75%, and 75-100%. These thresholds conform to the Daubenmire cover scale when cover is greater than 25% and, with minor exceptions, to the Domin-Krajina cover scale when cover is below 25% (Mueller-Dombois and Ellenberg 1974).

The relationship between mode of dispersal and species richness was tested by Wilcoxon rank sum tests, by row. Three classes of species richness (number of species) were established for the

analysis: "high" (≥56 taxa per quadrat), "intermediate" (29-55 taxa per quadrat), and "low" (≤ 28 taxa per quadrat). The thresholds for the "high" and "low" classes were taken, arbitrarily, to be the 75% and 25% quantiles of species richness, respectively.

Analyses were performed in JMP, Version 3.2.2., SAS Institute, Inc. The results are reported in Tables 3.16 to 3.18.

3.2.3.4 Pattern in Relation to Spatial Scale

The relationship between mode of dispersal and spatial scale was examined in relation to patch size and patch isolation.

In each case, the relationship was tested by Wilcoxon rank sum tests, by row. Three patch size classes were established for the analysis: "high" (≥122 ha), "intermediate" (43-121 ha), and "small" (≤42 ha). Three patch isolation classes were established for the analysis: "high" (mean distance to the nearest 8 woodlots, in 45^0 sectors, ≥477 metres), "intermediate" (mean distance 233-476 metres), "low" (mean distance ≤ 232 metres). The thresholds for the "high" and "low" classes were taken, arbitrarily, to be the 75% and 25% quantiles of patch size, and patch isolation, respectively.

Analyses were performed in JMP, Version 3.2.2., SAS Institute, Inc. The results are reported in Tables 3.19 and 3.20.

3.3 Results

Analyses for pattern in the tendency for modes of dispersal to be associated with particular states will be reported in relation to the following functional groupings: plant attributes, environmental variables, abundance variables and spatial scale.

3.3.1 Pattern in Relation to Plant Attributes

The tendency for dispersal modes to be associated with particular plant attributes are summarized

in relation to life form, life history, provenance, fruit type, and taxonomic rank. Each attribute has the potential to confound interpretations of the role of dispersal in structuring the composition and abundance of herb assemblages on the forest floor.

3.3.1.1 Life Form

The mode of dispersal varied by life form (Table 3.1). Most trees, and all ferns and fern allies, were dispersed by the wind, whereas most shrubs and vines were dispersed by animal ingestion. Most grasses were dispersed by animal adhesion. Herbs were the only life form to be dispersed by all modes and were dispersed primarily by vegetative expansion, animal vectors or unassisted means.

All life forms were dispersed by the wind and all but the trees achieved vegetative expansion by rhizomes or stolons. With the exception of the ferns and fern allies, all life forms were dispersed by animals and by prolonged dormancy in the soil. Only the grasses and herbs were dispersed by adhesion to animals, and only the herbs and one tree (*Robinia pseudoacacia*) were dispersed by mechanical expulsion. Only the herbs were dispersed by ants. A minority of shrubs, and a modest fraction of grasses and herbs, were dispersed by unassisted means. All but the ferns and fern allies were dispersed by more than one mode.

The dispersal modes of life forms also changed with the stratum of the forest. Canopy trees were dispersed primarily by the wind, whereas shrubs and vines were dispersed primarily by animal ingestion. All modes were present in the herb layer on the forest floor.

Taxa in these forests were dispersed primarily by animals (38.5 %), vegetative expansion (35.8 %), or the wind (30.5 %). Fewer taxa were dispersed by unassisted means (22.0 %), prolonged dormancy in the soil (15.5 %), and mechanical expulsion (4.6 %). Approximately 12 % of surveyed taxa were dispersed by more than mode.

These results are not supported by statistical analysis since the sparse data table did not permit

Table 3.1. Dispersal modes of surveyed taxa by life form. Legend: AI = animal ingestion, AA = animal adhesion, AC = animal conveyance, W = wind, PD = prolonged dormancy in the soil, ME = mechanical expulsion, U = unassisted, MM = multimodal, VE = vegetative expansion. Entries are the number of taxa recorded in 192, 10m x 10m quadrats.

Life Form		Dispersal Mode									
		Animal									
Form	# Taxa	AI[1]	AA[1]	AC[1]	Total	W[1]	PD[1]	ME[1]	U	MM	VE
tree	30	1	0	6	7	22	1	1	0	1	0
shrub	55	44	0	1	45	6	3	0	3	3	17
vine	9	8	0	0	8	1	1	0	0	1	2
fern	23	0	0	0	0	23	0	0	0	0	18
fern ally	8	0	0	0	0	8	0	0	0	0	4
grass	36	0	19	0	19	2	9	0	10	7	13
herb	252	17	34	33	80	64	50	18	78	39	94
Total	413	70	53	40	159	126	64	19	91	51	148
%	100	16.9	12.8	9.7	38.5	30.5	15.5	4.6	22.0	12.3	35.8

Notes:
1. Column values for a given dispersal mode include species that are multimodal.

chi-square tests of independence or homogeneity.

The finding that mode of dispersal differs among life forms has important implications for analyses of pattern since correlations with dispersal mode may be confounded with life form. For this reason, the results of subsequent analyses are either summarized by life form or relate strictly to herbs.

3.2.1.2 Life History

Approximately 90 % of taxa were perennial (Table 3.2). Trees, shrubs, vines, ferns and fern allies were strictly perennial. Annual and biennial grasses and herbs were dispersed by prolonged dormancy in the soil (45.7 %), wind (37.1 %), adhesion to animals (28.6 %), mechanical expulsion (17.1 %), unassisted means (14.3 %), and ants (11.4 %). None was dispersed by animal ingestion, seed caching or vegetative expansion. Approximately one-third of the species dispersed by multiple modes were annuals or biennials.

The number of herbs dispersed by animal adhesion, wind, prolonged dormancy, mechanical expulsion, and multiple modes varied with life history ($p<0.05$, chi-square tests of homogeneity by row, *df* 2, not shown; tests for prolonged dormancy, mechanical expulsion and multiple modes significant after Bonferroni correction for 8 row tests). The number of taxa dispersed by prolonged dormancy, mechanical expulsion and multiple modes was greater than expected for annual herbs, whereas, the number of taxa dispersed by animal adhesion, wind, prolonged dormancy, and multiple modes was greater than expected for biennial herbs ($p<0.01$, chi-square tests of homogeneity by cell). Analyses of pattern involving these modes of dispersal were therefore assessed for possible interactions with life history.

3.3.1.3 Provenance

Approximately 85% of taxa were native (Table 3.3). Among life forms, only the ferns and fern allies were strictly native. The percentage of alien taxa among other life forms was highest among

Table 3.2. Life History of surveyed taxa by dispersal mode and life form. Annual = annual *s.s.*; Biennial = annual/biennial, biennial *s.s.*; Perennial= annual/perennial, biennial/perennial, perennial s.s.. "-" = not applicable. Superscript[1]: total includes taxa with unknown life history. Superscript[2]: includes taxa dispersed by more than one mode.

Dispersal Mode		Life History					
Mode by Life Form	Taxa #	Annual #	Annual %	Biennial #	Biennial %	Perennial #	Perennial %
ALL TAXA	413[1]	13[2]	3.1	22[2]	5.3	372[2]	90.1
Animal s.l.	159[1]	3	1.9	9	5.6	146	91.8
Ingestion	70	0	0	0	0	70	100.0
Adhesion	53	3	5.7	7	13.2	42	79.2
Seed Caching	7	0	0	0	0	7	100.0
Ant	33	1	3.0	3	9.1	29	87.9
Wind	126	2	1.6	11	8.7	113	89.7
Prolonged Dormancy	64	6	9.4	10	15.6	50	78.1
Mechanical Expulsion	18	4	22.2	2	11.1	12	66.7
Unassisted	95	2	2.1	3	3.2	85	94.5
Multiple Modes	49	5	10.2	11	22.4	33	67.3
Vegetative Expansion	148	0	0	0	0	148	100.0
TREES	30	-	-	-	-	30	100.0
Ingestion	1	-	-	-	-	1	100.0
Seed Caching	6	-	-	-	-	6	100.0
Wind	22	-	-	-	-	22	100.0
Prolonged Dormancy	1	-	-	-	-	1	100.0
SHRUBS	55	-	-	-	-	55[2]	100.0
Ingestion	44[2]	-	-	-	-	44	100.0
Seed Caching	1	-	-	-	-	1	100.0
Wind	6[2]	-	-	-	-	6	100.0
Prolonged Dormancy	3[2]	-	-	-	-	3	100.0
Multiple Modes	3	-	-	-	-	3	100.0

Table 3.2. Life history of surveyed taxa by dispersal mode and life history (cont'd).

Dispersal Mode		Life History					
Mode by Life Form	Taxa #	Annual #	%	Biennial #	%	Perennial #	%
VINES	9	0	0	0	0	9[2]	100.0
Ingestion	8[2]	0	0	0	0	8	100.0
Wind	1	0	0	0	0	1	100.0
Prolonged Dormancy	1[2]	0	0	0	0	1	100.0
Multiple Modes	1	0	0	0	0	1	100.0
FERN / FERN ALLIES	31	-	-	-	-	31	100.0
Wind	31	-	-	-	-	31	100.0
GRASSES	36[1]	1	2.8	0	0	32[2]	88.9
Adhesion	19[2]	0	0	0	0	19	100.0
Wind	2[2]	1	50.0	0	0	1	50.0
Prolonged Dormancy	9[2]	0	0	0	0	9	100.0
Unassisted	10[1,2]	0	0	0	0	9	90.0
Multiple Mode	7	0	0	0	0	7	100.0
HERBS	252[1]	12[2]	4.8	22[2]	8.7	215[2]	85.3
Ingestion	17[2]	0	0	0	0	17	100.0
Adhesion	34[1,2]	3	8.8	7	20.6	23	67.6
Ants	33[2]	1	3.0	3	9.1	29	87.9
Wind	64[2]	1	1.6	11	17.2	52	81.3
Prolonged Dormancy	50[2]	6	12.0	10.0	20.0	34	68.0
Mechanical Expulsion:	18[2]	4	22.2	2	11.1	12	66.7
explosive dehiscence	11[2]	3	27.3	1	9.1	7	63.6
wind-push	5[2]	1	20.0	1	20.0	3	60.0
splash-cup	2[2]	0	0	0	0	2	100.0
Unassisted	78[1]	2	2.5	3	3.8	72	91.1
Multiple Modes	39	5	12.8	110	28.2	23	59.0

Table 3.3. Provenance of surveyed taxa by dispersal mode and life form. Elements do not sum to group totals when taxa dispersed by more than one mode.

Dispersal Mode		Provenance					
Mode by Life Form	Taxa	Native		Alien		Unknown	
	#	#	%	#	%	#	%
ALL TAXA	413	349	84.5	60	14.5	4	1.0
Animal s.l.	159	142	89.3	16	10.1	1	0.6
Ingestion	70	65	92.9	5	7.1	0	0
Adhesion	53	43	81.1	9	17.0	1	1.9
Seed Caching	7	7	100.0	0	0	0	0
Ant	33	30	90.9	3	9.1	0	0
Wind	126	107	84.9	19	15.1	0	0
Prolonged Dormancy	64	26	40.6	38	59.4	0	0
Mechanical Expulsion	18	13	17.2	5	27.7	0	0
Unassisted	91	83	91.2	8	8.8	3	0
Multiple Modes	51	28	54.9	23	45.1	0	0
Vegetative Expansion	148	132	89.2	16	10.8	0	0
TREES	30	29	96.7	1	0.1	0	0
Ingestion	1	1	100.0	0	0	0	0
Seed Caching	6	6	100.0	0	0	0	0
Wind	22	22	100.0	0	0	0	0
Prolonged Dormancy	1	0	0	1	100.0	0	0
SHRUBS	55	51	92.7	4	7.3	0	0
Ingestion	44	40	90.9	4	9.1	0	0
Seed Caching	1	1	100.0	0	0	0	0
Wind	6	6	100.0	0	0	0	0
Prolonged Dormancy	3	2	66.7	1	33.3	0	0
Multiple Modes	3	2	66.7	1	33.3	0	0

Table 3.3. Provenance of surveyed taxa by dispersal mode and life history (cont'd).

Dispersal Mode		Life History					
Mode by Life Form	Taxa #	Native #	Native %	Alien #	Alien %	Unknown #	Unknown %
VINES	9	8	88.9	1	11.1	0	0
Ingestion	8	7	87.5	1	12.5	0	0
Wind	1	1	100.0	0	0	0	0
Prolonged Dormancy	1	0	0	1	100.0	0	0
Multiple Modes	1	0	0	1	100.0	0	0
FERN / FERN ALLIES	31	31	100.0	0	0	0	0
Wind	31	31	100.0	0	0	0	0
GRASSES	36	27	75.0	7	19.4	2	5.6
Adhesion	19	17	89.5	2	10.5	0	0
Wind	2	2	100.0	0	0	0	0
Prolonged Dormancy	9	5	55.6	4	44.4	0	0
Unassisted	10	7	70.0	3	30.0	0	0
Multiple Mode	7	5	71.4	2	28.6	0	0
HERBS	252	203	80.6	47	18.7	2	0.8
Ingestion	17	17	100.0	0	0	0	0
Adhesion	34	26	76.5	7	20.6	1	2.9
Ants	33	30	9.9	3	9.1	0	0
Wind	64	45	70.3	19	29.7	0	0
Prolonged Dormancy	50	19	38.0	31	62.0	0	0
Mechanical Expulsion:	18	13	72.2	5	27.7	0	0
explosive dehiscence	11	9	81.8	2	18.2	0	0
wind-push	5	2	40.0	3	60.0	0	0
splash-cup	2	2	100.0	0	0	0	0
Unassisted	78	70	89.7	5	6.4	3	3.8
Multiple Modes	39	20	51.3	19	48.7	0	0

the grasses (19.4%) and herbs (18.7%), followed by the vines (11.1%), shrubs (7.3%) and trees (0.1%).

The number of herbs dispersed by animal ingestion, wind, prolonged dormancy, multiple modes and unassisted means varied with provenance ($p<0.05$, chi-square tests of homogeneity by row, df 1, not shown; tests for prolonged dormancy and multiple modes significant after Bonferroni correction for 9 tests). Dispersal modes with a higher than expected number of alien taxa were wind ($p<0.05$), prolonged dormancy in the soil ($p<0.001$), and multiple agents ($p<0.001$) (chi-square tests of homogeneity by cell). Analyses of pattern involving these modes of dispersal were therefore assessed for possible interactions with species provenance.

3.3.1.4 Modality

Approximately 12% of taxa were dispersed by more than one mode (Table 3.4). Among life forms, only the ferns and fern allies were unimodal. The percentage of multimodal taxa among other life forms was highest among the grasses (19.4%) and herbs (15.5%), followed by the vines (11.1%), shrubs (5.5%) and trees (3.3%).

The number of herbs dispersed by animal adhesion, wind, prolonged dormancy, and mechanical expulsion varied with modality ($p<0.001$, chi-square test of homogeneity by row, df 1, not shown; all tests significant after Bonferroni correction for 7 tests). In each case, the number of herbs dispersed by multiple modes was significantly higher than expected (chi-square tests of homogeneity by cell; all tests significant after Bonferroni correction for 14 tests). Analyses of pattern involving these modes of dispersal were therefore assessed for possible interactions with species modality.

3.3.1.5 Fruit Type

Among the herbs, the most abundant fruit types were the achene (49.8 %) and capsule (21.1 %) (Table 3.5). Minor fruit types in descending order of abundance were the schizocarp, berry, nutlet,

Table 3.4. Modality of surveyed taxa by dispersal mode and life form. Unimodal = taxon dispersed by one mode; multimodal = taxon dispersed by more than one mode.

Dispersal Mode		Modality			
Mode by Life Form	Taxa #	Unimodal #	%	Multimodal #	%
ALL TAXA	413	362	87.6	51	12.4
Animal s.l.	160	133	83.1	27	16.8
Ingestion	70	66	94.3	4	5.7
Adhesion	53	35	66.0	18	34.0
Seed Caching	7	7	100.0	0	0
Ant	33	25	75.7	8	24.2
Wind	126	106	84.1	20	15.9
Prolonged Dormancy	64	25	39.1	39	60.1
Mechanical Expulsion	18	8	44.4	10	55.6
Unassisted	91	91	100.0	0	0
Multiple Modes	51	0	0	51	100.0
Vegetative Expansion	148	132	89.2	16	10.8
TREES	30	29	96.7	1	3.3
Ingestion	1	1	100.0	0	0
Seed Caching	6	6	100.0	0	0
Wind	22	22	100.0	0	0
Prolonged Dormancy	1	1	100.0	0	0
SHRUBS	55	52	94.5	3	5.5
Ingestion	44	42	95.5	2	4.5
Seed Caching	1	1	100.0	0	0
Wind	6	5	83.3	1	16.7
Prolonged Dormancy	3	0	0	3	100.0
Multiple Modes	3	0	0	3	100.0

Table 3.4. Modality of surveyed taxa by dispersal mode and life history (cont'd).

Dispersal Mode		Modality			
Mode by Life Form	Taxa #	Unimodal #	%	Multimodal #	%
VINES	9	8	88.9	1	11.1
Ingestion	8	7	87.5	1	12.5
Wind	1	1	100.0	0	0
Prolonged Dormancy	1	0	0	1	100.0
Multiple Modes	1	0	0	1	100.0
FERN / FERN ALLIES	31	31	100.0	0	0
Wind	31	31	100.0	0	0
GRASSES	36	30	81.6	6	19.4
Adhesion	18	13	72.2	6	33.3
Wind	2	1	50.0	1	50.0
Prolonged Dormancy	9	4	44.4	5	55.6
Unassisted	12	12	100.0	0	0
Multiple Mode	6	0	0	6	0
HERBS	252	213	84.5	39	15.5
Ingestion	17	16	94.1	1	5.9
Adhesion	34	22	64.7	12	35.3
Ants	33	25	75.7	8	24.2
Wind	64	46	71.9	18	28.1
Prolonged Dormancy	50	21	42.0	29	58.0
Mechanical Expulsion:	18	8	44.4	10	55.6
explosive dehiscence	11	4	36.4	7	3.6
wind-push	5	2	40.0	3	60.0
splash-cup	2	2	100.0	0	0
Unassisted	78	78	100.0	0	0
Multiple Modes	39	0	0	39	100.0

Table 3.5. Fruit type of surveyed herbs (N=251) by dispersal mode. Legend: AI = animal ingestion, AA = animal adhesion, AC = animal conveyance, W = wind, PD = prolonged dormancy in the soil, ME = mechanical expulsion, U = unassisted, MM = multimodal, VE = vegetative expansion. Entries are the total # taxa recorded in 192, 10m x 10m quadrats. Drupe *s.l.* = drupe, berry-like-drupe, resembles-drupe. Superscript[1] denotes that column values include taxa that are multimodal.

			Dispersal Mode									
			Animal									
Fruit Type	# Taxa	% n=251	AI[1]	AA[1]	AC[1]	Total	W[1]	PD[1]	ME[1]	U	MM	VE
achene	125	49.8	3	17	8	26	53	23	0	46	21	43
berry	13	5.2	10	0	3	13	0	0	0	0	0	7
capsule	53	21.1	0	2	15	17	4	10	12	17	7	28
capsular	11	4.4	0	0	3	3	4	4	1	0	1	6
drupe *s.l.*	4	1.6	4	0	0	4	0	0	0	0	0	1
follicle	5	2.0	0	0	0	0	3	3	1	0	2	2
legume	7	2.8	0	1	2	3	0	4	2	1	3	0
nutlet	12	4.8	0	1	0	1	0	3	0	8	0	4
schizocarp	19	7.6	0	13	2	13	0	3	2	4	5	2
silique	2	0.8	0	0	0	0	0	0	0	2	0	1
Total	251	100	17	34	33	80	64	50	18	78	39	94

capsular fruit, legume, follicle, drupe *s.l.*, and silique. The number of modes by which a given fruit type was dispersed varied from one to six (excluding multiple modes and vegetative expansion). No fruit type was dispersed by all modes. Fruit types dispersed by a variety of modes were the achene (6), capsule (6), schizocarp (5) and capsular fruit (4). Two fruit types were dispersed by one mode: drupe *s.l.* and silique.

Each dispersal mode deployed the seeds of more than one fruit type but no mode deployed the seeds of all ten fruit types. The modes deploying the seeds of the greatest range of fruit types were animals *s.l.*, (8), and prolonged dormancy in the soil (7). The modes deploying the seeds of the least number of fruit types were animal ingestion (3) and wind (4).

The predominant mode by which a given fruit type was dispersed varied. Achenes were dispersed primarily by the wind; berries by animal ingestion; capsules by unassisted means and ants; capsules by wind and prolonged dormancy; drupes *s.l.* by animal ingestion; follicles and legumes by prolonged dormancy in the soil; nutlets and siliques by unassisted means; and, schizocarps by animal adhesion.

The data table summarizing the relationship between fruit type and dispersal mode was too sparse to test the overall relationship with standard statistical tests. However, selective row tests (not shown) revealed that the number of herbs with achene and capsule fruits differed by dispersal mode ($p<0.001$, chi-square tests of homogeneity by row, df 8). In particular, the number of herbs dispersed by wind ($p<0.001$) was significantly greater than expected for achene fruits; the number of herbs dispersed by mechanical expulsion ($p<0.001$) and by ants ($p<0.01$) were significantly greater than expected for herbs with capsule fruits (chi-square tests of homogeneity by cell).

Collectively, these results suggest that fruit type may have influenced the frequency of dispersal modes in these forests. Further analysis is required, however, since this data table could not be tested comprehensively.

3.3.1.6 Taxonomic Rank

The distribution dispersal modes by taxonomic rank is presented in Tables 3.6 (genus), 3.7 (family), and 3.8 (order). The most important trend for this thesis is that the number of taxa dispersed by more than one mode increases with taxonomic rank: species (12.3 %), genus (25.8 %), family (33.3 %), and order (57.4 %). This pattern has consequences for the number of degrees of freedom associated with linear regression analyses reported in Chapter 4. The contribution of phylogeny to species richness in vegetation samples will be discussed there.

3.3.2 Pattern in Relation to Environmental Variables

The analysis for pattern in relation to environmental variables was restricted to the herbs since it was the one life form that was dispersed by all modes. The results are summarized in relation to habitat affinity, moisture affinity, shade tolerance, environmental gradients, and microhabitats.

3.3.2.1 Habitat Affinity

The number of herbs dispersed by animal ingestion, ants, wind, prolonged dormancy, wind-push mechanisms, unassisted means, and multiple modes varied with the habitat affinity of the taxon (Table 3.9). Herbs dispersed by animal ingestion, ants, and splash-cup mechanisms were over-represented in taxa with an affinity for forest habitats, whereas, herbs dispersed by wind, prolonged dormancy, wind-push, and multiple modes were over-represented in taxa with an affinity for open habitats. The number of herbs dispersed by animal adhesion, explosive mechanisms, and vegetative expansion did not vary with habitat affinity. The strongest evidence was found for herbs dispersed by prolonged dormancy and by multiple modes (chi-square tests of homogeneity by cell, $p<0.001$, Bonferroni correction for 52 cell tests).

The significance of zero values in the data is difficult to assess since absence may be due to sampling error associated with small samples or to habitat related factors constraining dispersal, germination, establishment and/or persistence. The absence of herbs dispersed by animal ingestion and splash-cup mechanisms in taxa with affinity for open habitats, and by wind-push mechanisms

Table 3.6. Distribution of dispersal modes by taxonomic rank I (genus). Legend: AI=animal ingestion; AA=animal adhesion; AC=animal conveyance (ants, seed caching); W=wind; PD=prolonged dormancy; ME=mechanical expulsion; U=unassisted; MM=dispersed by >2 modes. Cell entries are the number of genera dispersed by the given mode(s). Only the lower half of matrix is shown. "-" denotes combination not observed in vegetation samples. All life forms included in analysis. N = 208 genera.

GENUS	AI n=35	AA n=31	AC n=20	W n=65	PD n=59	ME n=14	U n=44	MM n=6
AI	32							
AA	-	16						
AC	1	-	11					
W	-	2	1	45				
PD	2	9	2	13	15			
ME	-	-	1	-	7	5		
U	-	-	-	1	6	1	33	
MM	-	4	4	3	5	-	3	6[1]

Notes:

1. Genera dispersed by more than two modes:
   Carduus: AC, AA, W, PD
   Carex: AC, W, U
   Cirsium: AA, W, PD
   Galium: AA, AC, PD
   Melilotus: AC, PD, U
   Poa: AA, PD, U.

Table 3.7. Distribution of dispersal modes by taxonomic rank II (family). Legend: AI=animal ingestion; AA=animal adhesion; AC=animal conveyance (ants, seed caching); W=wind; PD=prolonged dormancy; ME=mechanical expulsion; U=unassisted; MM=dispersed by >2 modes. Cell entries are the number of families dispersed by the given mode(s). Only the lower half of the matrix is shown. "-" denotes combination not observed in vegetation samples. All life forms included in analysis. N = 78 families.

FAMILY	AI n=19	AA n=11	AC n=14	W n=27	PD n=27	ME n=11	U n=25	MM n=15
AI	12							
AA	-	1						
AC	-	-	7					
W	-	-	-	18				
PD	1	-	-	2	4			
ME	-	-	1	-	3	2		
U	1	-	-	-	3	1	8	
MM	5	10	6	7	14	4	13	15[1]

Notes:

1. Families dispersed by more than two modes:
   Apiaceae: AA, PD, U
   Asteraceae: AA, W, PD, U
   Betulaceae: AC, W, PD
   Caprifoliaceae: AI, PD, U
   Caryophyllaceae: PD, ME, U
   Cucurbitaceae: PD, ME, U
   Cyperaceae: AA, AC, W, U
   Fabaceae: AA, AC, PD, ME, U
   Liliaceae: AI, AC, U
   Onagraceae: AA, W, PD
   Poaceae: AA, W, PD, U
   Ranunculaceae: AI, AC, W, PD, ME, U
   Rosaceae: AI, AA, PD, U
   Rubiaceae: AI, AA, AC, PD
   Urticaceae: AA, W, PD, U
   Verbenaceae: AA, PD, U.

Table 3.8. Distribution of dispersal modes by taxonomic rank III (order). Legend: AI=animal ingestion; AA=animal adhesion; AC=animal conveyance (ants, seed caching); W=wind; PD=prolonged dormancy; ME=mechanical expulsion; U=unassisted; MM=dispersed by >2 modes. Cell entries are the number of orders dispersed by the given mode(s). Only the lower half of the matrix shown. "-" denotes combination not observed in vegetation samples. All life forms included in analysis. Nomenclature follows Mabberly 1997. N = 47 orders.

ORDER	AI n=15	AA n=9	AC n=12	W n=19	PD n=25	ME n=9	U n=20	MM n=19
AI	5							
AA	-	-						
AC	-	-	4					
W	1	-	-	7				
PD	-	-	-	2	2			
ME	-	-	-	-	1	-		
U	2	-	-	-	2	-	-	
MM	7	9	8	9	18	9	16	19[1]

Notes:

1. Orders dispersed by more than two modes:
   Apiales: AI, AA, PD, U
   Asterales: AA, W, PD, ME, U
   Caryophyllales: AC, PD, ME, U
   Cyperales: AA, AC, W, PD, U
   Dipsacales: AI, PD, U
   Fabales: AA, AC, W, PD, ME, U
   Fagales: AC, W, PD
   Gentianales: W, PD, U
   Lamiales: AA, PD, U
   Liliales: AA, PD, U
   Malvales: W, PD, ME
   Myrtales: AA, W, PD
   Ranunculales: AI, AC, W, PD, ME, U
   Rosales: AI, AA, PD, ME, U
   Rubiales: AI, AA, AC, PD, U
   Scrophulariales: W, PD, ME, U
   Solanales: AI, PD, U
   Urticales: AA, W, PD, U
   Violales: AC, PD, ME, U

Table 3.9. Dispersal modes of surveyed herbs by habitat affinity. "Forest": taxa occur only in forested or shaded habitats; "Forest-Open": taxa occur primarily in forested habitats but move into open habitats (including thickets); "Open-Forest": taxa occur primarily in open habitats but move into forested habitats; "Open": taxa occur only in open habitats. N = 234 herbs. Expected number of taxa = (# taxa dispersed by mode ÷ 234) x (# taxa in habitat category). Habitat assignments based on descriptions in: Voss 1972, 1985, 1996; Cody and Britton 1989; Dore and McNeill1980, Gleason and Cronquist 1991. Dispersal mode and observed value marked by an asterisk when differences among habitat classes significant at $p<0.05$, chi-square tests of homogeneity by row, *df* 3, and cell, *df* 1; dispersal mode and observed value in bold when differences significant after Bonferroni correction for the total number of tests (13 tests by row; 52 tests by cell).

Dispersal Mode	# Taxa (n=234)	Habitat Class							
		Forest (n=55)		Forest-Open (n=54)		Open-Forest (n=82)		Open (n=43)	
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Animal	76	29*	17.9	27*	17.5	11*	26.6	9	14.0
ingestion*	17	9*	4.0	5	3.9	3	6.0	0	3.1
adhesion	31	8	7.3	10	7.2	5	10.9	8	5.7
ant	31	13*	7.3	13*	7.2	3*	10.9	2	5.7
Wind	62	6*	14.6	6*	14.3	28	21.7	22*	11.4
Prolonged Dormancy	50	**0**	11.8	4*	11.5	21	17.5	**25**	9.2
Mechanical Expulsion	17	3	4.0	3	3.9	6	6.0	5	7.9
explosive	10	1	2.4	3	2.3	5	3.5	1	1.8
splash-cup	2	2*	0.5	0	0.5	0	0.7	0	0.4
wind-push	5	0	1.2	0	1.2	1	1.8	4*	0.9
Unassisted	69	19	16.2	18	15.9	27	24.2	5*	12.7
Multimodal	39	3*	9.2	5	9.0	11	13.7	**20**	7.2
Vegetative Expansion	92	22	21.6	23	21.2	37	32.2	10	16.9

in taxa with affinity for closed habitats, cannot be assessed owing to the small number of taxa involved. The absence of herbs dispersed by dormancy among taxa with forest affinity may be due to habitat related factors since their absence is consistent with factors hypothesized to favor the evolution of seed dormancy (Venable and Brown 1988, 1993).

The dispersal mode of herbs seldom varied with the known moisture affinity of the taxon (Table 3.10). Herbs dispersed by animal vectors *s.l.* were under-represented in taxa with an affinity for wetland habitats whereas herbs dispersed by unassisted means were over-represented in taxa with an affinity for wetland habitats (chi-square tests of homogeneity by cell, $p<0.05$, uncorrected for the number of tests). The number of herbs dispersed by other modes did not vary with the moisture affinity of the taxon.

The dispersal mode of herbs did vary, however, with the known shade tolerance of the taxon (Table 3.11). Herbs dispersed by animal ingestion were over-represented in taxa with high shade tolerance, whereas, herbs dispersed by wind, prolonged dormancy, and multiple modes were strongly over-represented in taxa with low shade tolerance, and, strongly under-represented in taxa with high shade tolerance. The number of herbs dispersed by adhesion, ants, mechanical expulsion, and vegetative expansion did not vary with the shade tolerance of the taxon.

3.3.2.2 Environmental Gradients

Pattern in relation to environmental gradients was investigated by univariate and multivariate methods. The former revealed the degree to which dispersal modes were associated with particular gradients and portions of gradients, whereas, the latter revealed affinities among quadrats dominated by a particular mode of dispersal and among species with similar environmental affinities.

Univariate Analysis

In general, the proportion of herbs in a 10m x 10m quadrat dispersed by a given mode varied in relation to the principal environmental gradients examined in this study (Wilcoxon rank sum tests,

Table 3.10. Dispersal modes of herbs by moisture affinity. N = 233 herbs. Moisture affinity classification based on Oldham *et al.* 1995. Expected number of taxa = (# taxa dispersed by mode ÷ 233) x (# taxa in moisture affinity class). Dispersal mode marked by an asterisk when differences among habitat classes significant at $p<0.05$, chi-square tests of homogeneity by row, *df* 2; observed value marked by an asterisk when departure from expectation significant at $p<0.05$, chi-square tests of homogeneity by cell, *df* 1; no test significant after Bonferroni correction for the total number of tests (13 tests by row; 39 tests by cell).

Dispersal Mode	# Taxa (n=233)	Moisture Affinity					
		Upland (n=116)		Intermediate (n=42)		Wetland (n=75)	
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Animal*	75	48	37.3	13	13.5	14*	24.1
ingestion	17	12	8.5	4	3.1	1	5.5
adhesion	31	19	15.4	3	5.6	9	10.0
ant	31	20	15.4	6	5.6	5	10.0
Wind	60	33	29.9	7	10.8	20	19.3
Prolonged Dormancy	49	27	24.4	12	8.8	10	15.8
Mechanical Expulsion	18	11	9.0	3	3.2	4	5.8
explosive	11	6	5.5	1	2.0	4	3.5
splash-cup	2	1	1.0	1	0.4	0	0.6
wind-push	5	4	2.5	1	0.9	0	1.6
Unassisted*	69	23	34.4	13	12.4	33*	22.2
Multimodal	38	25	18.9	6	6.8	7	12.2
Vegetative Expansion	91	45	45.3	16	16.4	30	29.3

Table 3.11. Dispersal modes of herbs by shade tolerance. N = 143 herbs. Shade tolerance classification based on Nimerfro and Brand (1993) and Ellenberg (1988). Expected number of taxa = (# taxa dispersed by mode ÷ 143) x (# taxa in shade tolerance class). "High" = shade tolerance class 1,2; "Intermediate = shade tolerance class 3; "Low" = shade tolerance class 4,5. Dispersal mode and observed value marked by an asterisk when differences among tolerance classes significant at $p<0.05$, chi-square tests of homogeneity by row, df 2, and cell, df 1 : dispersal mode in bold when differences among classes significant after Bonferroni correction for the total number of tests (13 tests by row).

Dispersal Mode	# Taxa (n=143)	Shade Tolerance					
		High (n=43)		Intermediate (n=19)		Low (n=81)	
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Animal	54	28*	16.2	8	7.2	18*	30.6
ingestion*	15	9*	4.5	2	2.0	4	8.5
adhesion	22	10	6.6	3	2.9	9	12.5
ant	17	9	5.1	3	2.3	5	9.6
Wind	42	2*	12.6	5	5.6	35*	23.8
Prolonged Dormancy	43	3*	12.9	1	5.7	39*	24.4
Mechanical Expulsion	12	4	3.6	3	1.6	5	6.8
explosive	6	2	1.8	3	0.8	1	3.4
splash-cup	2	2	0.6	0	0.3	0	1.1
wind-push	4	0	1.2	0	0.5	4	2.3
Unassisted	25	8	7.5	3	3.3	14	14.2
Multimodal	29	2*	8.7	1	3.9	26*	16.4
Vegetative Expansion	65	21	19.5	8	8.6	36	36.8

independent samples) (Table 3.12). Most modes varied along each gradient ($p<0.01$, Bonferroni correction for 5 row tests; $p<0.001$, Bonferroni correction for 50 tests). The major exception was dispersal by vegetative expansion which did not vary in relation to any gradient.

All modes were present on each portion of the gradients examined. Patterns associated with particular gradients are summarized below.

Canopy Closure: Under low canopy closure (high light), the largest proportion of herbs for a given mode was dispersed by animal adhesion, wind, prolonged dormancy, unassisted means, and multiple modes. These results reflect an underlying interaction between dispersal mode and habitat affinity since herbs dispersed by these modes are over-represented by taxa with open habitat affinities. Animal ingestion was the dominant mode of dispersal under high canopy closure (low light) whereas dispersal by ants was the dominant mode under medium canopy closure. Dispersal by mechanical expulsion did not vary with canopy closure.

Moisture: In quadrats with seasonally dry depressions, the largest proportion of herbs for a given mode was dispersed by animal ingestion and ants. In quadrats with seasonally moist depressions, the dominant mode was dispersal by prolonged dormancy. In quadrats with seasonally wet depressions, the predominant modes were animal adhesion, wind, mechanical expulsion, unassisted and multiple modes. Moisture conditions in quadrats with seasonally moist and wet depressions were typically dry, however, since the latter habitats occupied less than 50% of the quadrat, on average. The percentages for dispersal modes, therefore, tend to be higher in quadrats with moist and wet depressions since they include taxa with an affinity for mesic soils.

Percent Soil Organic Matter (% SOM): In quadrats with low and medium soil organic matter, the largest proportion of herbs for a given mode was dispersed by animal ingestion and by ants, respectively. In quadrats with high soil organic matter, the predominant modes were dispersal by animal adhesion, wind, prolonged dormancy, mechanical expulsion, unassisted means and multiple modes. Higher percentages of soil organic matter in these forests tend to be associated with tree pits

Table 3.12. Distribution of herbs in 10m x 10m quadrats by environmental attribute and dispersal mode (mean %). Cell values: mean % of taxa in 10m x 10m quadrats dispersed by mode. Wilcoxon Rank Sum Tests by attribute and mode. Highest value in bold when differences among modes significant at $p<0.01$ (Bonferroni correction for 5 column tests); highest value underlined when differences among modes significant after Bonferroni correction for 50 tests. Notes: **1**. Canopy closure: low = <80% closure, medium = 80-94% closure, high = >94% closure (fish-eye photography); **2**. Moisture class: dry = forest depressions dry spring and summer; moist = forest depressions moist spring and/or summer; wet = forest depressions with standing water spring and/or summer; **3**. % SOM: percent soil organic matter in upper 15 cm of soil profile: low = <6% SOM; medium = 6-14% SOM; high = >14% SOM; **4**. Cover type: 1 = red or white oak, no sugar maple; 2 = sugar maple + red, white oak; 3 = sugar maple, no red, white oak, no wet mesic or wet tree species; 4 = sugar maple + black ash, silver maple or American elm; 5 = black ash, silver maple, American elm, no sugar maple, no red, white oak. **5**. Disturbance: trail, regenerating field or canopy gap present in 10m x 10m quadrat. N = 252 herbs. Values do not sum to 100% when the tolerance of species is broader than category thresholds.

Dispersal Mode	Environmental Attribute															
	Canopy Closure[1]			Moisture Class[2]			% SOM[3]			Cover Type[4]					Disturbance[5]	
	Low	Med	High	Dry	Moist	Wet	Low	Med	High	1	2	3	4	5	Yes	No
ANIMAL	22.4	**28.7**	27.5	**29.2**	22.7	23.6	24.3	**29.3**	23.9	10.5	25.5	**32.2**	23.8	13.9	24.5	27.9
ingestion	6.9	10.9	**11.4**	**12.0**	7.8	5.7	**11.7**	10.6	7.1	3.5	**13.0**	10.7	7.7	2.8	7.9	**10.9**
adhesion	**7.2**	5.7	4.3	4.5	7.1	**8.4**	3.3	5.5	**8.6**	3.5	2.9	6.6	6.9	**8.7**	**7.1**	5.1
ant	8.4	**12.4**	12.0	**13.0**	7.8	9.5	9.4	**13.5**	8.2	5.3	9.7	**15.3**	9.3	2.4	9.6	12.0
WIND	**14.6**	8.8	8.4	8.3	12.2	**14.3**	7.9	10.1	**12.4**	21.1	7.1	8.7	12.2	**22.9**	**13.7**	8.6
PROLONGED DORMANCY	**9.0**	4.3	3.3	3.5	**8.0**	7.8	3.5	4.8	**7.9**	12.3	1.7	4.9	7.2	**13.8**	**8.1**	4.0
MECHANICAL EXPULSION	3.8	3.0	2.9	1.8	5.0	**6.0**	2.0	2.2	**6.4**	**7.0**	1.4	3.1	5.1	4.0	3.7	3.0

Table 3.12. Distribution of herbs in 10m x 10m quadrats by environmental attribute and dispersal mode (mean %) (cont'd).

Dispersal Mode	Environmental Attribute															
	Canopy Closure[1]			Moisture Class[2]			% SOM[3]			Cover Type[4]					Disturbance[5]	
	Low	Med	High	Dry	Moist	Wet	Low	Med	High	1	2	3	4	5	Yes	No
UNASSISTED	**12.4**	10.7	8.7	8.5	12.5	**15.9**	7.9	10.6	**13.3**	3.5	6.5	10.8	13.1	**18.1**	11.9	10.0
MULTIMODAL	**7.6**	4.7	3.4	3.5	6.9	**8.3**	2.8	4.6	**8.3**	**12.3**	1.6	5.2	7.0	11.4	**7.3**	4.1
VEGETATIVE EXPANSION	25.9	27.1	26.9	27.5	25.4	26.0	27.5	27.1	25.4	21.1	27.5	27.6	26.0	21.8	26.3	27.0

and with moist to wet topographic depressions, which typically occupied less than 50% of a given quadrat, when present. The percentages for dispersal modes therefore tend to be higher in quadrats with medium and high soil organic matter since they typically include taxa with affinity for low to medium percent soil organic matter.

Cover Type: The predominant modes under cover type "1" (red or white oak, no sugar maple) were dispersal by mechanical expulsion and by multiple modes. The dominant mode under cover type "2" (sugar maple + red or white oak) was dispersal by animal ingestion, whereas the dominant mode under cover type "3" (sugar maple, no red or white oak, no wet mesic or wet tree species) was dispersal by ants. No modes were dominant under cover type "4" (sugar maple + black ash, silver maple, or American elm). The predominant modes under cover type "5" (black ash, silver maple, American elm, no sugar maple, no red or white oak) were dispersal by animal adhesion, wind, prolonged dormancy, and unassisted means.

Disturbance: In quadrats with a trail, regenerating field, or canopy gap, the predominant modes of dispersal were animal adhesion, wind, prolonged dormancy, and multiple modes. This pattern reflects differences in the proportion of herbs with affinity for "open+forest" and "open" habitats ($p<0.001$, Wilcoxon rank sum test, independent samples, data not shown), rather than invasion by alien taxa. The proportion of alien taxa did not vary with disturbance class ($p>0.05$, Wilcoxon rank sum test, independent samples, data not shown). The dominant mode in quadrats without disturbance features was animal ingestion. The proportion of herbs dispersed by ants, mechanical expulsion and unassisted means did not vary with disturbance class.

Multivariate Analysis

Further evidence of the tendency for dispersal modes to be associated with particular environmental states is provided by the distribution of dispersal modes in the ordination space of detrended correspondence analysis (DCA). DCA is an ordination technique which arranges vegetation samples along gradients (axes) that maximize their dispersion on the basis of differences in species

composition and abundance. Quadrats that are close together in stand ordination space (Figures 3.1-3.5) are more similar in species composition than quadrats that are far apart. Quadrats separated by more than 4 standard deviations in these figures have few if any species in common.

The distribution of dispersal modes in ordination space reveals that quadrats in which animal ingestion, ants, and vegetative expansion are the predominate mode of dispersal are largely confined to the right side of the stand ordination (Figures 3.1, 3.2, 3.5) whereas quadrats in which the predominate modes of dispersal are animal adhesion, wind, prolonged dormancy, mechanical expulsion, unassisted, and multiple modes are concentrated on the left side of the ordination (Figures 3.1-3.5).

Quadrats in which the predominate modes are animal adhesion, wind or prolonged dormancy often overlap (50% of occurrences) (not shown). Quadrats in which animal ingestion, ants and vegetative expansion are the predominate modes also tend to overlap (62% of occurrences) (not shown). In contrast, dispersal by wind, prolonged dormancy and mechanical expulsion are rarely major constituents in quadrats where animal ingestion is the predominate mode of dispersal (Figures 3.2, 3.3). This is true even in the central portion of ordination where all modes are present. This suggests that the environments in which animal ingestion predominates are well defined and different from other modes.

Inspection of the survey data reveals that quadrats in which animal ingestion predominates are characterized by moderate to high canopy closure, mesic soils, moderate to low percent soil organic matter, low disturbance, and forest cover types 2 and 3. In contrast, quadrats in which wind, prolonged dormancy, and mechanical expulsion predominate are characterized by moderate to low canopy closure, moist to wet soils, moderate to high percent organic matter, high disturbance, and forest cover types 4 and 5. Unlike the latter modes, dispersal by animal ingestion is often the predominate mode of dispersal on glacial fluvial parent materials and never achieves predominance on calcareous outwash or lacustrine parent materials.

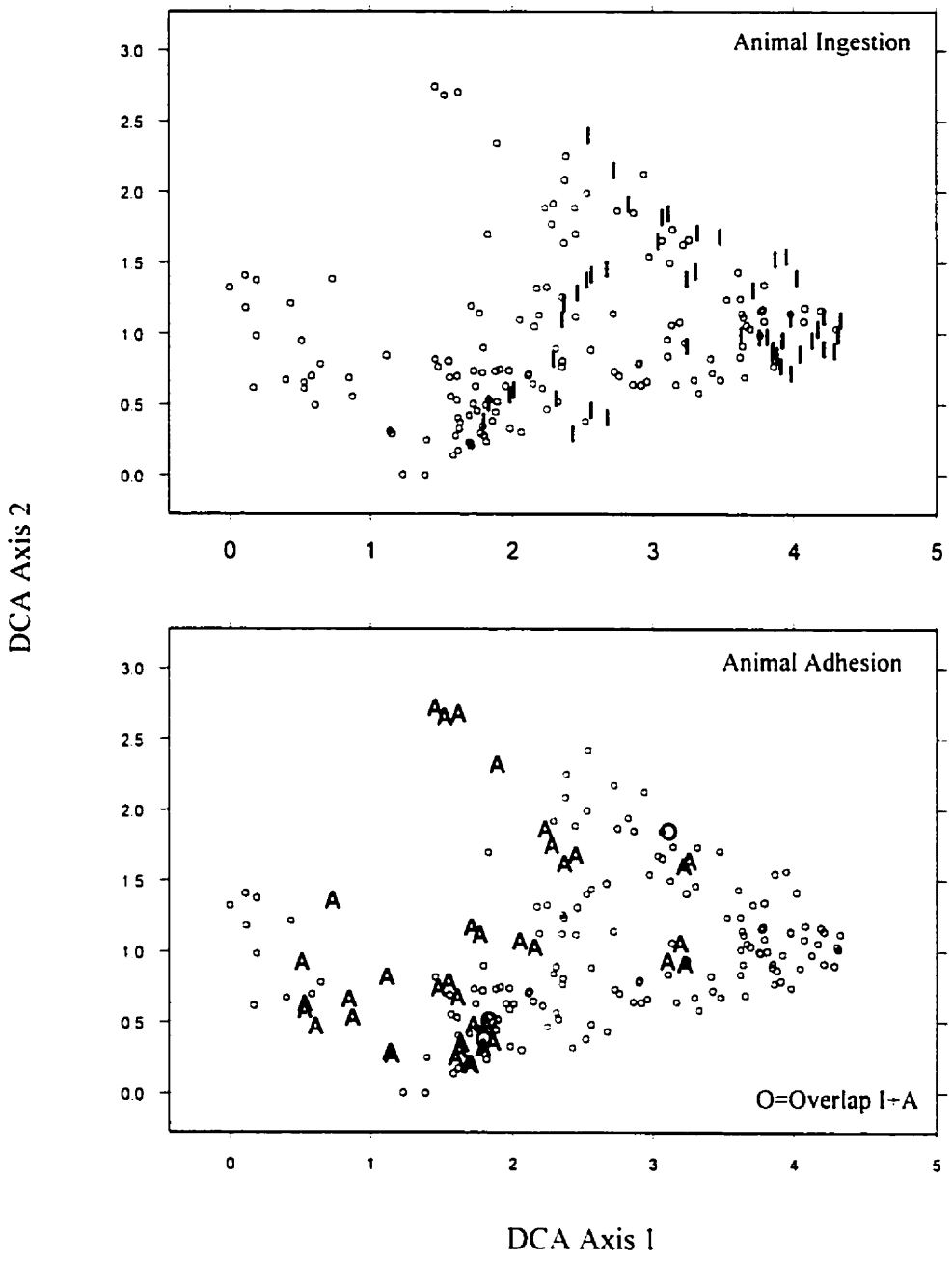

Figure 3.1. Distribution of herbs dispersed by animal ingestion (I) and by animal adhesion (A) in relation to DCA axes 1 and 2. Only quadrats in which the proportion of herbs dispersed by designated mode is $\geq$ 75% quartile are labeled. Note minor overlap (O) in quadrats where animal ingestion and animal adhesion predominate.

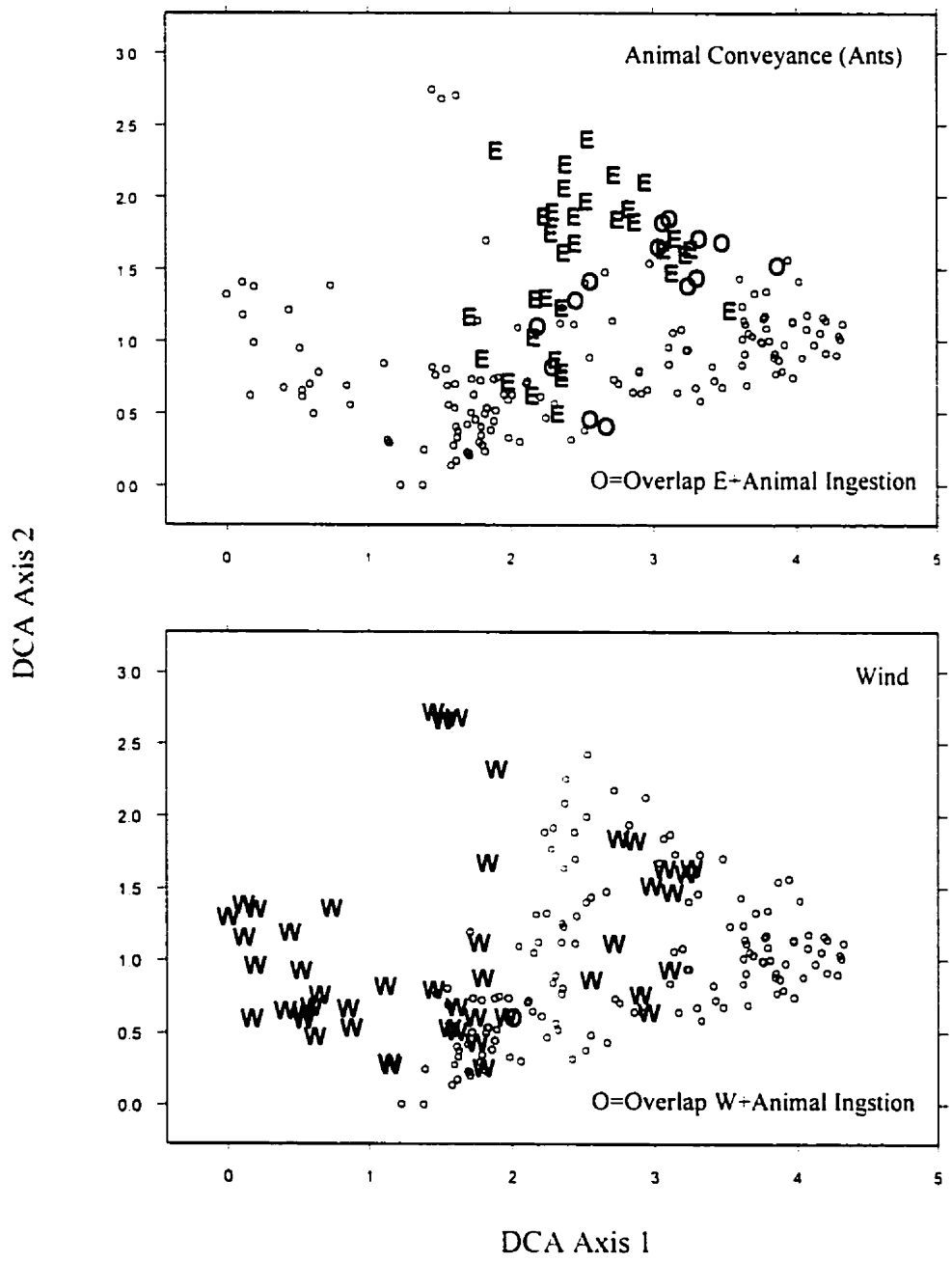

Figure 3.2. Distribution of herbs dispersed by ants (E) and by wind (W) in relation to DCA axes 1 and 2. Only quadrats in which the proportion of herbs dispersed by designated mode is ≥75% quartile are labeled. Note differences in the degree of overlap (O) in quadrats where designated modes and animal ingestion predominate.

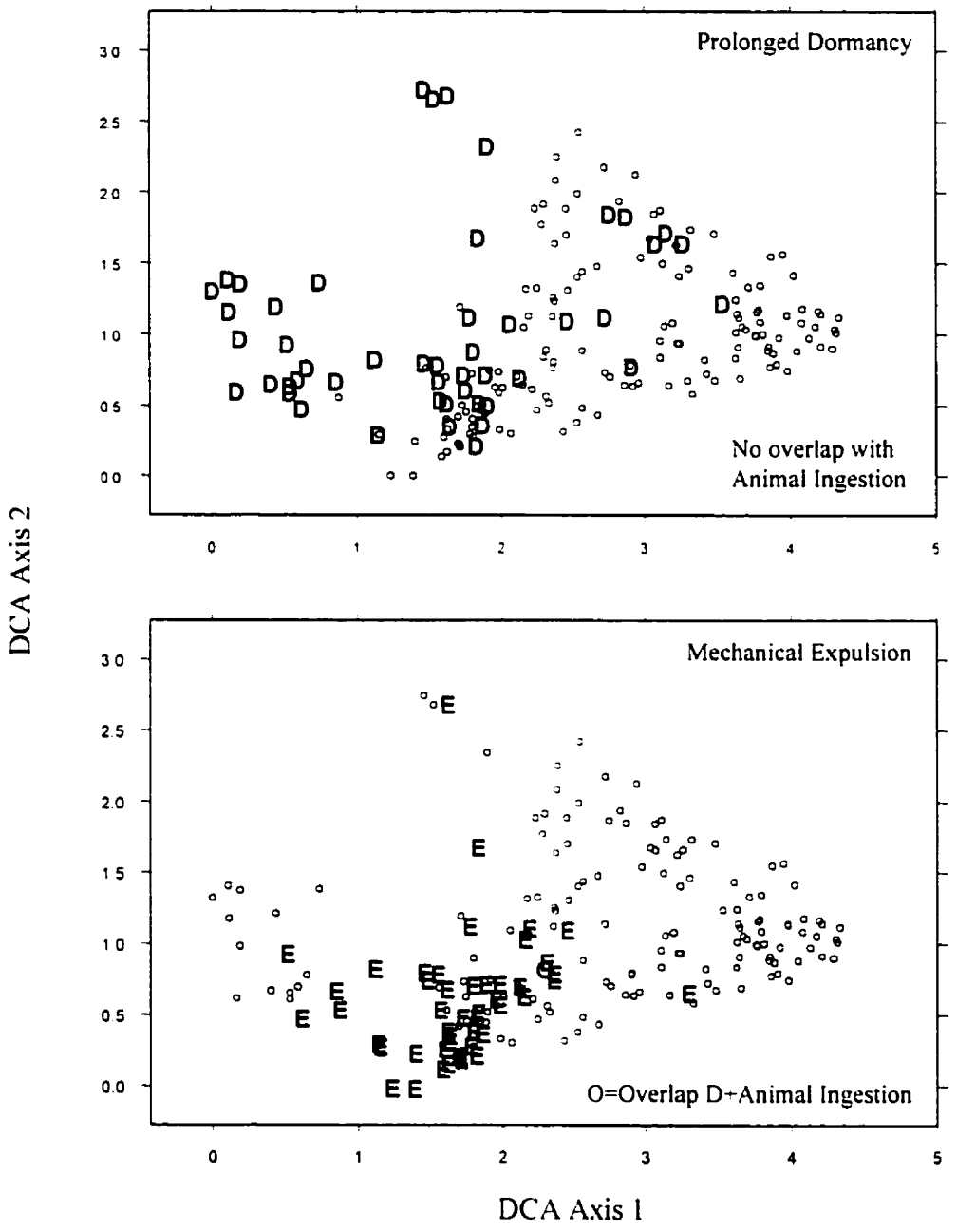

Figure 3.3. Distribution of herbs dispersed by prolonged dormancy in the soil (D) and by mechanical expulsion (E) in relation to DCA axes 1 and 2. Only quadrats in which the proportion of herbs dispersed by designated mode is ≥ 75% quartile are labeled. Note minor or no overlap (O) in quadrats where designated modes and animal ingestion predominate

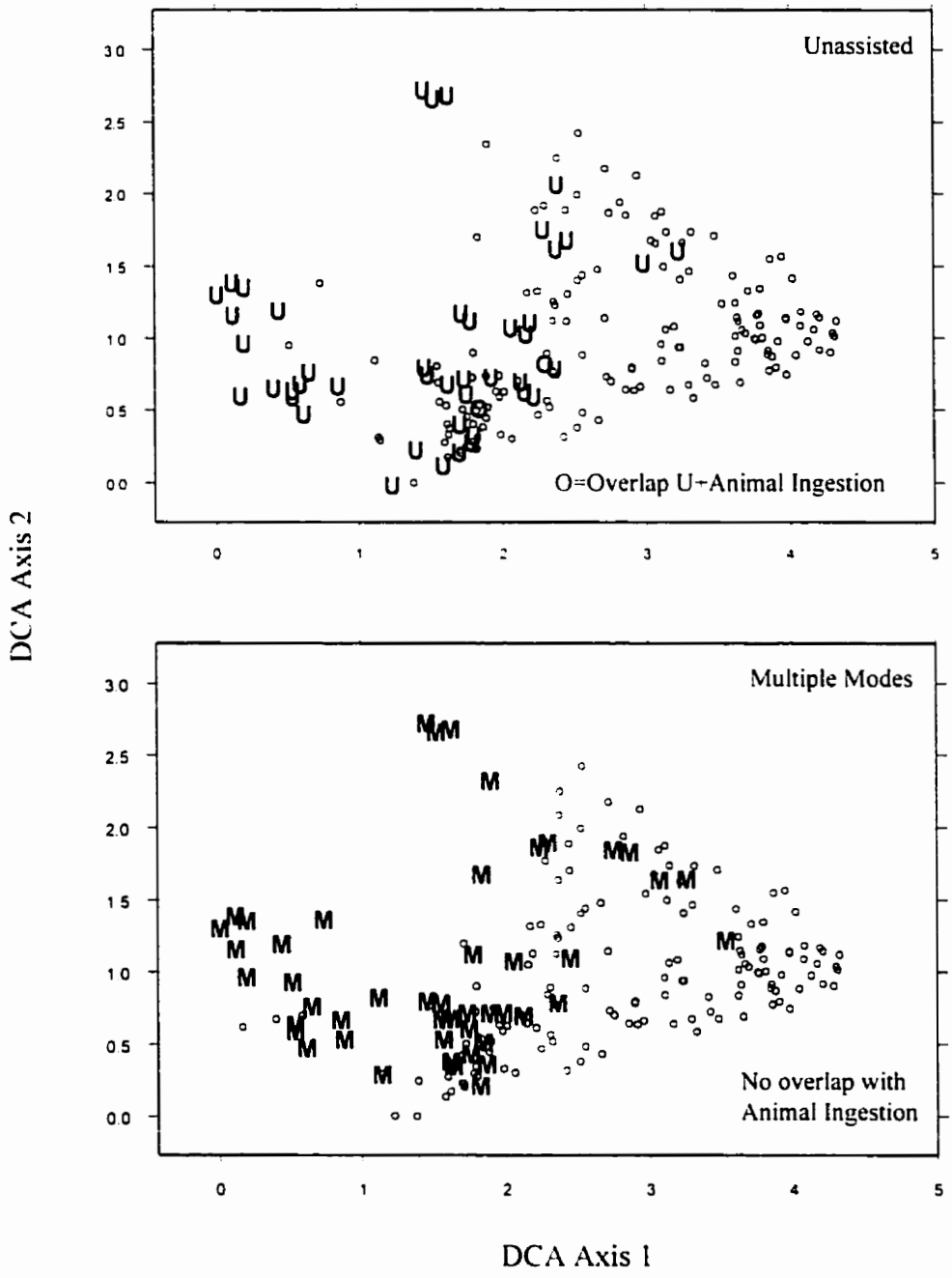

Figure 3.4. Distribution of herbs dispersed by unassisted means (U) and by multiple modes (M) in relation to DCA axes 1 and 2. Only quadrats in which the proportion of herbs dispersed by designated mode is ≥ 75% quartile are labeled. Note minor or no overlap (O) in quadrats where designated modes and animal ingestion overlap.

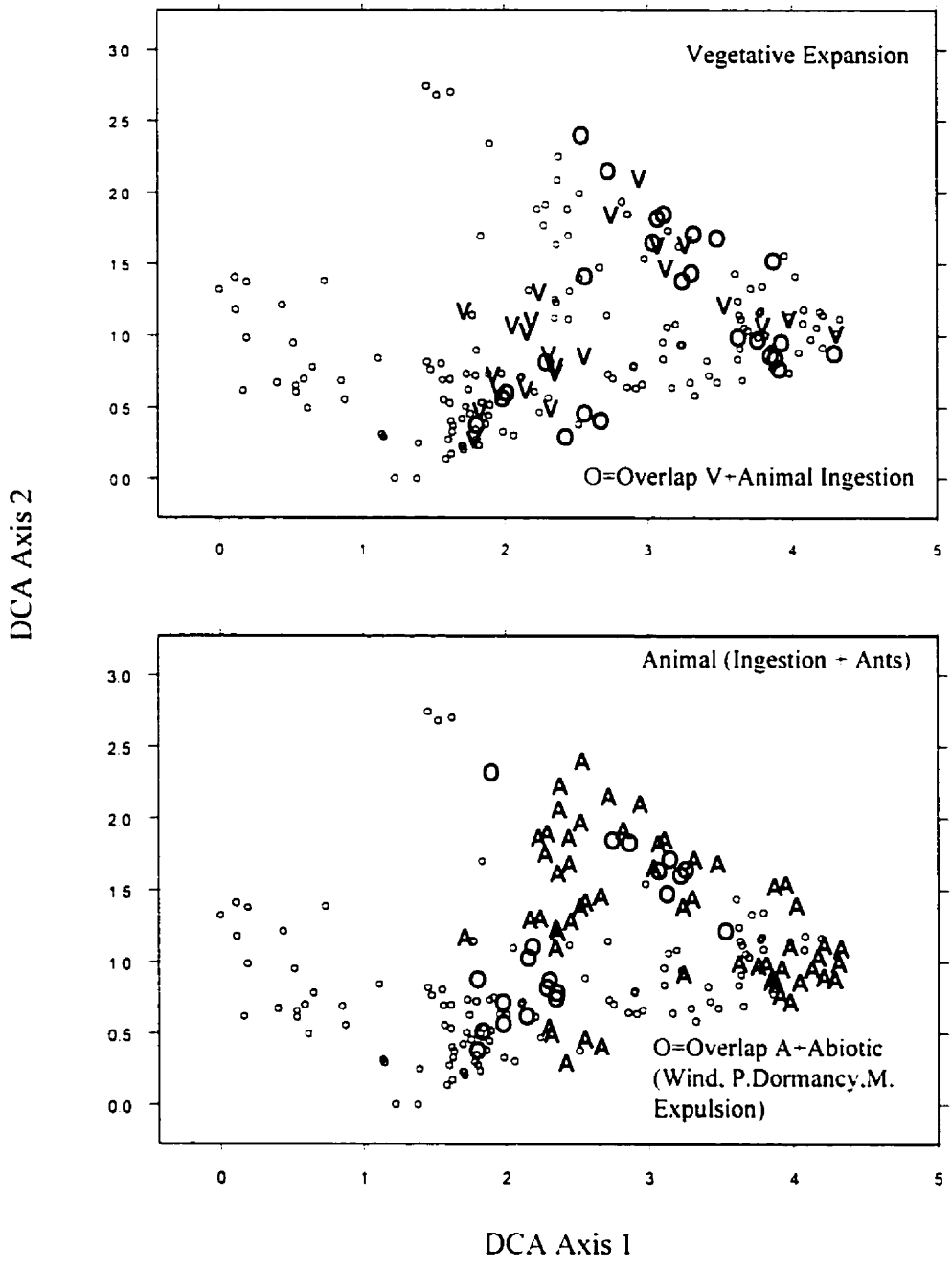

Figure 3.5. Distribution of herbs dispersed by vegetative expansion (V) and by selected animal agents (A) in relation to DCA axes 1 and 2. Only quadrats in which the proportion of herbs dispersed by designated modes is ≥75% quartile are labeled. Note substantial overlap (O) in quadrats where animal ingestion and abiotic agents predominate.

The environments in which dispersal by ants predominates are similar to animal ingestion (Figure 3.2). Unlike the latter, however, dispersal by ants was predominate in quadrats with wet depressions and in quadrats on calcareous outwash parent materials. The environments in which dispersal by mechanical expulsion predominates are similar to dispersal by wind and prolonged dormancy (Figures 3.2, 3.3), but trend towards the closed and wet ends of the environmental continuum. The quadrats in which dispersal by animal ingestion and ants predominate rarely overlap with quadrats in which dispersal by wind, prolonged dormancy or mechanical expulsion predominate (Figure 3.5).

An important trend in the data which has been masked by the decision to label only those quadrats in which the mode predominates is that some modes are more frequent than others. Herbs dispersed by vegetative expansion, animal ingestion and ants occur in virtually every quadrat whereas herbs dispersed by prolonged dormancy, mechanical expulsion and multiple modes are absent from more than 30 % of quadrats. Herbs dispersed by unassisted means, wind and animal adhesion are absent from 6 %, 10 % and 17 % of quadrats, respectively. Most absences occur in closed, dry, undisturbed habitats on calcareous till and glacio-fluvial parent materials.

The tendency for modes of dispersal to predominate in particular environmental states is readily apparent in the CCA ordination presented in Figure 3.6. In keeping with the pattern in the DCA ordination, the portion of ordination space occupied by herbs dispersed by animal ingestion and by ants is widely separated from the portion occupied by herbs dispersed by wind, prolonged dormancy, unassisted means, animal adhesion and multiple modes. Herbs dispersed by animal ingestion and by animal conveyance were most frequent in quadrats with a closed canopy, mesic soils, and large trees, whereas, herbs dispersed by wind and by prolonged dormancy were most frequent in disturbed habitats and quadrats with an open canopy. Herbs dispersed by unassisted means, adhesion to animals, and by multiple modes, were most frequent in quadrats with a high number of young stems, high soil organic matter, Gleysolic soils, and calcareous outwash or lacustrine parent materials.

Taken together, these results reveal that dispersal modes of herbs of the forest understory tend to be associated with particular environmental states at the quadrat scale. The mechanisms contributing

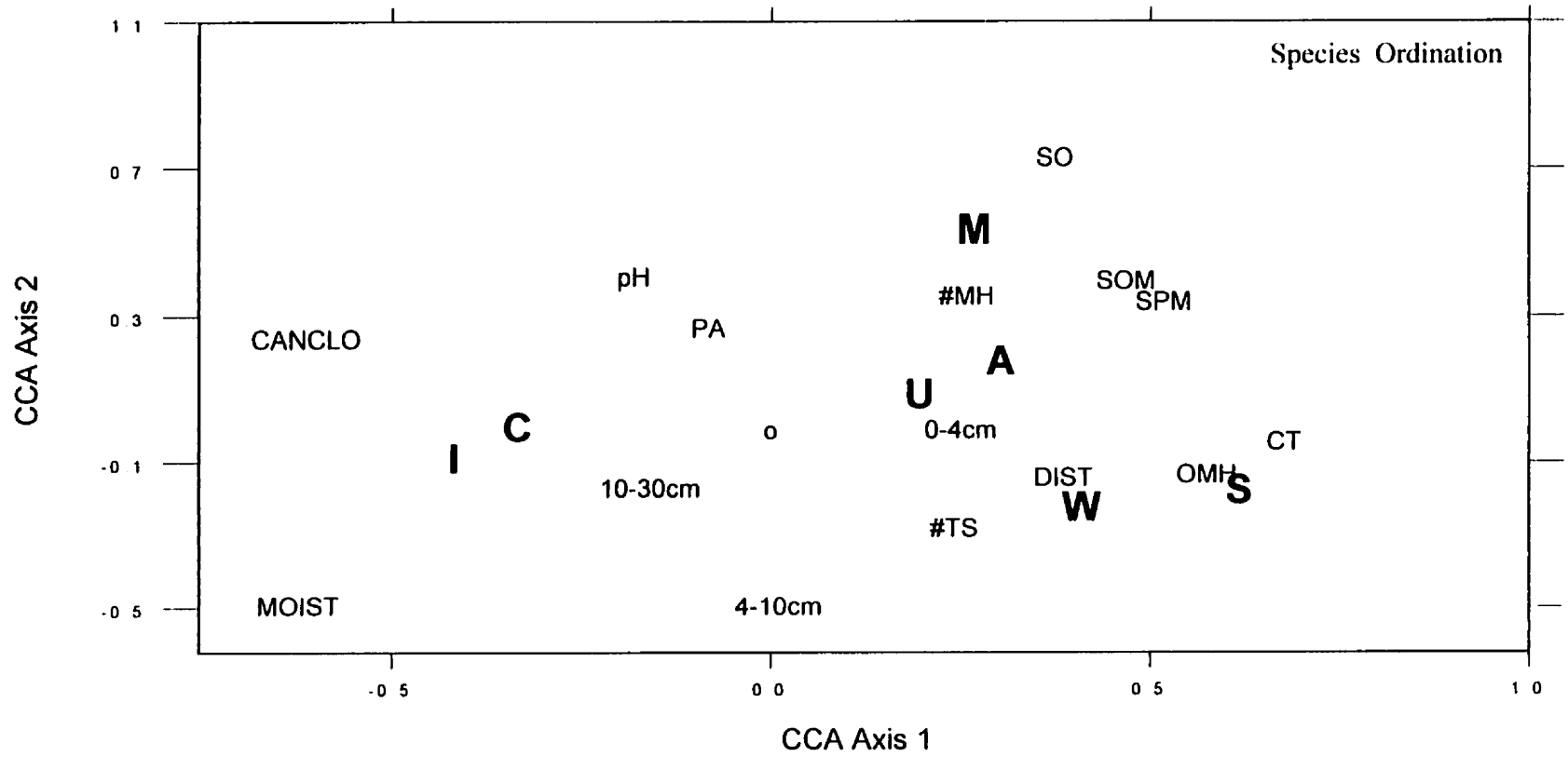

Figure 3.6. Distribution of dispersal modes of herbs in relation to environmental variables (CCA). Legend: Dispersal modes: **A** = animal adhesion, **C** = animal conveyance (ants), **I** = animal ingestion, **M** = mechanical expulsion, **S** = prolonged dormancy in soil, **U** = unassisted means, **W** = wind; Environmental variables: CANCLO = % canopy closure, CT = forest cover type, DIST = disturbance (closed and open canopy gaps, lanes, regenerating fields), MOIST = soil moisture, OMH = open microhabitats, pH = soil pH, PA = patch area (ha), 0-4 cm = # tree stems 0-4 cm dbh, 4-10 cm = # tree stems 4-10 cm dbh, 10-30 cm = # tree stems 10-30 cm dbh, #TS = # tree species. Environmental variables explain 51.6% of dispersion of dispersal modes in ordination space.

to this pattern require further analysis since the observed associations may be caused by differential dispersal, germination and establishment success. Nevertheless, the finding that all modes were present in each portion of the gradients examined suggests that the distribution of herbs in these forests has not been constrained by dispersal, or at least, has not been constrained absolutely.

3.3.2.3 Microhabitats

Environmental conditions within quadrats(10m x 10m) were rarely uniform. The relations between dispersal mode and environmental states were reassessed at the microhabitat scale in order that patterns may be examined in relation to more uniform states of forest cover, moisture, and disturbance. Definitions and descriptions of examined microhabitats were presented in Chapter 2.

Pattern was investigated in relation to three contexts: difference in the total number of herbs recorded each microhabitat (Table 3.13); difference in the proportion of herbs in contrasting microhabitats, paired samples (Table 3.14); and, difference in the proportion of herbs in contrasting microhabitats, independent samples (Table 3.15). The first context clarified the degree to which differences in the proportions of herbs in contrasting habitats were due to differences in the number of herbs present. The paired sample analysis clarified the degree to which dispersal modes were associated with particular environmental states when dispersal is known to be non-limiting. The independent sample analysis extends the latter analysis to cases where the contribution of dispersal is not known.

Number of Herbs within Microhabitats

Typically, the number of herbs dispersed by a given mode did not vary among microhabitats (Table 3.13). The exception was dispersal by animal ingestion which was over-represented in closed, dry, disturbed microhabitats (canopy gaps, tip-up mounds, tree pits, logs, stumps, farm lanes/access roads), closed seasonally dry forest floors, closed seasonally moist forest depressions, and, closed raised root mats ($p<0.05$, chi-square tests of homogeneity by column, df 38, Bonferroni correction for 9 modes). Among open microhabitats, the number of herbs dispersed by animal ingestion

Table 3.13. Number of observed and expected herbs in surveyed microhabitats by dispersal mode. Cell values: # herbs dispersed by mode in specified microhabitat (upper); departure from expectation (lower). Modes: AI = animal ingestion, AA = animal adhesion, AC = animal conveyance (ants), W = wind, PD = prolonged dormancy, ME = mechanical expulsion, U = unassisted, MM = multiple modes, VE = vegetative expansion. Chi-square tests of homogeneity by column and row. Dispersal mode in bold when the number of herbs differs from expectation across microhabitats, chi-square tests of homogeneity by column, *df* 38, Bonferroni correction for 9 modes. Microhabitat marked by asterisk when number of herbs differs by dispersal mode, chi-square tests of homogeneity by row, *df* 8 ($p<0.05$*, $p<0.01$**, $p<0.001$***); microhabitat in bold when difference from expectation significant after Bonferroni correction for 39 row tests. Cell value marked by asterisk when number of herbs for a given mode differs from expectation at $p<0.05$*, $p<0.01$**, $p<0.001$***. Expected cell value (not shown) = (proportion of herbs in data set dispersed by mode) x (# classified herbs in microhabitat). % SA = % of total area surveyed (19,200 m^2). # Herbs = number classified herbs in microhabitat. Closed microhabitats (-cc); open microhabitats (-oc). N=234 herbs.

Microhabitat			Dispersal Mode								
Variable	% SA	# Herbs	**AI** n=17	AA n=31	AC n=31	W n=62	PD n=50	ME n=17	U n=69	MM n=39	VE n=92
seasonally dry forest floors/rises-cc*	54.3	143	16* +6.3	23 +4.7	28* +9.7	26 -9.3	22 -6.5	12 +2.3	35 -4.3	19 -3.3	60 +7.6
seasonally dry forest floors/rises-oc	5.2	121	12 +3.2	18 +3.0	19 +4.0	32 +2.1	24 -0.1	9 +0.8	31 -1.2	22 +3.2	48 +3.6
seasonally moist forest floors/rises-cc	5.4	115	11 +3.2	15 +0.8	13 -1.2	31 +2.6	20 -2.9	7 -0.8	33 +1.4	14 -3.9	51 +8.8
seasonally moist forest floors/rises-oc	2.2	95	9 +2.6	10 -1.7	11 -0.7	28 +4.5	16 -2.9	7 +1.6	28 +1.9	14 -0.8	46 +11.2
seasonally moist forest depressions-cc	4.1	79	10* +4.6	10 +0.2	11 +1.2	18 -1.5	13 -2.7	5 -0.4	23 +1.3	10 -2.3	36 +7.0

Table 3.13. Number of observed and expected herbs (n=234) in surveyed microhabitats by dispersal mode (cont'd).

Microhabitat			Dispersal Mode								
Variable	% SA	# Herbs	**AI** n=17	AA n=31	AC n=31	W n=62	PD n=50	ME n=17	U n=69	MM n=39	VE n=92
seasonally moist forest depressions-oc	0.2	20	1 -0.4	6* +3.5	1 -1.5	5 +0.1	4 0.0	3 +1.6	4 -1.5	4 +0.9	5 -2.3
seasonally wet forest floors/rises-cc*	0.6	50	1 -2.4	5 -1.2	1* -5.2	12 -0.4	10 0.0	2 -1.4	24** +12.3	5 -2.8	17 -1.3
seasonally wet forest depressions-cc	4.0	66	5 +0.5	7 -1.2	7 -1.2	20 +3.7	8 -5.1	6 +1.5	22 +3.9	9 -1.3	30 +5.8
seasonally wet forest depressions-oc	1.0	24	1 -0.6	4 +1.0	1 -2.0	7 +1.1	5 +0.2	3 +1.4	10 +3.4	7 +3.3	7 -1.8
seep-cc	0.9	19	0 -1.3	2 -0.3	1 -1.3	4 -0.7	2 -1.8	2 +0.7	9 +3.8	1 -2.0	8 +1.0
seep-oc	0.3	19	1 -0.3	3 +0.7	0 -2.3	5 +0.3	0 -3.8	2 +0.7	9 +3.2	1 -2.0	5 -2.0
seasonally dry gap-cc **	2.2	59	12*** +8.0	6 -1.3	9 +1.7	13 -1.6	7 -4.8	5 +1.0	13 -3.2	5 -4.2	30 +8.4
seasonally dry gap-oc	6.9	125	12 +3.5	20 +4.6	21 +5.6	34 +4.9	24 -0.9	9 +0.5	30 -4.4	23 +3.6	50 +4.2
seasonally moist gap-cc	0.5	38	5 +2.4	6 +1.7	5 +0.3	10 +0.6	4 -3.6	4 +1.4	10 -0.4	6 +0.1	16 +2.1

Table 3.13. Number of observed and expected herbs (n=234) in surveyed microhabitats by dispersal mode (cont'd).

Microhabitat			Dispersal Mode								
Variable	% SA	# Herbs	**AI** n=17	AA n=31	AC n=31	W n=62	PD n=50	ME n=17	U n=69	MM n=39	VE n=92
seasonally moist gap-oc	3.0	93	8 +1.7	11 -0.5	11 -0.5	28 +5.0	17 -1.5	7 +0.7	26 0.4	15 0.5	46* +11.9
seasonally wet gap-oc	1.0	24	1 -0.6	4 +1.0	1 -2.0	7 +1.1	5 +0.2	3 +1.4	10 +3.4	7 +3.3	7 -1.8
mound-cc	3.6	91	13** +6.2	9 -2.2	20** +8.8	21 -1.5	10 -8.2	9 +3.8	21 -4.0	12 +2.1	44 +9.6
mound-oc	0.4	49	10*** +6.3	7 +0.9	9 +2.9	13 +0.9	11 +1.2	1 -2.3	9 -4.4	10 +2.4	24 +6.0
seasonally dry pit-cc	1.5	37	9*** +6.5	5 +0.4	11** +6.4	5 -4.1	2* -5.4	3 +0.5	5 -5.2	3 -2.7	21* +7.4
seasonally dry pit-oc	0.1	15	3* +2.0	4 +2.1	3 +1.1	4 +0.3	3 0.0	1 0.0	1 -3.1	3 +0.7	6 +0.5
seasonally moist pit-cc	0.3	5	0 -0.3	2 +1.4	1 +0.4	1 -0.2	0 -1.0	1 +0.7	0 -1.4	0 -0.2	3 +1.2
seasonally wet pit-cc	0.2	11	2 +1.3	2 +0.6	3 +1.6	1 -1.7	1 -1.2	2 +1.3	2 -1.0	2 +0.2	4 0.0
seasonally wet pit-oc	0.1	1	0 -0.1	0 -0.1	0 -0.1	0 -0.2	0 -0.2	1* +0.9	0 -0.3	0 -0.2	0 -0.4

Table 3.13. Number of observed and expected herbs (n=234) in surveyed microhabitats by dispersal mode (cont'd).

Microhabitat			Dispersal Mode								
Variable	% SA	# Herbs	AI n=17	AA n=31	AC n=31	W n=62	PD n=50	ME n=17	U n=69	MM n=39	VE n=92
log-cc	0.5	61	10** +5.9	8 +0.5	10 +2.5	12 -3.1	10 -2.2	6 +1.9	15 -1.8	10 +0.5	30 +7.6
log-oc	0.2	38	4 +1.4	7 +2.3	5 +0.3	12 +2.6	5 -2.6	4 +1.4	8 -2.4	8 +2.1	20 +6.1
stump-cc*	0.2	28	6** +4.1	3 -0.5	4 +0.5	6 -0.9	3 -2.6	4 +2.1	7 -0.7	5 +0.6	16 +5.7
stump-oc	0.1	23	3 +1.4	2 -0.8	2 -0.8	9 +3.3	2 -2.6	2 +0.4	5 -1.3	2 -1.6	12 +3.6
raised root mat-cc	1.3	73	10* +5.1	13 +4.0	8 -1.0	15 -3.0	8 -6.5	5 +0.1	23 +3.1	9 -2.3	30 +3.2
raised root mat-oc	0.6	57	6 +2.1	9 +2.0	7 0.0	9 -5.1	12 +0.6	5 +1.1	12 -3.7	12 +3.1	25 +4.1
stone-cc	0.1	11	1 +0.3	1 -0.4	3 +1.6	4 +1.3	0 -2.2	0 -0.7	1 -2.0	0 -1.7	5 +1.0
lane/road-cc*	2.3	50	9** +5.6	6 -0.2	9 +2.8	8 -4.4	4 -6.0	2 -1.4	16 +2.3	4 -3.8	25 +6.7
lane/road-oc	1.3	123	6 -2.3	18 +2.8	15 -0.2	36 +5.6	36* +11.5	8 -0.3	33 -0.8	26 +6.9	47 +1.9

Table 3.13. Number of observed and expected herbs (n=234) in surveyed microhabitats by dispersal mode (cont'd).

Microhabitat			Dispersal Mode								
Variable	% SA	# Herbs	**AI** n=17	AA n=31	AC n=31	W n=62	PD n=50	ME n=17	U n=69	MM n=39	VE n=92
ditch-cc	0.3	44	3 0.0	2 -3.4	6 +0.6	14 +3.1	6 -2.8	1 -2.0	16 +3.9	4 -2.8	22 +5.9
ditch-oc	0.1	20	1 -0.4	1 -1.5	1 -1.5	8 +3.1	3 -1.0	1 -0.4	6 +0.5	1 -2.1	11 +3.7
regenerating field-cc	1.3	72	3 -1.9	7 -1.9	7 -1.9	27* +9.2	19 +4.7	4 -0.9	20 -0.2	14 +2.8	30 +4.6
regenerating field-oc*	1.3	86	2 -3.8	9 -1.6	5 -5.6	33** +11.8	24 +6.9	8 +2.2	24 +0.4	17 +3.6	32 +0.5
riparian meadow-oc	0.7	42	1 -1.8	5 -0.2	3 -2.2	14 +3.6	9 +0.6	3 +0.2	13 +3.5	6 -0.5	15 -0.4
riparian marsh-oc	0.4	26	0 -1.7	6 +2.8	1 -2.2	10 +3.6	4 -1.2	2 +0.2	7 -0.1	4 0.0	9 -0.5
riparian thicket-oc	0.1	23	0 -1.6	7 +4.2	1 -1.8	8 +2.3	3 -1.6	1 -1.6	6 -0.3	3 -1.6	4 -4.4

departed from expectation only in dry tree pits.

Within microhabitats, the number of herbs rarely varied with mode of dispersal. The exceptions were seasonally dry or wet forest floors under closed canopies, disturbed microhabitats under closed canopies (canopy gaps with seasonally dry soils, tree pits with seasonally dry soils, stumps, lanes/access roads), and open regenerating fields ($p<0.05$, chi-square tests of homogeneity by row, *df* 8, rarely significant after Bonferroni correction for 39 row tests). The modes typically associated with this pattern were dispersal by animal ingestion and by ants.

The microhabitats in which modes of dispersal were significantly over (under) represented varied by mode. Dispersal by animal ingestion was over-represented in eleven microhabitats (see table), whereas dispersal by animal adhesion was over-represented only in open, seasonally moist, forest depressions. Dispersal by ants was over-represented on closed seasonally dry forest floors, and in closed or open seasonally moist depressions, whereas, dispersal by wind was over-represented in both closed and open regenerating fields. Dispersal by prolonged dormancy in the soil was over-represented on open lanes/access roads and under-represented in dry closed tree pits. Dispersal by unassisted means was over-represented on closed seasonally wet floors, whereas, dispersal by vegetative expansion was over-represented in open seasonally moist gaps and in closed seasonally dry tree pits. Dispersal by mechanical expulsion and by multiple modes did not differ from expectation in any microhabitat.

All modes of dispersal were represented in most microhabitats. The exceptions were seven rare microhabitats with seasonally saturated or shallow soils (number of missing modes in brackets): closed seeps (1), open seeps (2), closed seasonally moist tree pits (4), open seasonally wet tree pits (8), boulders (3), open riparian marshes (1), and open riparian thickets (1). The modes most frequently absent from these habitats were dispersal by animal ingestion (5 habitats), prolonged dormancy (4 habitats) and multiple modes (3 habitats). The modes least absent from these habitats were dispersal by animal adhesion, wind, mechanical expulsion and vegetative expansion. These modes were absent only from open seasonally wet tree pits.

The trends in Table 3.13 are broadly consistent with the trends reported in Section 3.3.2.2.

Proportion of Herbs in Contrasting Microhabitats within the Same Quadrat

Within quadrats, the dispersal modes of herbs were often associated with particular microhabitats (Wilcoxon signed rank tests by cell, paired comparisons) (Table 3.14). This suggests that herb assemblages in these samples were affected more by factors governing germination, establishment, and persistence than by dispersal, *per se*, since herbs dispersed by each mode were already present in each quadrat.

The following patterns were observed:

i) Under closed canopy conditions, the proportion of herbs dispersed by animal ingestion, mechanical expulsion and vegetative expansion was significantly higher on disturbance features with organic substrates such as logs, stumps and raised root mats than on the adjacent dry forest floor. The proportion of herbs dispersed by these modes on mineral substrates, such as pit/mound complexes, and on features created by anthropogenic disturbance, such as lanes, access roads, and regenerating fields, did not differ from the proportion on the adjacent forest floor.

ii) Under closed canopy conditions, the proportion of herbs dispersed by animal adhesion, ants, and unassisted means was significantly lower on natural disturbance features with organic substrates than on the adjacent forest floor. As in the previous case, the proportion of herbs dispersed by these modes on mineral substrates, such as pit/mound complexes, and on features created by anthropogenic disturbance, did not differ (or rarely differed) from the proportion on the adjacent floor. The proportion of herbs dispersed by wind, prolonged dormancy and multiple modes did not differ from the adjacent forest floor under any conditions.

iii) The proportion of herbs recorded under open canopy conditions did not differ from the proportion recorded in the same habitat under closed canopy conditions.

Table 3.14. Difference in mean percent of herbs (n=234) dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats. Wilcoxon signed-ranks tests, by cell, paired comparisons. AI = animal ingestion, AA = animal adhesion, A= ant, W = wind, PD = prolonged dormancy, ME = mechanical expulsion, U = unassisted, MM = multiple modes, VE = vegetative expansion. Difference = lower case habitat - upper case habitat. Values marked with an asterisk when difference significant: |t| * $p<0.05$, ** $p<0.01$, *** $p<0.001$; value in bold when difference significant after Bonferroni correction for n=9 tests per row. Quadrats with difference = "0" excluded from analysis. N=192 10m x 10m quadrats; n = maximum # quadrats in analysis. Suffixes: "-cc" = closed canopy; "-oc" = open canopy.

Microhabitat	(n=)	Dispersal Mode								
		AI	AA	A	W	PD	ME	U	MM	VE
DRY FOREST FLOOR/RISE-CC										
dry forest floor/rise-oc	13	+2.8	+1.4	-5.9	+2.6	+5.5	+1.4	-0.9	+5.7	-2.8
natural disturbance-cc	83	+6.1*	-3.1*	-4.5*	+2.7	+1.6	+6.3*	**-5.6****	+1.4	+5.7'
pit/mound-cc	61	+3.7	-2.1	-1.5	+4.3	+2.8	-0.4	-4.6*	+2.7	+2.4
log/stump-cc	37	+15.1*	**-7.3*****	**-16.6*****	-0.3	+3.9	**+24.1*****	**-10.9*****	+3.7	**+17.0*****
log/stump/root mat-cc	42	**+13.8****	**-6.0*****	**-13.7*****	+2.0	+4.2	**+16.3*****	**-9.4*****	+4.6	**+13.0*****
human disturbance-cc	9	+1.0	-4.8	-3.7	+5.5	+1.8	-10.4	+14.2	+2.4	-3.7
ALL FOREST FLOORS/RISES/DEPRESSIONS-CC										
all forest F/R/D-oc	16	+2.0	+0.5	-5.8	+1.9	+1.3	+1.6	+1.5	+2.9	-3.0
natural disturbance-cc	100	+5.2*	-2.8*	-3.6*	+0.9	+2.4	+6.2*	**-5.8*****	+1.2	**+5.8*****
natural disturbance-oc	11	-3.6	-3.7	-0.1	-2.7	-2.4	+19.1*	-2.2	+1.7	-2.6

Table 3.14. Difference in mean percent of herbs (n=234) dispersed by various modes in contrasting microhabitats (cont'd).

Microhabitat	(n=)	Dispersal Mode								
		AI	AA	A	W	PD	ME	U	MM	VE
DRY FOREST FLOOR/RISE-CC										
moist forest depressions-cc	18	-3.8	+5.7	**-10.2****	+4.8	-2.4	-2.8	+4.2	-3.5	-4.3
wet forest depressions-cc	11	-2.5	-1.5	**-17.1****	+14.5	+6.7	+9.1	-0.4	+9.2	-11.7*
NATURAL DISTURBANCE-CC										
natural disturbance-oc	8	-4.9	+1.5	+7.7	+3.9	-5.0	-5.5	+3.8	+5.2	-4.0
MOUND-CC										
pit-cc	36	+8.7	+3.6	+1.1	-10.7*	-11.0**	+7.6	-6.5	-9.0	+5.9
PIT/MOUND-CC										
log/stump/raised root mat-cc	16	+8.6	-9.5*	**-11.3***	+4.9	+10.3	+13.6	-7.3	+9.8	+6.6
LOG/STUMP-CC										
raised root mat-cc	20	-1.1	+5.0	+2.6	+3.6	-1.3	-15.3*	+6.0	-1.4	-10.4*

iv) The proportion of herbs dispersed by ants was significantly lower in moist and wet depressions under closed canopy conditions than on the adjacent dry forest floor.

v) The proportion of herbs dispersed by animal adhesion, ants, wind and prolonged dormancy on disturbance features varied with the feature and the nature of the substrate.

Proportion of Herbs in Contrasting Microhabitats, Independent Samples

The number of contrasting conditions that could be evaluated in paired samples was constrained by sample size and within-quadrat habitat combinations. By relaxing the requirement that contrasting habitats be present in the same quadrat, the analysis can be extended to the more general case: does the proportion of herbs dispersed by various modes change under contrasting habitat conditions. The greater generality achieved by this approach is offset by greater uncertainty regarding causal mechanism, since differences among sites cannot be controlled to the same degree, and, the degree to which dispersal is limiting is not known.

In general, the proportion of herbs dispersed by a given mode varied in response to contrasting habitat conditions (Wilcoxon rank sum tests, independent samples)(Table 3.15). Habitat contrasts that produced the most significant differences were the following (number of modes where the difference was significant in brackets): closed vs open dry forest floors (6); closed vs open forest floors/depressions (6), closed forest floors/depressions vs open human disturbance features (6), closed forest floors/depressions vs open natural disturbance features (5), dry vs moist closed forest floors (4), and, natural vs human disturbance features under an open forest canopy (4). Habitat contrasts in which the proportion of herbs did not vary for any mode were moist floors versus moist depressions, and, closed versus open pit/mound complexes. Modes of dispersal that were most sensitive to changes in habitat conditions were animal ingestion, prolonged dormancy in the soil, ants, and wind (difference in response was significant in >50% of habitat contrasts). Modes that were least sensitive to changes in habitat conditions were dispersal by unassisted means and by multiple modes (difference in response was significant in ≤20% of habitat contrasts).

Table 3.15. Mean percent of herbs (n=234) dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats. Wilcoxon rank sum tests, independent samples. AI = animal ingestion, AA = animal adhesion, A= ant, W = wind, PD = prolonged dormancy, ME = mechanical expulsion, U = unassisted, MM = multiple modes, VE = vegetative expansion. Quadrats with mode in each habitat excluded from analysis. Mean % for microhabitat presented for summary purposes. Larger value marked by an asterisk when difference between habitats significant: |t| * p<0.05, ** p<0.01, *** p<0.001, **** p<0.0001; larger value in bold when difference significant after Bonferroni correction for n=9 tests per comparison. N = 192 quadrats; n = maximum number of quadrats in analysis. Suffixes: "-cc" = closed canopy; "-oc" = open canopy.

		Dispersal Mode								
Microhabitat	(n=)	AI	AA	A	W	PD	ME	U	MM	VE
dry forest floor/rise-cc	126	**26.3*****	12.4	27.9	17.9	11.2	9.2	19.7	10.8	60.4*
dry forest floor/rise-oc	12	13.4	16.9*	22.0	25.1*	20.6**	9.5	18.4	**20.5****	49.2
dry forest floor/rise-cc	138	**26.4*****	12.6	**28.4******	18.2	11.0	9.3	19.7	10.7	**60.4*****
moist forest floor/rise-cc	18	15.7	15.2	11.2	25.4**	14.8	13.5	21.6	13.5*	47.6
moist forest floor/rise-cc	18	17.6	16.2	13.5	26.2	16.2	11.6	23.4	13.2	45.0
moist forest depressions-cc	19	15.6	19.0	16.4	33.7	17.0	16.4	25.4	15.9	47.4
all forest floors/rises/ depressions-cc	143	**27.1******	13.5	25.5	21.0	12.0	9.7	21.1	12.2	58.1**
all forest floors/rises/depressions-oc	18	12.1	17.4*	19.7	26.7*	18.4*	10.7	19.6	**19.2****	47.6

Table 3.15. Mean per cent of herbs dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats (cont'd).

Microhabitat	(n=)	Dispersal Mode								
		AI	AA	A	W	PD	ME	U	MM	VE
all forest floors/rises/depressions-cc	147	25.0	13.0	26.4*	19.7	11.7	9.7	21.0	12.0	58.6
all natural disturbance features-oc	12	23.3	**24.9****	17.9	34.0*	19.7*	22.5	20.1	22.2*	61.3
all forest floors/rises/depressions-cc	157	**25.1****	13.3	**26.6****	20.1	11.7	9.9*	20.7	12.0	57.9
all human disturbance features-oc	7	8.3	16.3	15.0	**42.3****	**28.5****	6.8	19.9	**21.9****	50.5
all natural disturbance features-oc	19	**21.6****	23.4	**25.2****	29.9	20.2	24.5*	21.6	22.7	55.8
all human disturbance features-oc	10	5.6	15.2	8.9	39.1	30.1*	8.5	21.3	22.7	41.6
natural disturbance-cc	96	33.2*	16.8	28.7	26.8	15.9	19.7	20.1	17.2	66.2
natural disturbance-oc	15	20.3	**26.7****	23.4	31.7	20.7	25.0	19.3	23.2	62.5
pit/mound-cc	59	32.2	15.7	33.5	26.9	15.6	12.8	19.5	16.5	66.5
pit/mound-oc	5	32.0	18.4	29.1	25.6	22.6	14.3	20.1	20.8	70.1
pit/mound-cc	50	30.6	15.1	34.6*	26.9	14.5	13.1	20.0	15.6	66.1
log/stump-cc	37	42.9	21.4*	21.5	30.5	**22.3****	**35.3*****	29.2*	**25.5*****	66.8

Table 3.15. Mean per cent of herbs dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats (cont'd).

Microhabitat	(n=)	Dispersal Mode								
		AI	AA	A	W	PD	ME	U	MM	VE
pit/mound-cc	53	32.4	15.2	**34.5*****	27.9	16.0	13.4	19.1	16.8	66.9**
raised root mat-cc	19	27.1	19.8	16.9	25.5	19.4	16.5	23.2	19.7	652.6
log/stump-cc	52	**49.0****	21.3	23.5	34.1	27.2*	35.4	29.2	30.0	69.9
log/stump-oc	8	12.8	29.2	23.3	30.0	13.1	31.3	22.2	20.6	58.8
lane/road-cc	9	27.2**	13.7	30.0*	16.8	8.5	9.5	22.2	11.0	59.2
lane/road-oc	6	6.8	16.1	17.8	**35.5****	32.3*	7.0	22.3	24.0	48.5
lane/road-cc	10	26.1*	14.8	**29.1****	16.1	9.0	7.4	23.4	12.6	58.6
regenerating field-cc	5	8.4	9.7	8.5	**42.3****	30.2*	7.7	24.0	20.7	47.4
lane/road-oc	6	8.7	17.7	23.2	30.9	32.1	7.4	19.9	25.1	51.6
regenerating field-oc	5	6.5	11.9	8.0	45.6**	28.0	8.7	21.4	19.3	44.5

Herbs dispersed by animal ingestion were most strongly associated with closed, dry forest floors; logs and stumps under closed canopies; and with natural rather human disturbance features ($p<0.05$, Bonferroni correction for 9 tests per comparison). In contrast, herbs dispersed by animal adhesion were most strongly associated with open natural disturbance features, whereas, herbs dispersed by ants were most strongly associated with closed forest floors, closed pit/mound complexes, lanes and access roads under closed canopies, and, with natural rather than human disturbance features. Herbs dispersed by the wind were most strongly associated with open human disturbance features such as lanes, access roads and regenerating fields, whereas, herbs dispersed by prolonged dormancy in the soil were most strongly associated with human disturbance features under an open canopy and with closed logs and stumps. Herbs dispersed by mechanical expulsion and by unassisted means were most strongly associated with closed logs and stumps. Herbs dispersed by multiple modes were most strongly associated with open forest floors, human disturbance features under open canopies, and closed logs and stumps. In contrast, herbs dispersed by vegetative expansion were most strongly associated with closed, dry forest floors.

The patterns of association revealed by independent and paired samples were similar in cases where direct or indirect comparison was possible. The sole exception was the affinity of selected modes for open habitats. In contrast to the pattern in paired samples, the proportion of herbs dispersed by animal adhesion, wind, prolonged dormancy, and multiple modes was often significantly higher under open than closed canopy conditions.

The latter result is intuitively more satisfying given that many of these herbs have affinities for open habitats. The difference in results is primarily in the relative strength of the outcome, however, since the proportion of herbs in open habitats was also greater in the paired samples analysis. If the positive, but non-significant, difference in richness in the paired samples simply reflects the low probability that a new taxon may land or germinate in a canopy opening before it closes, then the difference in results may be due to the larger sample size, and the different unit of measure, in the analysis of independent samples. The greater number of closed forests with low species richness in the independent samples analysis may also have strengthened the statistical relationship in that

analysis.

3.3.3 Pattern in Relation to Abundance Variables

The tendency for dispersal modes to be associated with particular states of plant abundance was examined in relation to frequency class, cover class and species richness class.

3.3.3.1 Frequency Class

The frequency class of herbs rarely varied with dispersal mode (Table 3.16). The sole exception were herbs dispersed by animal ingestion which were over-represented in the high frequency class ($\geq$25 quadrats) ($p<0.001$, chi-square tests homogeneity by row and cell, Bonferroni correction for 10 row tests and 30 cell tests). The tendency for herbs dispersed by animal ingestion to occur with high frequency is consistent with the mobility and variety of animal taxa that consume fleshy fruits, and, with the capacity of these herbs to germinate and persist under closed canopy conditions.

Surprisingly, the frequency of wind dispersed herbs did not differ from expectation. Given the mobility of wind dispersed diaspores, one might have expected wind dispersed herbs to be over-represented in the high frequency class. The capacity for these taxa to colonize and persist in closed habitats is limited, however, and these factors may have offset the extended dispersal reach of these species.

3.3.3.2 Cover Class

The cover of a given herb within a 10m x 10m quadrat often varied with the mode of dispersal (chi-square tests of homogeneity by row and column) (Table 3.17). Herbs dispersed by the wind were over-represented in cover class 1 whereas herbs dispersed by animal ingestion, and by vegetative expansion, were over-represented in cover classes 4 and 5. Herbs dispersed by prolonged dormancy were over-represented in cover class 1 and under-represented in cover classes 2 and 4. Herbs dispersed by ants were over-represented in cover class 5 (chi-square tests of homogeneity by cell).

Table 3.16. Dispersal modes of herbs (n=252) by frequency class. Cell values are the number of observed and expected herbs dispersed by a given mode at the designated frequency. Expected = (# herbs dispersed by mode ÷ 252) x (# herbs in the frequency class). Dispersal mode and observed value marked by asterisk(s) when departure from expectation significant: *p<0.05, **p<0.01, ***p<0.001, chi-square tests of homogeneity by row (*df*2) and cell (*df*1), respectively; dispersal mode and observed value in bold when departure from expectation significant after Bonferroni correction for 10 row tests and 30 cell tests, respectively. N=192 10m x10 quadrats.

Dispersal Mode		Frequency Class					
Mode	# Herbs	High ≥25 quadrats n=49 herbs		Intermediate 3-24 quadrats n=127 herbs		Low 1-2 quadrats n=76 herbs	
		Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Animal	81	23	15.8	38	40.8	20	24.4
Ingestion	17	**10*** **	3.3	4	8.6	3	5.1
Adhesion	34	5	6.6	20	17.1	9	10.3
Conveyance (ant)	33	8	6.4	16	16.6	9	10.0
Wind	64	11	12.4	35	32.3	18	19.3
Prolonged Dormancy	50	5	9.7	31	25.2	14	15.1
Mechanical Expulsion	18	3	3.5	8	9.1	7	5.4
Unassisted	78	12	15.2	39	39.3	27	23.5
Multiple Modes	39	5	7.6	24	19.7	10	11.8
Vegetative Expansion	95	23	18.5	49	47.9	23	28.7

Table 3.17. Dispersal modes of herbs (n=252) by cover class. Legend: # = number of herbs dispersed by mode; Trace = 1-5 individuals or small clumps; Obs. = # species observed in 10m x 10m quadrats; Exp. = # species expected in 10m x 10m quadrats [expected number = (# herbs dispersed by mode÷252) X (# herbs in cover class)]; chi-square tests of homogeneity by column (*df* 8), row (*df* 6) and by cell (*df* 1): * p<0.05, ** p<0.01, *** p<0.001, no correction for number of tests; dispersal mode and cover class in bold when p<0.05 after Bonferroni correction for number of tests.

Dispersal Mode	#	Cover Class															
		1 (Trace) n=195		2 (<1%) n=209		3 (1-5%) n=133		**4 (5-15%) n=46**		5 (15-25%) n=15		6 (25-50%) n=9		7 (50-75%) n=3		8 (75-100%) n=0	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Animal Ingestion**	17	15	13.2	14	14.1	13	9.0	8**	3.1	3*	1.0	2	0.6	1	0.2	0	0
Animal Adhesion	34	28	26.3	23	28.2	14	17.9	3	6.2	1	2.0	1	1.2	0	0.4	0	0
Animal Conveyance (Ants)	33	24	25.5	31	27.4	18	17.4	8	6.0	5**	2.0	3	1.2	1	0.4	0	0
Wind	64	60***	31.0	56	53.1	37	33.8	13	11.7	1	3.8	1	2.3	0	0.8	0	0
Prolonged Dormancy	50	22***	10.1	24**	41.5	17	26.4	2*	9.1	1	3.0	0	1.8	0	0.6	0	0
Mechanical Expulsion	18	14	13.9	14	14.9	6	9.5	6	3.3	3	1.1	2	0.6	1	0.2	0	0
Unassisted	78	51	40.2	64	64.7	43	41.2	10	14.2	1	4.6	0	2.8	0	0.9	0	0
Multiple Modes	39	33	30.2	30	32.3	17	20.6	4	7.1	0	2.3	0	1.4	0	0.5	0	0
Vegetative Expansion	95	75	73.5	82	78.8	58	50.1	30**	17.3	11*	5.7	7	3.4	3	1.1	0	0

The tendency for herbs dispersed by animal ingestion, ants and vegetative expansion to be over-represented in the higher cover classes is consistent with their greater tolerance for deep shade and capacity for clonal growth. The tendency for herbs dispersed by wind and prolonged dormancy to be over-represented in cover class 1 is consistent with their mobility in space, or time, and their affinity for high light environments. Both recruitment and extinction processes may contribute to the tendency for the latter species to be found as isolated individuals or in small clumps.

3.3.3.3 Richness Class

The mean proportion of herbs in a 10m x 10m quadrat dispersed by a given mode varied with the number of taxa in the quadrat (Table 3.18). The proportion of herbs dispersed by animal ingestion and by ants was highest in quadrats with low species richness, whereas, the proportion dispersed by animal adhesion, wind, prolonged dormancy, mechanical expulsion, unassisted means, and multiple modes was highest in quadrats with high richness(Wilcoxon rank sum tests by row). The proportion of herbs dispersed by vegetative expansion did not vary with the species richness of the quadrat.

This pattern is broadly consistent with the tendency for taxa dispersed by these modes to be associated with closed or open habitats (Tables 3.9 and 3.12). Closed forest habitats tend to be comparatively species poor since taxa with affinity for open habitats cannot germinate or persist under a closed canopy. Open forest habitats, on the other hand, provide opportunities for colonization by taxa with affinities for high light conditions, and, retain taxa with affinity for moderate and low light conditions (since open canopy conditions are short-lived) and thus tend to be comparatively species rich.

3.3.4 Pattern in Relation to Spatial Scale

The tendency for the dispersal modes of herbs to vary in relation to the spatial scale of their surroundings was examined in relation to patch size and patch isolation.

Table 3.18. Dispersal modes of herbs (n=252) by species richness class. Cell value: mean percent of herbs in 10m x 10m quadrats dispersed by mode. Dispersal mode and class with the highest mean ranked sum marked by asterisk(s) when differences among richness classes significant: *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001, Wilcoxon rank sum tests by row, *df* 2); dispersal mode and cell value in bold when differences significant after Bonferroni correction for 10 tests. N=192 quadrats.

Dispersal Mode	Richness Class		
Mode	High ≥56 taxa/quadrat n=49quadrats	Intermediate 29-55 taxa/quadrat n=93quadrats	Low ≤28 taxa/quadrat n=50quadrats
Animal	21.9	26.7	**32.5******
Ingestion	6.6	9.4	**14.5******
Adhesion	**6.7******	6.6	3.1
Conveyance (ant)	8.6	10.7	**14.9******
Wind	**15.4******	9.9	5.6
Prolonged Dormancy	**10.1******	4.4	2.0
Mechanical Expulsion	**4.0******	3.6	1.7
Unassisted	**14.9******	10.3	7.1
Multiple Modes	**8.6******	4.8	2.1
Vegetative Expansion	25.7	25.8	29.6

3.3.4.1 Patch Size

The proportion of herbs dispersed by a given mode often varied in relation to patch size (Wilcoxon rank sum tests) (Table 3.19). The proportion of herbs dispersed by animals, ants, prolonged dormancy, and multiple modes was highest in patches of intermediate size, whereas, the proportion of herbs dispersed by mechanical expulsion, unassisted means, and vegetative expansion was highest in small patches. The proportion of herbs dispersed by animal ingestion, animal adhesion, and wind did not vary with patch size.

The causal mechanisms for these patterns are not immediately apparent. However, the pattern is consistent with the tendency for small patches to have wet depressions (Table 2.12), and, for patches of intermediate size to be rich in sugar maple (Wilcoxon rank sum test, not shown). The former may explain the greater frequency of herbs dispersed by unassisted means, mechanical expulsion and prolonged dormancy in small patches, given their apparent affinity for moist and wet soils, whereas, the latter may explain the greater frequency of herbs dispersed by ants patches of intermediate size, given their apparent affinity for sugar maple stands on mesic soils (Tables 2.12 and 3.12).

Only the most mobile modes did not vary with patch size: animal ingestion, animal adhesion, and wind. The degree to which this pattern is due to dispersal is unclear since the environmental states most strongly associated with these modes did not vary with patch size: canopy closure, mesic soils, high soil organic matter, cover type 5, and disturbance (Tables 2.12 and 3.12).

3.3.4.2 Patch Isolation

The dispersal modes of herbs rarely varied with patch isolation (Wilcoxon rank sum tests) (Table 3.20). The exceptions were dispersal by unassisted means and by vegetative expansion. The former were more abundant in quadrats in patches of intermediate isolation whereas the latter were more abundant in quadrats in patches of low isolation. These differences were not significant after Bonferroni correction for the number of tests. The mechanisms responsible for this result are not apparent.

Table 3.19. Dispersal modes of herbs (n=252) by patch size class. Cell value: mean percent of herbs in 10m x 10m quadrats dispersed by mode. Dispersal mode, and class with the highest mean ranked sum, marked by asterisk(s) when differences among size classes significant: *p<0.05, **p<0.01, ***p<0.001, ****p<0.0001. Wilcoxon rank sum tests by row; dispersal mode and cell value in bold when differences significant after Bonferroni correction for 10 tests. N=192 quadrats.

Dispersal Mode	Patch Size Class		
Mode	Large ≥ 122 ha n=48 quadrats	Intermediate 43-121 ha n=88 quadrats	Small ≤ 42 ha n=56 quadrats
Animal**	22.8	29.4**	26.9
Ingestion	10.2	10.5	9.1
Adhesion	5.7	5.7	5.9
Conveyance (ant)	7.0	**13.2****	11.9
Wind	8.5	10.8	11.1
Prolonged Dormancy*	3.4	5.9*	5.9
Mechanical Expulsion	3.4	2.4	**4.4****
Unassisted	8.3	10.4	**13.0****
Multiple Modes*	3.4	5.8*	5.5
Vegetative Expansion*	24.6	27.3	27.7*

Table 3.20. Dispersal modes of herbs (n=252) by isolation class. High: mean distance to nearest 8 woodlots in 45^0 sectors ≥ 477m; Intermediate: mean distance 233-476 m; Low: mean distance ≤ 232 m. Cell value: mean percent of herbs in 10m x 10m quadrats dispersed by mode. Dispersal mode, and class with the highest mean ranked sum, marked by asterisk(s) when differences among richness classes significant: *p<0.05, **p<0.01, ***p<0.001, **** p<0.0001,Wilcoxon rank sum tests by row; differences among classes not significant after Bonferroni correction for 10 tests. N=192 quadrats.

Dispersal Mode	Isolation Class		
Mode	High ≥477 m n=48quadrats	Intermediate 233-476 m n=96quadrats	Low ≤232 m n=48quadrats
Animal	56.1	51.8	55.7
Ingestion	20.7	21.2	22.3
Adhesion	12.0	10.0	9.8
Conveyance (ant)	23.4	20.6	23.7
Wind	18.9	19.3	20.1
Prolonged Dormancy	11.4	9.1	8.1
Mechanical Expulsion	7.0	5.7	6.1
Unassisted*	18.6	22.0*	18.2
Multiple Modes	11.5	8.2	8.6
Vegetative Expansion**	48.0	54.0	60.3**

3.4 Discussion

Limitations of the Methodology

The composition and relative abundance of herbs in a given assemblage may be influenced by the composition, size and frequency of the seed rain; differential germination and establishment success; competitive interactions, and other factors. In principle, the distribution of plants will resemble the distribution of diaspores only when the probability of recruitment and persistence are independent of where a seed may land. In practice, this probability is not independent, and determination of the degree to which the composition of an assemblage has been influenced by dispersal limitation, site limitation, and persistence, is a complex undertaking. Inferences with respect to causal mechanism that may be drawn from pattern in the attributes and distribution of established plants, therefore, are limited.

In this study, the composition of an assemblage was deemed to have been influenced by dispersal if: i) the proportion of herbs dispersed by a given mode was significantly greater than its proportion in the sampled flora; and, ii) there was evidence of directed dispersal; or, iii) there was reason to conclude that the composition of the assemblage was not the result of differential germination, establishment, or persistence. This test of causality limits the accepted cases of influence to those in which seeds are dispersed beyond the immediate vicinity of the maternal plant, and, seedlings aggregate in sufficient numbers to be detected in a chi-square test of homogeneity or a Wilcoxon rank sum test. Seeds that are dispersed close to the maternal plant will be excluded from consideration since dispersal at this spatial scale is non-limiting and pattern in the established vegetation will be due to differential germination, establishment or persistence. Seeds that are dispersed at random beyond the immediate vicinity of the maternal plant will often be excluded since they will fail to aggregate in sufficient numbers to be detected in statistical tests.

Taken together, these conditions remove most seeds from consideration when evaluating the potential contribution of dispersal to the distribution and composition of herb assemblages in the forest understory (Portnoy and Willson 1993).

Has Dispersal Mode been a Limiting Factor in Sampled Herb Assemblages?

One inference that may be drawn, when modes of dispersal are consistently present in the sampled vegetation, is that the assemblage has not been constrained by the mode of dispersal, or at least, has not been constrained absolutely. This inference, while necessarily true, is not trivial when interpreted in the context of reported differences in the maximum reach of dispersal modes (Appendix 11) and concern that dispersal may be limiting in fragmented landscapes (Curtis 1956, Matlack 1994, Kalisz *et al.* 1997, Tilman 1997, Ehrlen and Eriksson 2000).

By this test, the composition of herb assemblages in these forests has not been constrained by the *mode* of dispersal, or at least, has not been constrained absolutely. Each mode of dispersal was represented on each portion of the environmental gradients examined (Table 3.12), and, with few exceptions (7 rare habitats with extreme conditions), in each type of microhabitat (Table 3.13). Although most modes were absent from at least one 10m x 10m quadrat, each mode of dispersal was present in all but one sampled patch (summaries of survey data, not shown). This pattern suggests that at least some seeds from each functional group were able to reach most patches and to germinate in most conditions recorded there.

Contrary to my expectations at the beginning of this study, the number of herbs recorded at low, intermediate and high frequencies was in proportion to their representation in sampled patches (Table 3.16). This suggests that the frequency of herbs in the sampled landscape was not constrained by mode of dispersal. The sole exception were herbs dispersed by animal ingestion, which were significantly over-represented in the high frequency class. Unlike other herbs, herbs dispersed by animal ingestion are both mobile and comparatively shade-tolerant and thus may experience greater colonization success in the forest understory. Taken together, these findings support the inference that mode of dispersal has not been a *limiting* factor in sampled patches.

The inference that mode of dispersal has been a non-limiting factor in the composition of sampled herb assemblages may depend critically on the level of generality in the analysis. Therefore, what may be true for functional groups may not apply to individual populations and species. Similarly,

what may be true for environmental states may not apply to individual localities. Or, at least, not at all temporal and spatial scales (Matlack 1994, Brunet and von Oheimb 1988, Cain *et al.* 1998).

Has the Composition of Herb Assemblages been Mediated by Dispersal?

The tendency for the dispersal modes of herbs to be associated with particular environmental states (Figures 3.1-3.6, Tables 3.12-3.15) is consistent with a dispersal mediated process that has facilitated the colonization of taxa in certain habitats but not others. According to this hypothesis, the observed tendency for herbs dispersed by animal ingestion to be over-represented in former canopy gaps, and on natural disturbance features associated with former canopy gaps (tip-up mounds, tree pits, logs and stumps) (Table 3.13), may be attributed to the habitat preferences and foraging behavior of their dispersal agents and to the methods by which seeds were processed. Similarly, the tendency for herbs dispersed by the wind to be found in open habitats may be attributed to higher wind speeds and the greater dispersal reach of diaspores in open vs closed habitats (Hughes *et al.* 1994). The evidence for such an hypothesis is examined below.

The pattern of colonization by herbs dispersed by fleshy fruits does appear to be consistent with a dispersal mediated process. First, birds that consume fleshy fruits are known to forage preferentially in canopy gaps (Thompson and Willson 1978, Willson *et al.* 1982, Malmborg and Willson 1988) and to regurgitate or excrete the majority of ingested seeds within and near gaps (Hoppes 1988). Moreover, forests and advanced second-growth habitats are known to support a greater diversity and abundance of frugivorous birds than early successional habitats and grasslands (Willson 1986, McDonnell and Stiles 1983). While the foraging patterns of mammals are apparently less defined (Willson and Whelan 1990), the scat of both mammals and birds has often been observed in tree pits (Thompson 1980) and on logs and stumps (Whelan *et al.* 1990, personal observation).

Second, all fleshy-fruited herbs observed in tree pits, or on tip-up mounds, logs and stumps, were also recorded on forest floors (summaries of survey data, not shown). And, all but two fleshy-fruited herbs recorded on forest floors were present in tree pits, or on tip-up mounds, logs and stumps. Thus there is little evidence that the distribution of fleshy-fruited herbs on these features has been

constrained by differential germination or persistence.

Third, inspection of the normative and compositional data (Tables 3.13 and 3.14, respectively) reveals that the over-representation of fleshy-fruited herbs on these features is due to an increase in the number of taxa rather than to an increased proportion of the taxa capable of colonizing these features. This suggests the principal mechanism contributing to this pattern has been dispersal enrichment. Although the direction of dispersal is unknown, the higher frequency and proportions of fleshy-fruited herbs on closed vs open features (Tables 3.13 and 3.15) suggests that the features were colonized over time and primarily from the forest floor. This pattern, and inference, are consistent with the patterns of herb colonization reported for tree pits and logs in three Illinois woodlands (Thompson 1980), and, with the seed rain reported for Trelease Woods, Illinois, (Willson *et al.* 1982, Hoppes 1988).

Interpretation of the colonization pattern of herbs dispersed by ants is less transparent. Although present in every patch, and in virtually every quadrat (189/192), herbs with elaiosomes were consistently over-represented on closed dry forest floors, tip-up mounds and dry tree pits (Table 3.13) and strongly under-represented (in selected habitat contrasts) on closed wet forest floors, logs and stumps, moist or wet depressions, and regenerating fields (Tables 3.13, 3.14, 3.15).

Aspects of this pattern are consistent with a dispersal mediated process. First, ants are known to carry elaiosome-bearing seeds back to the nest where the elaiosome is eaten and the seed is discarded unharmed (e.g. Handel 1978, Beattie and Culver 1981). In forests of the US northeast, nests of these species may be located in the soil (n=13 species), on decaying wood such as logs and stumps (n=3 species), or in both soil and decaying wood (n=2 species) (Appendix13). Most taxa excavate their nests in dry mineral soils (Creighton 1950). However, nests of *Myrmecina americana* and *Prenolepis imparis* are typically found in moist and damp soils, respectively (Creighton 1950), and, nests of *Formica neogagates, F. subsericea, Lasius alienus*, and *Tapinoma sessile* have been observed on organic soils in southern Quebec (Letendre *et al.* 1971). These tendencies are consistent with both the widespread occurrence and observed frequencies of elaiosome-bearing herbs. This

inference, however, depends on the unproved assumption that similar taxa and frequencies occur in sampled forest patches.

Second, ants that forage primarily in forest habitats have been shown to be less tolerant of elevated temperatures than taxa associated with old-field or other open habitats (Lynch 1981). Although the habitat affinities of known myrmecochores have not been widely assessed, most evaluated species show an affinity for forested habitats (Lynch 1981). However, at least one known myrmecochore, *Tapinoma sessile*, has an apparent affinity for recently abandoned fields, and two predominately forest litter species, including one of the most common ant species of the eastern deciduous forest, *Aphaenogaster rudis* (Lynch *et al.* 1980), have been recorded there (Lynch 1981). If these species were to nest in old-fields, then differences in the frequency and habitat affinity of dispersal vectors may contribute to the observed scarcity of elaiosome-bearing herbs in regenerating old-field habitats.

Third, the over-representation of elaiosome-bearing herbs on closed forest floors, tip-up mounds and dry tree pits was due to a greater number of herbs rather than to a higher proportion of taxa that were able to colonize these habitats (Table 3.13). Moreover, 21 of 26 species recorded on closed dry forest floors were also recorded on tip-up mounds and in tree pits; all taxa recorded in the latter habitats were recorded on closed dry forest floors (summaries of survey data, not shown). Taken together, these data provide little evidence of limitation by other factors and suggest that the principal mechanism contributing to this pattern has been dispersal enrichment.

The case for dispersal limitation as the principal mechanism in habitats where elaiosome-bearing herbs were under-represented is less strong. Although somewhat fewer species were recorded in regenerating fields, stumps, and open moist depressions (Table 3.13), the strength of the relationship was due primarily to differences in the proportion of elaiosome-bearing taxa in the contrasting habitat (Tables 3.14, 3.15). This was also the case for closed and open logs where more, rather fewer, species were present (Tables 3.13, 3.14). Taken together, these results suggest that dispersal was not the principal mechanism responsible for the under-representation of elaiosome-bearing herbs in these habitats. However, the under-representation of elaiosome-bearing herbs on closed wet

floors is consistent with a dispersal mediated process, since significantly fewer species were recorded in this habitat (Table 3.13) and comparatively few species of ants nest in such conditions.

The presumption that elaiosome-bearing herbs are dispersed exclusively by ants is not strictly true. Yellow jacket wasps in Oregon state have been observed transporting diaspores of *Trillium ovatum* to their nests (Jules 1996), and in Washington state, Pellmyr (1985) has observed yellow jacket wasps dispersing elaiosome-bearing seeds of *Vancouveria hexandra* (Berberidaceae). Elaiosomes represent a rich source of lipids in the forest understory and it is likely that deer and other animals consume and passively disperse the diaspores of many "ant-dispersed" herbs. Infrequent but chance (or consistent but unrecognized) dispersal by insect and animal vectors may therefore be an important mechanism for longer-distance dispersal of these herbs and may account for their rapid apparent rate of post-glacial migration in eastern North America (Cain *et al.* 1998).

The degree to which dispersal has contributed to patterns of association for other modes is less certain. Herbs dispersed by the wind, for example, were consistently associated with open microhabitats and with human disturbance (Tables 3.12 and 3.15). While propagules with wings and plumes may travel farther in these habitats than under a closed forest canopy (Hughes *et al.* 1994), the tendency for wind-dispersed herbs to be poorly represented in forest habitats is more likely to be have been caused by differential germination success arising from differences in seed weight (Salisbury 1942, 1974; Baker 1972, Luftensteiner 1979, Mazer 1990, Saverimuttu and Westoby 1996). Species of open habitats tend to have lower seed mass than congener species of closed habitats and thus lack sufficient reserves to sustain seedling growth in dense shade during the critical cotyledon stage (Saverimuttu and Westoby 1996). According to this view, species should differentially occupy habitats on the basis of seed size (Mazer 1990) rather than on the basis of dispersal reach.

Published data were not sufficient to test the seed size (seed reserve) hypothesis. However, in keeping with this hypothesis, approximately 10 % of the wind-dispersed herbs in this study had an affinity for closed habitats (Appendix 2): *Aster macrophyllus*, *Boehmeria cylindrica*, *Galearis*

spectabilis, *Prenanthes* sp., *Solidago caesia*, and *Solidago flexicaulis*. The reported mean seed mass for congeners of closed vs. open habitats (*sensu lato*) is consistent with the predictions of the seed size (seed reserve) hypothesis: 0.847 mg (n=1) vs 0.250 mg (n=5) for classified species of *Aster*; 0.346 mg. (n=1) vs. 0.090 mg. (n=7) for classified species of *Solidago* (Mazer 1990).

In addition, the mean frequency of wind-dispersed herbs in sampled patches was higher for herbs with affinity for "forest" habitats ($\bar{x}$ = 18.0 quadrats, n=6 herbs) than for herbs with affinity for "open" habitats ($\bar{x}$ = 6.4 quadrats, n=22 herbs) (p=0.03, Wilcoxon rank sum test, not shown). Herbs with affinities for intermediate conditions were present at higher frequencies ($\bar{x}$ =43.2 quadrats, n=6 herbs with affinity for "forest + open habitats"; $\bar{x}$=16.8 quadrats, n=28 herbs with affinity for "open + forest habitats"). These data suggest that lower wind speeds in forest interiors do not pose a colonization constraint for wind-dispersed herbs with affinities for closed habitats (*sensu lato*). The dispersal reach of asters and goldenrods may be enhanced by late season flowering and by higher wind speeds associated with a senescing canopy. The higher mean frequency of herbs with affinity for "forest+open" habitats may indicate that the dispersal reach of forest dependent taxa is constrained by their greater seed mass.

Wind-dispersed herbs were present in every sampled forest patch but were absent from 10 % of quadrats within patches. Closed canopy conditions were present in most of these quadrats. In the remaining cases, canopy gaps were either small (<2% of sampled area) or in a large forest stand where the sole wind dispersed herb was *Solidago flexicaulis*.

Taken together, these results suggest that closed canopy conditions pose less of a constraint for herbs with affinities for closed habitats ("forest", "forest+open") than for open habitats ("open", "open + forest"). While the colonization success of wind-dispersed herbs may be mediated to some extent by dispersal processes, the overall evidence from this study suggests that the principal mechanisms governing their distribution are differential germination, establishment or persistence.

Herbs dispersed by animal adhesion were over-represented in open seasonally moist depressions

(Table 3.13) and were consistently associated with open habitats in contrasting habitat comparisons (Table 3.15). While these habitats are associated with animal activity, the more likely explanation for this pattern is differential germination, establishment or persistence since dispersal by animal adhesion is primarily a stochastic process (Agnew and Flux 1970, Bullock and Primack 1977, Sorensen 1986, Williams and Guries 1994, Kiviniemi 1996). The habitat affinities of herbs dispersed by adhesion are broadly consistent with this inference: 74.2% of taxa have affinities for open habitats (*sensu lato*) and 30.4 % of these taxa have affinities for moist and wet habitats.

Herbs dispersed by mechanical expulsion were over-represented in open seasonally wet tree pits (Table 3.13) and were strongly associated with logs and stumps under closed canopies in habitat comparisons (Tables 3.14). At the local scale, dispersal by mechanical expulsion should be primarily a non-limiting process since most seeds land in the immediate vicinity of the parent plant (Appendix 11). The principal contributors to pattern in the local herb assemblage should therefore be differential germination, establishment and persistence. In keeping with this inference, only 50% of the ballochores recorded on closed forest floors were present on logs and stumps (summaries of survey data, not shown). The ballochores occupying open seasonally wet tree pits were habitat generalists that were recorded in more than 60% of classified habitats.

Although the dispersal reach of herbs dispersed by mechanical expulsion is typically less than 5 metres (Appendix 11), ballochores were present in 23 of 24 sampled patches. Longer-distance dispersal may therefore be achieved by ingestion by birds, mammals or insects. Interestingly, herbs dispersed by mechanical expulsion in this study were never secondarily dispersed by animal adhesion.

Herbs dispersed by unassisted means were over-represented on closed seasonally wet forest floors (Table 3.13) and under-represented on closed logs and stumps in habitat contrasts (Table 3.14). Although the diaspores of these herbs lack apparent features that may facilitate their dispersal, herbs dispersed by unassisted means were present in every patch and in 181 of 192 quadrats. The contribution of dispersal to this pattern is not known but presumably is mediated by animal vectors.

Herbs dispersed by prolonged dormancy were initially dispersed by some other agent: unknown vectors (36%), wind (34%), vegetative expansion (26%), adhesion to animals (16%), mechanical expulsion (14%), ants (6%), and ingestion by animals (2%)(percentages do not sum to 100 since certain herbs were dispersed by more than one mode). The distribution of propagules arising from dispersal in space has presumably been masked by patterns of recruitment in time, owing to the inherent requirement for high light conditions for germination and establishment. In keeping with this inference, the habitats in which dispersal by prolonged dormancy was most prominent were open microhabitats associated with human disturbance and former canopy gaps (closed logs and stumps) (Table 3.15).

Herbs dispersed by vegetative expansion were often dispersed by some other agent: animal ingestion (9.9%), animal adhesion (4.4%), ants (22.0%), wind (35.2%), prolonged dormancy (14.3%), mechanical expulsion (8.8%), and multiple modes (13.2%). Herbs dispersed by vegetative expansion were present in every quadrat and rarely were associated with particular microhabitats. Their numbers were over-represented, however, in open, moist, canopy gaps and in closed, dry, tree pits (Table 3.13). The former association is unique among dispersal modes whereas the latter association was also shared by herbs dispersed by animal ingestion and by ants. The distribution of herbs dispersed by vegetative expansion may therefore be mediated to some extent by animals.

Dispersal in Time

Dormancy enables plants to germinate when conditions are favorable and to delay germination when they are not. Delayed germination is predicted to be favored in taxa of open habitats since it allows species to avoid exposure to unfavorable conditions and to specialize on conditions that maximize reproductive success (Brown and Venable 1986, Cohen and Levin 1987). Delayed germination is predicted to be less favored in forest habitats, since the enhanced seed reserves that facilitate establishment in dense shade also enable forest plants to specialize on shaded conditions and to avoid the reduction in mean annual fitness that arises when dormancy constrains the number of seeds that can be produced in favorable years (Venable and Brown 1988). Selection pressure for the evolution of dormancy, therefore, is expected to be greatest in permanently open habitats, where

environmental quality varies more or less randomly in time, and to be intermediate in successional habitats, where the decline in environmental quality is progressive and persistent, and where non-seed-bank traits increasingly should be favored (Brown and Venable 1986). Plants with annual life histories are expected to benefit more from dormancy than plants with biennial or perennial life histories (Rees 1993, 1994).

Approximately 20 % of the herbs recorded in this study are known to disperse in persistent soil seed banks (Table 3.1). In keeping with models of the evolution of dormancy, the majority of these herbs (92%) were species with affinities for "open" or "open+forest" habitats, and no herbs were species with an affinity for "forest" habitats (Table 3.9). Moreover, the number of taxa with capacity for prolonged dormancy increased with increasing affinity for open conditions (Table 3.9). These results, and current theory, suggest that in forested habitats, dispersal in time may be restricted to fugitive species and to sites of recent canopy disturbance. In keeping with this prediction, herbs with capacity for dormancy were significantly over-represented in the trace cover class (1-5 individuals) and under-represented in the higher cover classes (Table 3.17).

Unexpectedly, many seed-banking herbs (52%) in this study were also capable of long-distance dispersal (i.e., dispersal by wind, animal ingestion or animal adhesion). Typically, models of annual herbs in spatially and temporally variable environments predict an inverse relationship between dormancy and dispersal, since a reduction in the variance in reproductive success by dispersal should reduce selection pressure for the evolution of dormancy, and vice versa (e.g. Venable and Lawlor 1980, Cohen and Levin 1987). In plants with dimorphic seeds, reproductive success is maximized when low dispersal seeds have delayed germination and when high dispersal seeds have quick germination (Venable and Lawlor 1980). These combinations are also favored in plants with monomorphic seeds (Cohen and Levin 1987). A seed that is both dormant and mobile is therefore unexpected.

The most apparent explanation for taxa with the capacity for high dispersal and high dormancy is a seed polymorphism. In this study, such a species would be classified as having "high dispersal"

based on the morphology of the diaspore, and, as possessing "high dormancy" based on its demonstrated capacity to persist in the soil for ≥5 years. Based on the reasoning above, one would expect the dormant seeds to be dispersed close to the parent and the non-dormant seeds to be dispersed remote from the parent. The reverse pattern is less likely and has been observed only in selected species of Brassicaceae (Venable and Lawlor 1980). In keeping with this reasoning, one might also expect variability in the reported dormancy status of such species since their classification would depend on the morph that was sampled. All but one "high-dispersal, high-dormancy" taxa in this study (*Bidens frondosa*)were typically classified as "transient" or "short-term persistent" in Thompson *et al.* (1997). An assessment of seed polymorphism in these taxa, therefore, appears warranted.

Deterministic versus Stochastic Dispersal Processes

Most seeds of most North American herbs apparently land within a few metres of the parent plant (Portnoy and Willson 1993, Cain *et al.* 1998, Appendix 11). At this spatial scale, dispersal is primarily a deterministic, non-limiting, process and pattern in the structure of herb assemblages should be governed primarily by factors controlling germination, establishment and persistence. The maximum dispersal distance achieved by North American herbs is poorly understood but is apparently on the order of tens of metres for most herbs, and, rarely more than a thousand metres for seeds dispersed by the wind and animal adhesion (Appendix 11). Dispersal at these spatial scales is increasingly a stochastic process and may result in dispersal limitiation on short time scales. Dispersal by ants and by frugivorous birds may be important exceptions since these taxa have the potential for "directed"dispersal at these spatial scales.

When viewed from this perspective, dispersal is primarily a short-distance process that operates on the scale of metres to tens of metres. This is the scale where dispersal has the greatest control over where a seed may land, and, apparently is the scale at which reproductive success, on average, is maximized. Paradoxically, it is also the scale where differences in the dispersal reach of evolved morphologies are minimized. This is apparently true even for herbs of ephemeral habitats since most of their seeds, on average, also land in close proximity to the parent (Appendix 11). However, it is

these seeds in which dormancy is most often expressed and thus travel greater distances in time (Flint and Palmblad 1978. Olivieri and Berger 1985. Venable and Lawlor 1980. Venable *et al.* 1995). Taken together, these tendencies imply that, on average, the fitness benefits to be derived from long-distance dispersal are outweighed by the benefits to be derived from "controlled" dispersal at the micro-scale. Paradoxically, it would appear that dispersal is most successful when the movement of seeds is most constrained.

3.5 Principal Findings

1. Most plants in the forest understory were dispersed by animals (38.5 %), vegetative expansion (35.8 %), and the wind (30.5 %). Others were dispersed by unassisted means (22.0 %), prolonged dormancy in the soil (15.5 %), multiple modes (12.3 %), or mechanical expulsion (4.6 %). Of those dispersed by animals, 16.9 % were dispersed by animal ingestion, 12.8% were dispersed by animal adhesion, and 9.7% were dispersed by ants or by seed caching. These patterns are broadly consistent with reported dispersal profiles for temperate forest habitats in the Great Lakes region and northeast United States (Table 1.1).

   The proportion of taxa dispersed by a given mode was found to be sensitive to environmental conditions at the micro spatial scale. Characterization of the dispersal profile at the patch or landscape spatial scale, therefore, may mask variation in dispersal frequencies that reflect differences in causal factors.

2. The mode by which plants were dispersed varied by life form. Most trees, and all ferns and fern allies, were dispersed by the wind, whereas most shrubs and vines were dispersed by animal ingestion. Most grasses were dispersed by animal adhesion. Herbs were the only life form to be dispersed by all modes and were dispersed primarily by vegetative expansion, animal vectors or unassisted means.

3. The mode by which plants were dispersed also varied by life history, provenance, modality, fruit type, habitat affinity, and shade tolerance. Pattern in the frequency of dispersal modes

was also observed in relation to environmental gradients, microhabitat, patch size and plant cover class. Dispersal by animal ingestion and by ants was associated with low species richness in 10m x 10m quadrats, whereas dispersal by animal adhesion, wind, prolonged dormancy, mechanical expulsion, unassisted means, and multiple modes were associated with high species richness.

4. The composition of herbs in sampled patches has not been constrained by the modes of dispersal employed by herbs, or at least, has not been constrained absolutely. Each mode of dispersal was represented on each of the environmental gradients examined, and, with few exceptions, in each type of microhabitat. Although most modes were absent from at least one 10m x 10m quadrat, each mode of dispersal was present in 23 of 24 surveyed patches. These patterns suggest that at least some seeds from each functional group were able to reach most patches and to germinate there.

5. The species composition of selected habitats has been enriched by dispersal by frugivorous birds and mammals and by ants. The strongest evidence for directed dispersal by animal ingestion was found in former canopy gaps and on disturbance features associated with canopy openings (tip-up mounds, tree pits, logs, stumps, forest lanes and access roads). The strongest evidence for directed dispersal by ants was found on closed tip-up mounds and tree-pits.

6. With few exceptions, the tendency for modes of dispersal to be correlated with particular environmental states cannot be attributed to dispersal processes. The supporting evidence for this conclusion is not definitive, however, since the methodology has limited capacity to differentiate between effects caused by dispersal and effects caused by germination, establishment and persistence.

7. Several herbs were classified as having the capacity for both long-distance dispersal and dormancy. This character combination is rare in the literature and counter to current theory

regarding the evolution of dormancy. The most apparent reason for this combination is seed heteromorphism, a property previously unreported for these species. Approximately 10 % of surveyed herbs, and 21% of herbs with the capacity for long-distance dispersal, possessed the traits of interest.

8. If most seeds of most herbs land within a few metres of the maternal plant, then dispersal is primarily a non-limiting, deterministic, process and pattern in established herb assemblages should be due primarily to differential germination, establishment, and persistence.

Evolved dispersal morphologies, however, enable at least some propagules to travel metres to hundreds of metres from the maternal plant, on short time scales. At this spatial and temporal scale, dispersal is increasingly a stochastic process and the structure of established herb assemblages may be mediated by the number and spatial distribution of dispersing seeds. Opportunities to detect change based on properties of the established vegetation are limited, however, since only rarely can the contribution of dispersal be differentiated from the effects of germination, establishment and persistence.

4.0 PATTERNS OF SPECIES RICHNESS

4.1 Introduction

The paradox posed by the apparent coexistence of many species in the same environment has attracted attention for more than a century. According to the competitive exclusion principle, two similar species cannot coexist indefinitely on a single limiting resource in a uniform environment (Grinnell 1904, Volterra 1926, Gause 1934). Under such conditions, one species should eventually exclude the other and the assemblage should be reduced to a single species (Hutchinson 1957, 1959, 1961; Hardin 1960). How is it, then, that so many natural habitats are species rich?

One productive approach to this question has been to examine the assumptions of the exclusion principle: what happens if species are not "similar", if interactions do not proceed to equilibrium, if there is more than one limiting resource, or, if the environment is not spatially and temporally uniform. This research effort has generated a vast literature and many alternative explanations (Connell 1978, Huston 1979, Pickett 1980, Sousa 1984, Petraitis *et al.* 1989, Hart and Horwitz 1991, Tilman and Pacala 1993, Ricklefs and Schluter 1993, Huston 1994, Palmer 1994, Heywood 1995, Grace 1999). A selected review of the principal themes follows.

Limiting Similarity: The Lotka-Volterra model of interspecific competition predicts the stable coexistence of species when competition between species is less significant than competition within species. One way this may be achieved is through niche differentiation. If competitors were to differ in their requirements for a limiting resource, or, were to consume that resource at a different time or in a different place, then the effects of competition would be concentrated more within than between species and coexistence would be favored (Begon *et al.* 1990).

The apparent necessity for coexisting species to possess distinct ecologies has been demonstrated in mathematical models in both uniform and variable environments (e.g. MacArthur and Levins 1967, May 1973, Chesson and Warner 1981, Pacala and Tilman 1994). An important prerequisite for coexistence is that populations be able to expand when rare. If individuals of different species in a competing assemblage were indistinguishable, then the competition experienced by individuals

would depend solely on the total density of individuals in the assemblage. Under these circumstances, individuals of rare species experience no less competition than individuals of abundant species. And, since individuals possess the same capacity to reproduce and disperse, and propagules have the same response to differences in environmental quality, each species has the same chance of recruiting offspring into the population. Under these circumstances, it is not apparent how populations recover from fluctuations that take them to low density, and thus, how the criterion for coexistence may be satisfied (Chesson 1991).

There would appear to be some limit, therefore, to the similarity in the way in which species in a competitive assemblage may use, and respond to differences in, available resources. That limit is is now expected to be both environment and species assemblage specific (Abrams 1983).

The niche differentiation hypothesis may constitute a necessary, but not sufficient, explanation of species richness, however, owing to the degree of resource partitioning that is implied for a species rich assemblage (Connell 1978, Silvertown and Law 1987). In spite of the apparent utility of concepts such as the regeneration niche (Grubb 1977, 1986), and the resource ratio hypothesis (Tilman 1982, 1988), a major difficulty in applied studies has been to identify the important resource axes that may permit coexistence at the local scale (Silvertown and Doust 1993, Tilman 1993, Hooper and Vitousek 1997, Busing and White 1997).

Non-Equilibrium Conditions: An important limitation of hypotheses that seek to explain species coexistence under equilibrium conditions is that assemblages are embedded in environments that are subject to more or less continuous change. In a variable environment, species densities are expected to fluctuate over time, rather than stabilize, in response to patch dynamics (Watt 1947, Oliver 1981, Pickett and White 1985) and to periodic disturbance (Connell 1978, Pickett 1980, Sousa 1984, Petraitis *et al.*1989). Under non-equilibrium conditions, community recovery from such processes is expected to be incomplete, owing to priority effects (Yodzis 1978, 1986), differences in the assembly sequence arising from chance colonization events (Drake 1991, Fastie 1995), and time lags in plant response (Davis 1981, 1986).

Hypotheses that account for spatial and temporal variability in the environment have proposed three general ways in which variability may facilitate species coexistence on ecological time scales: i) by slowing down the rate of competitive exclusion (e.g. Hutchinson 1941, Levin and Paine 1974, Connell 1978, Huston 1979, Shmida and Ellner 1984); ii) by reversing the order of competitive superiority among species (e.g. Hutchinson 1961, Chesson 1985, Pacala 1987); and, iii) by altering the availability of limiting resources (e.g. Tilman 1982, 1988). These processes are not mutually exclusive and may differentially apply in given circumstances (Warner and Chesson 1985). The first process emphasizes the conservation of existing species, whereas the latter processes emphasize how populations and diversity may increase (Chesson and Case 1986).

An important property of the slow dynamics hypothesis is that disturbance interrupts and sets back the process of competitive exclusion, by removing the competitive dominants and releasing resources for established species. This prevents competitive dominants from monopolizing available resources and promotes species coexistence by delaying the exclusion of inferior competitors. Factors expected to promote slow dynamics include: i) long life spans; ii) small differences in competitive strength; iii) highly aggregated or clumped distributions; iv) a surplus of suitable microsites; v) widely separated microsites; vi) intermittent competition; vii) slow growth rates; and, viii) intermediate rates of disturbance (Shmida and Ellner 1984, Huston 1979, Connell 1978). Related theories based primarily on small differences in competitive strength include the slow dynamics model of Hubbell and Foster (1986), and, the ecological and competitive combining ability model of Aarssen (1983).

Patterns and processes of diversity explained by this mechanism include: gap phase dynamics (Watt 1947, Oliver 1981, Pickett and White 1985); the initial floristic composition model of secondary succession (Egler 1954); species coexistence in the presence of keystone predators (Paine 1966, 1974); and, the displacement of characteristic species and assemblages in the absence of fire (Varga 1989, Kruger and Reich 1997), fluctuating water levels (Keddy and Reznicek 1982, 1986), herbivory (Whitney 1984, Grubb 1986), and land-use management (Gimingham 1972, Heil and Bruggink 1987).

An important property of the reversal in competitive rankings hypothesis is that a variable environment provides some place or time where competitors may perform poorly or not survive, and, where populations of low abundant species may expand. It is the latter process that distinguishes this explanation from the others and that provides the basis for the coexistence (Warner and Chesson 1985, Chesson 1986). Factors expected to promote reversals in competitive superiority in competing plant assemblages include: i) juvenile mortality rates that are sensitive to environmental conditions; ii) reproductive rates that are sensitive to environmental conditions; iii) adult survival rates that are insensitive to environmental conditions; iv) overlapping generations; v) iteroparity; and, vi) random dispersal (Chesson 1985, 1986; Pacala 1987).

In this analytical setting, species in strong competition may depress each other's recruitment rates. Nevertheless, each species may still be able to show positive average growth rates provided that it has periods when it is able to recruit well. In a variable environment, temporary reversals in the competitive advantage of species make this increasingly likely owing to the sensitivity of both juveniles and reproductive rates to changes in environmental conditions. This should lead to the strong recruitment of different species at different times, or in different places, and reverse the trend towards competitive exclusion for all species. Overlapping generations promote coexistence in this setting by ensuring that demographic gains made during favorable periods are "stored" in the surviving offspring and contribute to reproduction when favorable conditions return (Warner and Chesson 1985, Chesson 1985). Dispersal facilitates the reversal in competitive rankings through the randomization of neighbors in competing plant assemblages (Pacala 1987).

An important property of the resource availability hypothesis is that species utilize different portions of available habitats, or, differ in the range of habitats wherein they have a competitive advantage over other species, owing to differences in plant requirements and the differential availability of limiting resources (Whittaker 1965, Grime 1973, 1979; Tilman 1982, 1988; Comins and Noble 1985; Bazzaz 1991). In these models, coexistence is achieved primarily through the spatial segregation of competitors in a mosaic of suitable habitats. The C-S-R model of competition (Grime 1973, 1979) and the resource ratio hypothesis (Tilman 1982, 1988) emphasize competitive interactions among established plants, whereas, the lottery model of competition (Sale 1977,

Chesson and Warner 1981, Comins and Noble 1985) emphasizes the recruitment phase and the competition for suitable sites for establishment. Periodic disturbance facilitates coexistence and enriches local diversity by increasing spatial heterogeneity in the availability of limiting resources. In these models, the important consequence of disturbance is the change in the relative supply of limiting resources for which competition occurs. Competition is not so much interrupted as redirected.

Patterns explained by the differential availability of limiting resources include: the paradox of enrichment (Rosenzweig 1971, Al-Mufti *et al.* 1977, Tilman 1982, Wisheu and Keddy 1989, Abrams 1995); the facilitation model of plant succession (Connell and Slayter 1977, Finegan 1984); regeneration from persistent seed pools (Thompson *et al.* 1998), persistent seedlings, and serotinous cones; and, the differential composition and richness of plant assemblages along gradients of moisture (Spies and Barnes 1985, Caspersen *et al.* 1999), nutrients (Whitney 1991, Diekmann and Falkengren-Grerup 1998, Hutchinson *et al.* 1999), light (Thomas *et al.* 1999), and geomorpholgy (Pastor *et al.* 1984, Host and Pregitzer 1992, Reich *et al.* 1997).

Dispersal: The importance of environmental heterogeneity and periodic disturbance to species coexistence has awakened interest in the potential contribution of dispersal to the spatial and temporal segregation of competing species. Whereas the former segregates competitors by creating conditions locally suitable to different species, the latter may segregate competitors by chance dispersal to empty sites followed by population expansion of the favored species. Current models suggest that segregation by dispersal may arise at two spatial scales: the micro-scale of the competing plant assemblage (Atkinson and Shorrocks 1981, Shmida and Ellner 1984, Ives and May 1985, Pacala 1986, Geritz *et al.* 1988), and, the scale at which environmental heterogeneity enables each species to compete for establishment sites (Comins and Noble 1985, Pacala and Tilman 1994, Lavorel *et al.* 1994, Lavorel and Chesson 1995, Hurtt and Pacala 1995, Holmes and Wilson 1998, Bolker and Pacala 1999, Loreau and Mouquet 1999).

Rather than interact with a number of individuals in a plant assemblage, and thereby experience the average density of the population at large, plants interact primarily with individuals that lie within

a crown or root diameter (Harper 1977, Pacala and Silander 1985, Venable and Brown 1993). In the forest understory, this means that the distance over which most plants competitively interact is on the order of decimetres to metres (Pacala and Silander 1987). When the dispersal distance of plants is short, siblings tend to aggregate into monospecific clumps and competing species become segregated spatially. Under these circumstances, individuals tend to compete more with their own kind than with others and thus create the conditions for coexistence (Atkinson and Shorrocks 1981, Shmida and Ellner 1984, Ives and May 1985, Pacala 1986, 1987). An interesting property of these models is that the spatial heterogeneity required for coexistence is generated by the plants themselves.

When the dispersal distance extends beyond the immediate vicinity of the maternal plant, a declining number of conspecific seeds land in close proximity to one another and an increasing number of seeds land in environments that are less favorable than the home patch. These processes confer a competitive advantage to established plant assemblages by limiting the number of seeds from neighboring patches and by limiting the capacity of invading seeds to form aggregations of their own kind. These dynamics are expected to favor coexistence by enabling each species to be dominant in site establishment at some time or place (Shmida and Ellner 1984, Comins and Noble 1985, Loreau and Mouquet 1999).

The stochastic arrival of a diminishing number of seeds is expected to facilitate this process by randomizing the composition of neighbors in competing plant assemblages and by leaving a certain proportion of sites vacant for colonization (Pacala 1986, Geritz *et al.* 1988, Clark *et al.* 1998, Ehrlen and Eriksson 2000). The former process increases the likelihood that seeds germinate next to weaker competitors, or to stronger competitors weakened by a less favorable setting, whereas the latter process enables inferior competitors to win favorable sites in the absence of more dominant but recruitment limited competitors (Hurtt and Pacala 1995).

The degree to which long-distance dispersal is required for the persistence of competitively inferior species remains controversial. Recent modeling studies suggest that a long dispersal reach, *per se*, is not as important as regeneration niche, fecundity, disturbance, storage effects, and the spatial

pattern of suitable sites (Lavorel *et al.* 1994, Lavorel and Chesson 1995, Holmes and Wilson 1998, Bolker and Pacala 1999). In general, dispersal beyond the immediate vicinity of the maternal plant is favored whenever the distribution of the superior competitor is strongly clustered and the invading species is able to establish in the intervening gaps. The required dispersal distance to achieve this need not be great if both species are resident in the same habitat. Short distance dispersal is apparently favored in all other situations, owing to the competitive advantage that accrues when offspring are clustered and close to hand (Holmes and Wilson 1998, Bolker and Pacala 1999). With spatial segregation and environmental heterogeneity, these studies suggest that a mixed strategy which strongly favors short distance dispersal may offer the greatest return in most habitats.

Local versus Regional Processes: The assumption that the diversity of species in a given setting can be explained solely by properties of the local environment, and by interactions among resident species, has come under increasing scrutiny in recent years (e.g., MacArthur and Wilson 1967, Ricklefs 1987, Taylor *et al.* 1990, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Caley and Schluter 1997, Cornell and Karlson 1997, Zobel 1997, Loreau and Mouquet 1999). Examination of processes that operate at larger spatial and temporal scales has revealed that the composition and richness of local assemblages may be influenced by historical processes such as time lags in plant response to climate change (Davis 1981a, 1986), alternative sequences of community development arising from chance colonization events (Drake 1991, Fastie 1995), establishment opportunities/ constraints arising from past disturbance (Motzkin *et al.* 1996, Abrams and Orwig 1996), extirpation by herbivory (Whitney 1984) or pathogens (Davis 1981b), and, by spatial processes such as dispersal (Holt 1993) and the scale of heterogeneity in the local environment (McLaughlin and Roughgarden 1993).

Recent studies investigating the relationship between local and regional species diversity have argued that the principal direction of control should be from regional to local (Cornell and Lawton1992, Eriksson 1993, Partel *et al.* 1996, Caley and Schluter 1997, Karlson and Cornell 1998). The principal reason for this is that in a variable environment biological interactions may not be sufficient to limit the number of species in the local assemblage. In the presence of dispersal, the richness of the local assemblage should reflect the number of species in the surrounding region that

are capable of establishing there. Empirical evidence from plant communities has been reported by Keddy 1981, Partel *et al.* 1996, Tilman 1997, Duncan *et al.* 1998, and Ehrlen and Eriksson 2000).

An alternative explanation for the positive correlation between local and regional richness observed in these studies is that the composition of plant assemblages is in fact constrained by local processes and that limits to regional richness are set by the number of distinct habitats, each supporting a saturated assemblage (Cornell and Lawton 1992). In the presence of migration, differences in the richness of local assemblages should reflect properties of the local environment rather than the number of species in the surrounding region.

Summary: Niche differentiation, competitive exclusion, slow dynamics, weak competitive interactions, differential resource availability, short-distance dispersal, recruitment limitation, and the consequences of periodic and chance events, are prominent elements in the vast number of individual hypotheses that have been advanced to explain observed differences in the composition and richness of plant assemblages. In a spatially and temporally variable environment, however, the synthesis for which we strive may well be pattern and scale dependent. If so, then a useful way forward is to clarify which of the alternative mechanisms apply to the pattern at hand and to what extent.

Study Objectives: The objectives of this chapter are the following: i) to identify the environmental variables that best explain observed differences in species richness in 10m x 10m quadrats; ii) to identify the plant attributes that best explain observed differences in species richness in 10m x 10m quadrats; and, iii) to compare the degree to which environmental and plant attributes explain observed differences in species richness in the understory of sampled forest patches.

4.2 Methods

4.2.1 Environmental Correlates of Species Richness

Environmental correlates of species richness were assessed in relation to edaphic, forest stand structure, human disturbance, environmental heterogeneity, and landscape, variables. Methods

related to the identification and evaluation of environmental correlates are presented in the following sections.

4.2.1.1Generalized Linear Regression Models

Analysis #1: Environmental correlates of species richness in 10m x 10m quadrats were identified by simple linear regression. The normality of residuals was evaluated by the Shapiro-Wilk W test (SAS Institute Inc. 1997): environmental and response variables were transformed (square root, ln, logit) where necessary to achieve, and/or maximize, normality. Pair-wise interactions among environmental variables were evaluated and all significant interactions ($p<0.05$) recorded. Analyses were performed in JMP, Version 3.2.2., SAS Institute.

Alternative combinations of variables that maximally explained the variance in observed species richness were identified through generalized linear regression (GLM) models that were fit manually by forward and backward selection. Separate models were fit for edaphic, forest stand structure, human disturbance, environmental heterogeneity, and, landscape, variables. Summary models were also developed to identify an overall set of environmental variables that maximally explained observed differences in species richness. Candidate models were evaluated in relation to Mallow's *Cp* statistic (Neter *et al.* 1996, Ryan 1997, Hocking 1996, Mathsoft Inc.1998) to ensure that only the most parsimonious models were retained for further analysis. Only significant, non-interacting, terms were retained in each model.

A "Best Model" was identified for each set of variables, based on the amount of explained variance (r^2 adjusted statistic). Alternative models were retained for further analysis in cases where the next best model represented a better fit in relation to the Shapiro-Wilk W test, or, where an entirely different set of variables explained virtually the same amount of variance.

The results of this analysis are presented in Table 4.1. Scatter plots of important correlates of species richness are presented in Figures 4.1, 4.2, 4.3, 4.4. Mean species richness for categorical variables is presented in Table 4.2.

4.2.1.2 Contribution of Forest Stand Structure

Analysis #1: The contribution of stand structure to species richness (Table 4.1) was examined further to clarify the cause and effect relationship among selected variables. Of particular interest was the degree to which "number of tree species", and, "number of live stems 0-4 cm dbh", were causal mechanisms of species richness. Non-parametric correlations (Spearman's Rho) with selected stand structure variables, soil moisture, available calcium, and human disturbance, were computed with a view to identifying more proximate correlates of available moisture, nutrients and light on the forest floor.

Variables included in this analysis were: species richness; percent live tree stems *Acer saccharum*; percent live tree stems wet-mesic, or wet, tree species (*Abies balsamea*, *Acer negundo*, *Acer saccharinum*, *Fraxinus nigra*, *Fraxinus pennsylvanica*, *Populus balsamifera*, *Thuja occidentalis*, *Ulmus occidentalis*); percent live tree stems shade intolerant or very shade intolerant tree species (*Acer negundo*, *Acer saccharinum*, *Betula papyrifera*, *Populus balsamifera*, *Populus grandidentata*, *Populus tremuloides*, *Robinia pseudoaccacia*); percent canopy closure; soil moisture class (1 = seasonally dry depressions, 2 = seasonally moist or wet depressions; available calcium (cmols/kg); and, human disturbance (1 = no disturbance apparent in quadrat, 2 = trails, canopy gaps due to logging, or, regenerating fields, present in quadrat).

Trees associated with wet-mesic or wet soils were identified with reference to Oldham *et al.* (1996), Maycock (1963), and, Nimerfro and Brand (1993). Trees classified as obligate or facultative wetland species (wetland affinity rating = -1, -2, -3, -4, or -5)(Oldham *et al.* 1996) were chosen as representative indicators of wet-mesic or wet soils in this study. Trees that achieved their maximum average importance value in southern Ontario on wet-mesic soils (Maycock (1963) were typically rated as "facultative" or "facultative upland" species by Oldham *et al.* (1996), when abundant on other soils, and were not used as indicators in this study (*Betula papyrifera*, *Carpinus caroliniana*, *Carya cordiformis*, *Fraxinus americana*, *Tilia americana*, *Quercus macrocarpa*). Shade intolerant, and very shade intolerant, trees were identified with reference to Baker (1949), Barnes and Wagner (1981) and Oldham *et al.* (1996). The shade tolerance ratings of Barnes and Wagner (1981) were

adopted for *Acer negundo*, *Acer saccharinum* (owing to uncertainties in the Baker's ratings) and *Prunus serotina* (owing to its relative shade tolerance when young); the shade tolerance ratings of Baker (1949) were used for all other species.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. Results are presented in Table 4.3.

4.2.1.3 Contribution of Soil Fertility

Analysis #1: The interaction between available calcium and sugar maple abundance (Table 4.1) was investigated further to clarify the contribution of soil fertility to observed differences in species richness. This analysis was restricted to undisturbed forest stands on Brunisolic and Luvisolic soils, overlying calcareous till, in order to standardize samples with respect to soil parent material, soil moisture and recent site disturbance. Soils with free calcium carbonate in the upper 15 cm of the soil profile (positive reaction to 0.1N HCl) were excluded from this analysis in order to standardize samples with respect to exchangeable calcium (see contrasting treatment in Analysis 2). This analysis was further restricted to quadrats with cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, trees) in order to standardize samples with respect to forest cover. N = 29 10m x10m quadrats in 7 forest patches.

The contribution of available calcium to species richness, and to sugar maple abundance (% stems >1 m *Acer saccharum*, # stems >1m *Acer saccharum*), was evaluated by simple linear regression. Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of this analysis are presented in Figure 4.5.

Analysis #2: The interaction between available calcium and sugar maple abundance was re-examined in undisturbed forest stands on Brunisolic soils in order to standardize samples for soil parent material (calcareous till), soil order (Orthic Melanic Brunisol) and soil series (Otonabee loam). The analysis was restricted to quadrats with cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, trees) in order to standardize samples with respect to forest cover. These stands (N = 17 quadrats in 3 forest patches) provided

the most uniform subset of samples in which to assess the response of sugar maple to differences in available calcium.

The contribution of available calcium to species richness, and to sugar maple abundance, was evaluated by simple linear regression. Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of this analysis are presented in Figure 4.6.

Analysis #3: Stand history, edaphic variables, and available light, were examined further to determine whether one or more of these factors may have contributed to observed differences in species richness, or sugar maple abundance, in stands evaluated in Analysis #1. Indicators of potential differences in stand history were: stand structure (% stems in 0-4 cm dbh, 4-10 cm dbh, 10-30 cm dbh, and >30 cm dbh, size class); % live stems shade intolerant, very shade intolerant, trees; and, % canopy closure. Indicators of potential differences in soil properties were: available calcium, soil pH_{water}, and % soil organic matter. Indicators of potential differences in available light were: % canopy closure; % taxa shade tolerant herbs (Nimerfro and Brand light rating 1, 2; Ellenberg light rating 1,2,3,4); and, % taxa shade intolerant herbs (Nimerfro and Brand light rating 4,5; Ellenberg light rating 6,7,8,9).

Differences among soil orders were evaluated by Wilcoxon rank sum tests. Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of this analysis are presented in Figures 4.7, 4.8, and 4.9.

4.2.1.4 Contribution of Patch Isolation and Patch Size

Analysis #1: The contribution of patch isolation and patch size to species richness was evaluated by simple and multiple linear regression. The independent contribution of patch isolation and patch size to species richness was evaluated by testing their interaction with edaphic, stand structure, and human disturbance variables. A significant interaction with one or more variables was taken as evidence that patch isolation, or patch size, *per se*, did not contribute to species richness.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of this analysis are presented in Table 4.1.

4.2.1.5 Contribution of Microhabitats

Analysis #1: The contribution of microhabitats to species richness was evaluated at the quadrat, forest patch, and landscape spatial scale. The objective was to determine the degree to which a given microhabitat contained species that did not occur elsewhere in the reference area. Observed differences in species richness ["total # species in quadrat or patch" versus "total # species in quadrat or patch - # species unique to microhabitat"] were evaluated by paired t-test, when the distribution of differences was normal, and by Wilcoxon signed rank sum test, otherwise. A minium number of six elements was required for the latter analysis (Sokal and Rohlf 1995, p.444). Quadrats or patches that contained only one microhabitat were excluded from the analysis.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of this analysis are presented in Tables 4.4, 4.5 and 4.6.

Analysis #2: The proportion of the study area occupied by habitats of contrasting moisture and canopy closure states was determined in order to evaluate the contribution of sampled area to the relative importance of moisture and light in models of species richness.

The results of this analysis are presented in Table 4.7.

4.2.2 Plant Trait Correlates of Species Richness

Plant trait correlates of species richness were assessed in relation to mode of dispersal, life history, provenance, life form, habitat affinity, shade tolerance, and moisture affinity. Methods related to the identification and evaluation of plant trait correlates are presented in the following analysis.

Analysis #1. Plant trait correlates of species richness in 10m x 10m quadrats were identified by simple linear regression. The normality of residuals was evaluated by the Shapiro-Wilk W test (SAS

Institute Inc. 1997); plant trait and response variables were transformed (square root, ln, logit) where necessary to achieve, and/or maximize, normality. Pair-wise interactions among plant trait variables were evaluated and all significant interactions ($p<0.05$) noted. Analyses were performed in JMP, Version 3.2.2., SAS Institute.

Alternative combinations of variables that maximally explained the variance in observed species richness were identified through generalized linear regression (GLM) models that were fit manually by forward and backward selection. Separate models were fit for mode of dispersal, life history, provenance, life form, habitat affinity, shade tolerance, and moisture tolerance, variables. Summary models were also developed to identify an overall set of plant traits that maximally explained observed differences in species richness. Candidate models were evaluated in relation to Mallow's *Cp* statistic (Neter *et al.* 1996, Ryan 1997, Hocking 1996, Mathsoft Inc. 1998) to ensure that only the most parsimonious models were retained for further analysis. Only significant, non-interacting, terms were retained in each model.

A "Best Model" was identified for each set of variables, based on the amount of explained variance (r^2 adjusted) and normality of residuals. An additional model was identified for modes of dispersal to permit a comparison among life forms.

The results of this analysis are presented in Table 4.8. Scatter plots of selected dispersal correlates of species richness are presented in Figures 4.10 and 4.11.

4.2.3 Comparison of Alternative Models of Species Richness

Analysis #1: Alternative models of species richness, composed of environmental variables, dispersal variables, and both environmental and dispersal variables, were compared within and among functional groupings, in relation to four statistical properties: F-statistic, r^2adjusted value, mean square error, and, normality of residuals (Shapiro-Wilk W test). Interactions among explanatory variables prevented the use of a single evaluation criterion, such as Mallow's Cp statistic or the $PRESS_p$ statistic (Neter *et al.* 1996), to identify an overall best model. Models with a high p<W

value and a low mean square error were considered superior to models with a low p<W value and a high mean square error. Superior models with a higher r^2adjusted value were considered to be more informative than superior models with a lower r^2adjusted value. Models that could not otherwise be differentiated were considered to be comparable models for the purpose of explaining observed differences in species richness.

One outlier, quadrat #160, was removed from each model (Cooke's D statistic = 0.226). Species richness in this quadrat was sharply reduced by seasonal standing water that covered more than 85% of the forest floor during the spring and summer survey, resulting in a strongly outlying data point in models with dispersal variables.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results of the analysis are summarized in Tables 4.9 and 4.11.

Analysis #2: A graphical method (personal communication, Dr. Roger Hansell, Institute for Environmental Studies, University of Toronto) was subsequently employed to reveal the degree to which alternative models explained similar or dissimilar portions of sample space. Explanatory variables for each regression model were submitted to detrended correspondence analysis (DCA) (ter Braak 1987), and, the resulting "species" scores used to construct a polygon in ordination space. The ordination space enclosed by each polygon was interpreted to represent the portion of sample space maximally explained by each model. Regression models that overlapped in ordination space were considered less distinctive than models that did not.

The detrended correspondence analysis was performed in CANOCO, Version 3.12 (ter Braak 1991). The polygons were constructed in S-Plus, Version 4.5 (Mathsoft Inc. 1998). Representative results are presented in Figures 4.12 and 4.13. Summaries are presented in Tables 4.10 and 4.11.

4.2.4 Contribution of Phylogeny

Analysis #1: The contribution of phylogeny to explanations of variance in species richness (Table

4.8) was evaluated indirectly by refitting the regression models at more inclusive taxonomic ranks. Detection of a significant pair-wise interaction between terms was taken as indirect evidence of a phylogenetic contribution to observed differences in species richness.

The response variable in a given regression model was the number of species, genera, families, or orders, in a given 10m x 10m quadrat. The predictor variable for a plant trait was the number of species, genera, families, or orders with the trait of interest in a given 10m x 10m quadrat.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results are summarized in Table 4.12.

Analysis #2: The contribution of phylogeny to observed interactions among selected variables at more inclusive taxonomic ranks was examined further by determining the loss of degrees of freedom associated with evaluating selected plant traits at more inclusive ranks. The traits addressed in this analysis were moisture affinity, shade tolerance, and mode of dispersal.

Analyses were performed in JMP, Version 3.2.2., SAS Institute. The results are summarized in Table 4.13.

4.3 Results

4.3.1 Environmental Correlates of Species Richness

4.3.1.1 Generalized Linear Regression Models

Environmental correlates of species richness in 10m x 10m quadrats are reported in Table 4.1 in relation to the following groupings: edaphic variables, forest stand structure, human disturbance, environmental heterogeneity, landscape variables, and, overall model. Scatter plots of the most influential variables are presented in Figures 4.1, 4.2, 4.3, and 4.4; the mean species richness of categorical variables is presented in Table 4.2.

Table 4.1. Environmental correlates of species richness in 10m x 10m quadrats. Generalized linear regression (GLM) models, by row. See notes for interactions among predictor variables, and, for partial F statistics of selected models. See text for criteria for selection of "best" models. Legend: co=calcareous outwash; lac=lacustrine; ct=calcareous till; gf=glacio-fluvial; gb=gleyed brunsisol; gl=gleyed luvisol; b=brunisol; l=luvisol; g=gleysol; CT1= oak, no sugar maple, no red or white oak; CT2=sugar maple + oak; CT3=sugar maple; CT4=sugar maple + wet-mesic or wet species; CT5=wet mesic or wet species, no sugar maple, no red or white oak; ln p/q = ln [(proportion)÷(1-proportion)].

Model	Response Variable	F	p-Value	r^2 adj.	$p<W^1$	relationship
1. EDAPHIC VARIABLES						
soil parent material[3,5,8,10,16,24,26,31,35]	sqrt # spp	18.99	0.0001	0.2203	0.29	co>lac>ct>gf
soil order[2,4,10,15,16,33,34,35]	ln sqrt # spp	17.13	0.0001	0.2525	0.18	gb>gl>b>l>g
soil moisture[3,5,15,21,24,27,28,35]	sqrt # spp	32.32	0.0001	0.2469	0.58	wet>dry
ln % soil organic matter[2,4,10,13,16,18,19,20,29]	ln # spp	11.52	0.0008	0.0522	0.26	positive
soil pH[2,3,10,11,12,14,16,18,19,20,21]	sqrt # spp	28.91	0.0001	0.1403	0.06	positive
available calcium[2,10,14,18,19,24,27]	sqrt # spp	5.52	0.0194	0.0260	0.15	positive
Best Model: soil moisture + soil parent material[9]	sqrt # spp	29.36	0.0001	0.3557	0.71	
2. FOREST STAND STRUCTURE						
forest cover type[2,5,8,13,14,15,24,26,31,33,35]	sqrt # spp	19.25	0.0001	0.2765	0.99	CT5>CT1>CT4> CT3>CT2
% canopy closure (ln p/q)[3,8,16,21,35]	sqrt # spp	34.78	0.0001	0.1503	0.05	negative
ln # tree species (>1m)[8,14,15,27,35]	ln sqrt # spp	71.00	0.0001	0.2682	0.65	positive
ln # wet-mesic or wet tree species[4,5,8,10,16,17,25]	sqrt # spp	30.07	0.0001	0.2235	0.50	positive

Table 4.1. Environmental correlates of species richness (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
sqrt # live tree stems 0-4 cm dbh[8,10,12,15,18,24,27,29,35]	sqrt # spp	47.65	0.0001	0.1963	0.28	positive
sqrt # live tree stems 4-10 cm dbh[3,4,8,10,12,14,18,19,24,31,34]	sqrt # spp	1.49	0.2237	0.0026	0.07	positive
ln # live tree stems 10-30 cm dbh[2,3,5,11,13,20,29]	ln sqrt # spp	0.28	0.5990	0.0042	0.04	-
# live tree stems >30 cm dbh[13,33]	sqrt # spp	7.37	0.0072	0.0323	0.07	negative
sqrt % stems sugar maple[5,8,14,15,27,31,35]	sqrt # spp	66.55	0.0001	0.2555	0.28	negative
sqrt % stems sugar maple 0-4cm dbh[5,8,20,21,27,29,33,35]	sqrt # spp	66.01	0.0001	0.2539	0.74	negative
sqrt % stems sugar maple 4-10 cm dbh[5,8,15,16,20,24,29,35]	sqrt # spp	20.38	0.0001	0.0991	0.11	negative
% stems sugar maple 10-30 cm dbh[4,8,11,16,35]	sqrt # spp	19.14	0.0001	0.0959	0.07	negative
Best Model 1: ln # tree species (>1m) + canopy closure (ln p/q) + forest cover type[22]	sqrt # spp	39.67	0.0001	0.5485	0.68	
Best Model 2: sqrt # stems 0-4 cm dbh + canopy closure (ln p/q) + forest cover type[23]	sqrt # spp	32.52	0.0001	0.4975	0.92	
3. HUMAN DISTURBANCE						
open trail[2,10,14,15,20,25,27,29,33]	sqrt # spp	19.57	0.0001	0.0886	0.28	present > absent
closed trail[4,13,24,26,29]	sqrt # spp	9.59	0.0022	0.0431	0.06	present > absent
open regenerating field[2,10,25,27,29]	sqrt # spp	17.41	0.0001	0.0791	0.03	present > absent
open canopy gap[4,12,14,18,19,24,26,31]	sqrt # spp	9.21	0.0027	0.0412	0.04	present > absent

Table 4.1. Environmental correlates of species richness (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
closed canopy gap[4,29]	sqrt # spp	0.04	0.8371	0.0050	0.02	present > absent
disturbed microhabitats[5,14,16,20,24,25,26,28,31,34]	sqrt # spp	19.67	0.0001	0.0890	0.04	present > absent
Best Model: open trail + open regenerating field[30]	sqrt # spp	15.03	0.0001	0.1280	0.20	
4. ENVIRONMENTAL HETEROGENEITY						
# microhabitats[2,10,15,18,19,27,29]	ln sqrt # spp	11.84	0.0007	0.0537	0.05	positive
5. LANDSCAPE VARIABLES[32]						
% forest cover (within 5km x 5km square centered on study site)[3,10,17,18,19,24,34]	sqrt # spp	14.44	0.0002	0.0658	0.14	negative
ln mean distance to nearest forest patch (in 45° arcs)[3,10,15,29,33,35]	ln sqrt # spp	1.01	0.3169	0.0000	0.01	negative
sqrt patch area[2,3,4,10,11,12,14,18,19,20,21,34]	sqrt # spp	4.67	0.0319	0.0189	0.12	negative
Best model: % forest cover	sqrt # spp	14.44	0.0002	0.0658	0.14	negative
6. OVERALL MODEL: ENVIRONMENTAL CORRELATES						
Best Model 1: ln # tree species (>1m) + canopy closure (ln p/q) + forest cover type + open microhabitats[36]	sqrt # spp	39.04	0.0001	0.5823	0.66	
Best Model 2: canopy closure (ln p/q) + sqrt # stems 0-4 cm dbh +moisture class + soil parent material[37]	sqrt # spp	34.10	0.0001	0.5495	0.69	

Notes:

1. Shapiro-Wilk W test for normality of residuals (residuals normal when $p \geq 0.05$).

Notes (cont'd).

2. Significant interaction with soil parent material.
3. Significant interaction with soil order.
4. Significant interaction with soil moisture.
5. Significant interaction with ln % soil organic matter.
6. Significant interaction with available calcium.
7. 2^0 polynomial fit significant; relationship curvilinear, mode = 30% soil organic matter.
8. Significant interaction with soil pH.
9. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.0001$. Partial F statistics: soil moisture class: F=20.75; soil parent material: F=11.63.
10. Significant interaction with forest cover type.
11. Significant interaction with % canopy closure (ln p/q).
12. Significant interaction with ln # tree species (>1m).
13. Significant interaction with ln # wet-mesic and wet tree species (>1m).
14. Significant interaction with sqrt # live tree stems 0-4 cm dbh.
15. Significant interaction with sqrt # live tree stems 4-10 cm dbh.
16. Significant interaction with ln # live tree stems 10-30 cm dbh.
17. Significant interaction with # tree stems >30 cm dbh.
18. Significant interaction with sqrt % stems sugar maple >1m
19. Significant interaction with sqrt % stems sugar maple 0-4 cm dbh
20. Significant interaction with sqrt % stems sugar maple 4-10 cm dbh
21. Significant interaction with % stems sugar maple 10-30 cm dbh
22. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.03$. Partial F statistics: sqrt # stems 0-4 cm dbh: F=34.21; percent canopy closure (ln p/q): F=31.98; moisture class: F=22.52; soil parent material: F=7.77; disturbance, *sensu lato* (open or closed trails, gaps, regenerating fields: F=4.71.
23. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.0001$. Partial F statistics: ln # tree species (>1m): F=75.32; percent canopy closure (ln p/q): F=34.74; forest cover type: F=19.12.
24. Significant interaction with open trails.
25. Significant interaction with closed trails.
26. Significant interaction with open regenerating fields.
27. Significant interaction with open canopy gaps.
28. Significant interaction with closed canopy gaps.
29. Significant interaction with disturbed microhabitats (cut or snag gaps, lanes, regenerating fields - closed or open canopy).

Notes (cont'd).

30. Variables in model presented in descending order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.002$. Partial F statistics: open trail: F=11.67; open regenerating field: F=9.60.
31. Significant interaction with # microhabitats.
32. N=24 patches; interactions based on mean # elements in a given patch.
33. Significant interaction with % forest cover.
34. Significant interaction with ln mean distance to nearest forest patch (in 45^0 arcs)
35. Significant interaction with sqrt patch area.
36. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.0001$. Partial F statistics: ln # tree species (>1m): F=75.88; percent canopy closure (ln p/q): F=19.00; forest cover type: F=16.93; open microhabitats (cut or snag gap, lane, regenerating field, seep, riparian meadow, riparian thicket, riparian marsh - all features have clear view to sky): F=15.98.
37. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.0001$. Partial F statistics: ln (p/q) canopy closure: F=43.31; sqrt # tree stems 0-4 cm dbh: F=31.68; moisture class: F=22.80; soil parent material: F=8.81.

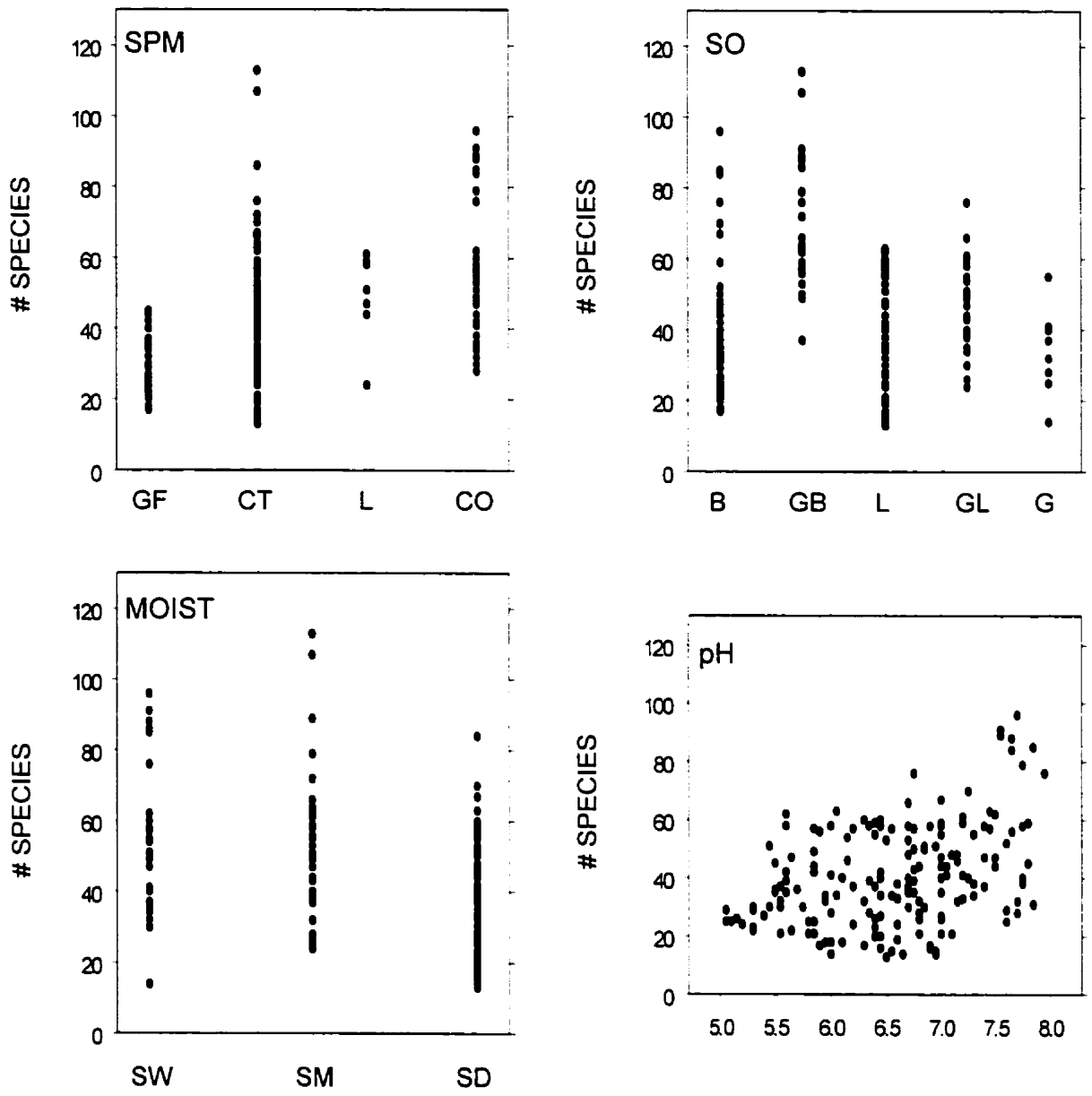

Figure 4.1. Scatter plots of selected correlates of species richness in 10m x 10m quadrats I. Legend: SPM = soil parent material: GF = glacio-fluvial, CT = calcareous till, L = lacustrine, CO = calcareous till; SO = soil order: G = gleysol, B = brunisol, GL = gleyed luvisol, GB = gleyed luvisol; MOIST = soil moisture: SD = seasonally dry depressions, SM = seasonally moist depressions, SW = seasonally wet depressions: pH = soil pH_{water} upper 15 cm soil profile.

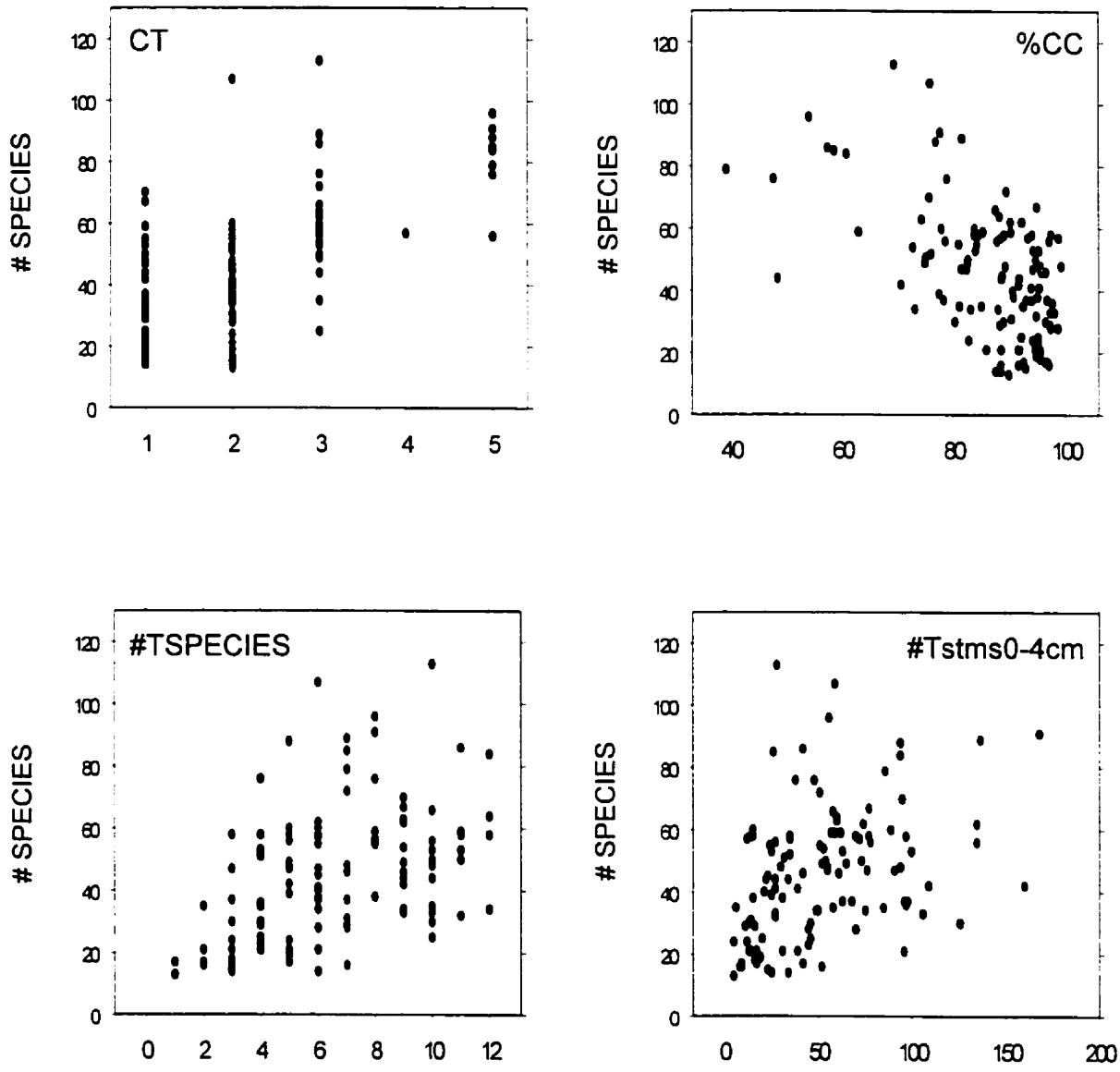

Figure 4.2. Scatter plots of selected correlates of species richness in 10m x 10m quadrats II. Legend: CT = forest cover type: 1 = sugar maple + red, white oak; 2 = sugar maple, no oak, no wet-mesic or wet species; 3 = sugar maple + wet-mesic or wet species, 4 = oak, no sugar maple (1 quadrat), 5 = wet-mesic or wet species, no sugar maple, no oak; %CC = % canopy closure; #TSPECIES = # tree species (>1m); #Tstms0-4cm = # tree stems 0-4 cm dbh.

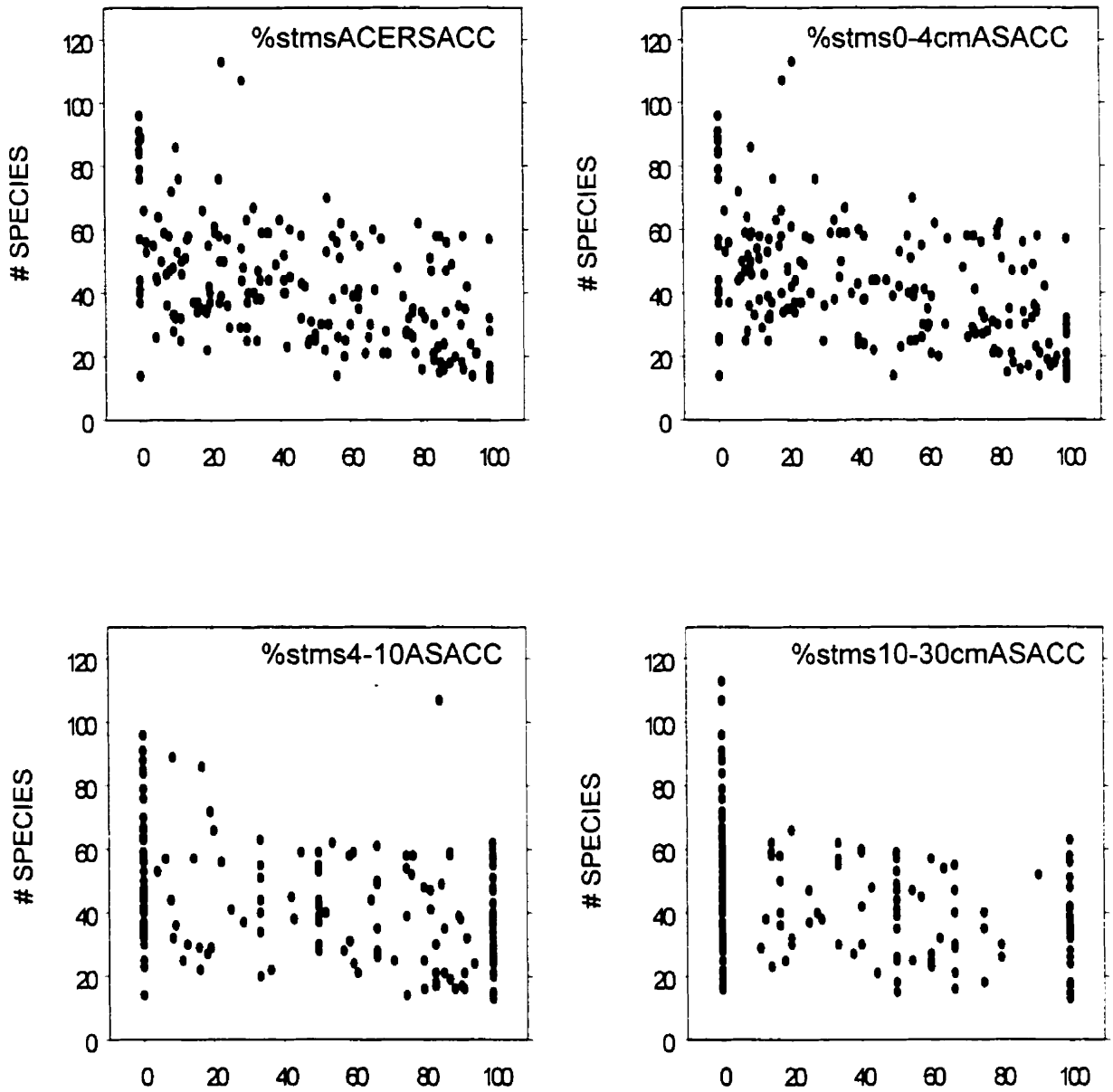

Figure 4.3. Scatter plots of selected correlates of species richness in 10m x 10m quadrats III. Legend: %stmsACERSACC = % live tree stms (> 1 m) in 10m x 10m quadrat *Acer saccharum*; %stms0-4cmASACC = % live tree stems 0-4 cm dbh in 10m x 10m quadrat *Acer saccharum*; %stms4-10cmASACC = % live tree stems 4-10 cm dbh in 10m x 10m quadrat *Acer saccharum*; %stms10-30cmASACC = % live tree stems 10-30 cm dbh in 10m x 10m quadrat *Acer saccharum*.

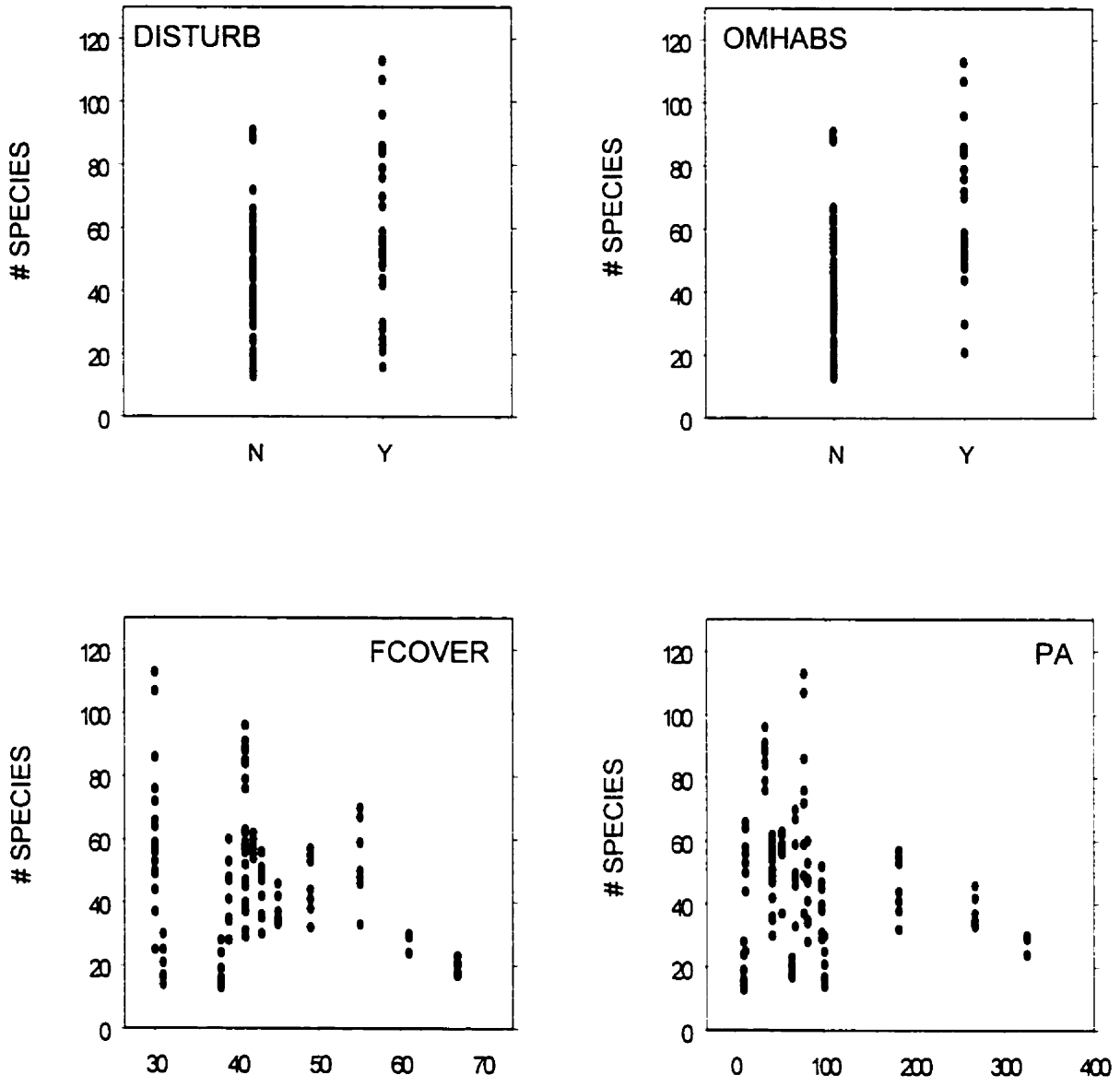

Figure 4.4. Scatter plots of selected correlates of species richness in 10m x 10m quadrats IV. Legend: DISTURB = disturbance absent/present (open or closed trails, canopy gaps, regenerating fields); OMHABS = open microhabitats absent/present (cut or snag canopy gaps, trails, regenerating fields, seeps, riparian meadow, riparian thicket, riparian marsh); FCOVER = % forest cover within a 5km x 5km square, centered on study site; PA = patch area (ha).

Table 4.2. Species richness (10m x 10m quadrats) of soil parent materials, soil orders, soil moisture classes, forest cover types, and disturbance classes. Wilcoxon rank sum tests, by attribute: ** $p<0.01$, **** $p<0.0001$. Highest mean value in attribute group in bold.

Attribute	# Quadrats	# Species Study Area	Mean # Species
1. SOIL PARENT MATERIAL****			
glacio-fluvial	40	116	27.8
calcareous till	104	334	42.6
lacustrine	8	104	48.5
calcareous outwash	40	307	**55.2**
2. SOIL ORDER****			
brunisol	70	280	36.6
gleyed brunisol	26	253	**67.0**
luvisol	57	258	36.6
gleyed luvisol	31	198	47.6
gleysol	8	92	34.0
3. SOIL MOISTURE CLASS****			
seasonally dry depressions	118	337	34.8
seasonally moist depressions	42	241	53.2
seasonally wet depressions	32	159	**56.2**
4. FOREST COVER TYPE****			
red oak, no sugar maple	1	57	57
sugar maple + red oak	54	188	33.6
sugar maple	74	305	36.4
sugar maple + wet-mesic/wet	50	287	54.9
wet-mesic + wet, no sugar maple	13	333	**63.9**
5. DISTURBANCE CLASS**			
human disturbance present (closed or open canopy gaps, lanes, regenerating fields)	61	345	**49.2**
human disturbance absent	131	355	39.2

i) Edaphic Variables

Edaphic variables that maximally explained observed differences in species richness in 10m x 10m quadrats were soil order (r^2adj.=0.253), soil moisture (r^2adj.=0.247), and soil parent material (r^2adj.=0.220) (Table 4.1). Significant, but less informative variables, were soil pH_{water} (r^2adj.=0.140), and, ln % soil organic matter (r^2adj.=0.052). Available calcium (free calcium carbonate + exchangeable calcium) was a significant but weak predictor of overall species richness (r^2adj.=0.026).

Quadrats on calcareous outwash parent materials (mean richness = 55.2 species) were approximately twice as rich in species as quadrats on glacio-fluvial parent materials (mean richness = 27.8 species) (Table 4.2). Quadrats on lacustrine parent materials (mean richness = 48.5 species) were more species rich than quadrats on calcareous till (mean richness = 42.6 species). The latter contrast, however, was not significant (Tukey-Kramer HSD test).

Quadrats on gleyed Brunisolic soils (mean richness = 67.0 species) were more species rich than quadrats on gleyed Luvisolic soils (mean richness = 47.6 species), and far more species rich than quadrats on Brunisolic soils (mean richness = 36.6 species), Luvisolic soils (mean richness = 36.6 species), or Gleysolic soils (mean richness = 34.0 species) (Table 4.2).

Quadrats with seasonally moist depressions (mean richness = 56.2 species) were marginally more species rich than quadrats with seasonally wet depressions (mean richness = 53.2 species), and significantly more species rich than quadrats with seasonally dry depressions (mean richness = 34.8 species)(Table 4.2)(Tukey-Kramer HSD test).

Species richness was positively correlated with percent soil organic matter, soil pH, and available calcium.

Soil moisture and soil parent material collectively explained 35.6% of the variance in species richness in 10m x 10m quadrats (Table 4.1).

Pair-wise interactions among edaphic variables (superscript 2-6), and with stand structure variables (superscript 10-21), were common (Table 4.1). Less common were interactions with human disturbance (superscript 24-29) and landscape variables (superscript 33-35).

ii) Forest Stand Structure Variables

Stand structure variables that maximally explained differences in species richness in 10m x10m quadrats were forest cover type (r^2adj.=0.277), # tree species (r^2adj.=0.268), % stems sugar maple (r^2adj.=0.256), % stems sugar maple 0-4 cm dbh (r^2adj.=0.254), # wet-mesic, wet, tree species (r^2adj.=0.224), and, # live tree stems 0-4 cm dbh (r^2adj.=0.196) (Table 4.1, variables variously transformed). Significant, but less informative, stand structure variables were % canopy closure (r^2adj.=0.150), % stems sugar maple 4-10 cm dbh (r^2adj.=0.099), % stems sugar maple 10-30 cm dbh (r^2adj.=0.096), and, # live tree stems >30 cm dbh (r^2adj.=0.032) (variables variously transformed). The number of live tree stems in the 4-10 cm dbh, and 10-30 cm dbh, size class were non-significant predictors of species richness.

Quadrats composed of wet-mesic or wet tree species (mean richness = 63.9 species), or composed of sugar maple and wet-mesic or wet tree species (mean richness = 54.9 species), were significantly more species rich than quadrats composed of sugar maple (no wet-mesic, wet, trees; no red or white oak) (mean richness = 36.4 species) or composed of sugar maple and red or white oak (mean richness = 33.6 species) (Table 4.2) (Tukey-Kramer HSD test).

Species richness was positively correlated with the number of tree species; the number of wet-mesic, wet, trees; the number of live stems 0-4 cm dbh; and, the number of live stems 4-10 cm dbh. Species richness was negatively correlated with the number of live stems >30 cm dbh; the percent stems sugar maple; the percent stems sugar maple 0-4 cm dbh; the percent stems sugar maple 4-10 cm dbh; and, the percent stems sugar maple 10-30 cm dbh.

The number of live tree species (>1m), degree of canopy closure, and type of forest cover, collectively explained 54.9 % of the variance in species richness in 10m x 10m quadrats (Table 4.1). The number of tree stems 0-4 cm dbh, degree of canopy closure, and type of forest cover type

collectively explained 49.8% of the variance in species richness. The latter model achieves a better statistical fit ($p<W = 0.92$ vs $p<W = 0.68$) and thus constitutes the "best" set of explanatory variables for this set of environmental variables.

Pair-wise interactions among stand structure variables (superscript 10-21), and with edaphic variables (superscript 2-6), were common (Table 4.1). Less common were interactions with human disturbance (superscript 24-29) and with landscape variables (superscript 33-35). Stand structure variables that interacted less frequently than other variables were # live tree stems >30 cm dbh, % canopy closure, # tree species (>1m), and, % stems 10-30 cm dbh.

iii) Human Disturbance

The disturbance variables that maximally explained differences in species richness in 10m x 10m quadrats were disturbed microhabitats (present/absent) (r^2adj.=0.089), open trails (r^2adj.=0.089), and open regenerating fields (r^2adj.=0.079). Significant, but less informative, variables were closed trails (r^2adj.=0.043) and open canopy gaps (r^2adj.=0.041) (Table 4.1). Closed canopy gaps did not explain observed differences in species richness.

Quadrats with human disturbance (closed or open canopy gaps, trails, regenerating fields) were significantly more species rich than quadrats with no apparent disturbance (mean richness = 49.2 species versus 39.2 species) (Table 4.2).

Open trails and open regenerating fields collectively explained 12.8% of the variance in species richness in 10m x10m quadrats (Table 4.1).

Pair-wise interactions among disturbance variables (superscript 24-29), and with edaphic variables (superscript 2-6), and with stand structure variables (superscript 10-21), were common (Table 4.1). Open conditions interacted more frequently with other environmental variables than did closed conditions.

iv) Environmental Heterogeneity

The number of microhabitats recorded in a given quadrat explained 5.4% of the variance in species richness in 10m x 10m quadrats (Table 4.1).

Pair-wise interactions occurred with soil parent material (superscript 2), selected stand structure variables (superscript 10-24), and selected disturbance variables (superscript 24-29)(Table 4.1).

v) Landscape Variables

The variables that maximally explained differences in species richness in 10m x 10m quadrats were percent forest cover in the surrounding landscape (r^2adj.=0.066), and, patch area (r^2adj.=0.019) (Table 4.1). The mean distance to the nearest forest patch (in 45^0 arcs) did not explain observed differences in species richness.

Species richness was positively correlated with the mean distance to the nearest forest patch (in 45^0 arcs), and, negatively correlated with the percent forest cover in the surrounding landscape, and, with patch area.

Pair-wise interactions occurred with soil parent material (superscript 2), soil order (superscript 3), soil moisture (superscript 4), selected stand structure variables (superscript 10-21), selected disturbance variables (superscript 24-29), and landscape variables (superscript 33-35).

vi) Overall Model

The combination of environmental variables that maximally explained differences in species richness in 10m x10m quadrats were the number of tree species (>1m), percent canopy closure, forest cover type, and open microhabitats (cut or snag gap, lane, regenerating field, seep, riparian meadow, riparian thicket, riparian marsh) (r^2adj.=0.582) (Table 4.1). An alternative model composed of percent canopy closure, number stems 0-4 cm dbh, soil moisture class, and soil parent material, was equally successful in explaining observed differences in species richness (r^2adj.=0.5495).

4.3.1.2 Contribution of Forest Structure

The contribution of stand structure to species richness (Table 4.1) was examined further to clarify the cause and effect relationship among selected variables. Of particular interest was the degree to which "number of tree species", and "number of live stems 0-4 cm dbh", were causal mechanisms of species richness. Non-parametric correlations (Spearman's Rho) with selected stand structure variables, soil moisture, available calcium, and human disturbance were computed with a view to revealing more proximate correlates of species richness (Table 4.3).

The number of tree species in a given 10m x 10m quadrat was negatively correlated with the percent stems that were sugar maple ($p<0.0001$), and, positively correlated with the percent stems that were wet-mesic, wet, trees ($p<0.0001$), or, shade intolerant, very shade intolerant, trees ($p<0.0001$)(Table 4.3). The number of tree species was not correlated with recent human disturbance ($p=0.95$) or with percent canopy closure ($p=0.27$).

The percent stems sugar maple in a given 10m x 10m quadrat was negatively correlated with seasonally moist or wet depressions on the forest floor ($p<0.0001$) and with the percentage of stems that were wet-mesic, wet trees ($p<0.0001$), or, shade intolerant, very shade intolerant, trees ($p<0.0001$) (Table 4.3). Sugar maple abundance was negatively correlated with available calcium ($p=0.0049$), owing to the strong positive correlation between available calcium and percent soil organic matter. Sugar maple abundance was positively correlated with percent canopy closure ($p=0.0029$) and weakly correlated with the absence of the human disturbance ($p=0.0655$).

Taken together, these results reveal that the number of tree species in given quadrat increased in the presence of seasonally moist or wet soils and in conditions that favored the establishment of shade intolerant and very shade intolerant trees, and, declined in the presence of sugar maple. This suggests that the number of tree species in a given quadrat is a complex variable that accounts for differences in soil moisture, stand history, and available light. Tree species number is thus a correlate of species richness and not its cause.

Table 4.3. Selected correlations involving # tree species, % stems sugar maple, and, # tree stems 0-4 cm dbh.

Variables		Correlation	
X	Y	Spearman Rho	Prob > |Rho|
# tree species	# species (all life forms)	0.5191	<0.0001
# tree species	% stems sugar maple	-0.5937	<0.0001
# tree species	% stems wet-mesic, wet, tree species	0.4430	<0.0001
# tree species	% stems shade intolerant, very shade intolerant, tree species	0.3220	<0.0001
# tree species	moisture class (1=dry, 2=moist,wet)	0.1382	0.0562
# tree species	% canopy closure	-0.0804	0.2677
# tree species	human disturbance (1=no, 2=yes)	-0.0044	0.9521
% stems sugar maple	# species (all life forms)	-0.4857	<0.0001
% stems sugar maple	# tree species	-0.6184	<0.0001
% stems sugar maple	% stems wet-mesic, wet tree species	-0.4521	<0.0001
% stems sugar maple	% stems shade intolerant, very shade intolerant, tree species	-0.3709	<0.0001
% stems sugar maple	moisture class (1=dry, 2=moist,wet)	-0.3512	<0.0001
% stems sugar maple	% canopy closure	0.2142	0.0029
% stems sugar maple	calcium (cmol/kg)	-0.2137	0.0049

Table 4.3. Selected correlations involving # tree species, % stems sugar maple, and, # tree stems 0-4 cm dbh (cont'd).

Variables		Correlation	
X	Y	Spearman Rho	Prob > |Rho|
% stems sugar maple	human disturbance (1=no, 2=yes)	-0.1332	0.0655
# tree stems 0-4 cm dbh	# species (all life forms)	0.4646	<0.0001
# tree stems 0-4 cm dbh	# tree species	0.5287	<0.0001
# tree stems 0-4 cm dbh	% stems sugar maple	-0.2503	0.0005
# tree stems 0-4 cm dbh	% stems wet mesic, wet, tree species	0.2659	0.0002
# tree stems 0-4 cm dbh	% stems shade intolerant, very shade intolerant	0.0256	0.7250
# tree stems 0-4 cm dbh	moisture class (1=dry, 2=moist,wet)	0.1602	0.0265
# tree stems 0-4 cm dbh	human disturbance (1=no, 2=yes)	0.1389	0.0546
# tree stems 0-4 cm dbh	% canopy closure	-0.0592	0.4150

The number of live tree stems 0-4 cm dbh was positively correlated with the number of tree species ($p<0.0001$) and with the percentage of stems that were wet-mesic, wet, trees ($p=0.0002$) (Table 4.3). The number of live tree stems in this size class was weakly correlated with recent human disturbance ($p=0.0546$) and negatively correlated with the percentage of stems that were sugar maple ($p=0.0005$). Stem number was neither correlated with percent canopy closure ($p=0.4150$) nor with the percentage of stems that were shade tolerant or very shade tolerant ($p=0.7250$).

Taken together, these results reveal the number of live tree stems, 0-4 cm dbh, was more strongly influenced by the number of tree species, the percentage of stems that were wet-mesic, wet, trees, and, the percentage of stems that were sugar maple, than by recent and past stand disturbance. In general, the number of stems in this size class increased with increasing soil moisture and declined with increasing sugar maple abundance. This suggests that the number of live tree stems, 0-4 cm dbh, is a complex variable that primarily accounts for differences in soil moisture and available light. The number of tree stems, 0-4 cm dbh, is thus a correlate of species richness and not its cause.

The capacity of each variable to explain observed differences in species richness, therefore, is a function of their correlation with differences in soil moisture and available light. The variance in richness explained by the number of tree species also reflects the influence of past disturbance events and thus explains marginally more variance in species richness than the number of live tree stems 0-4 cm dbh (Table 4.1).

4.3.1.3 Contribution of Soil Fertility

The interaction between available calcium and sugar maple abundance (Table 4.1) was investigated further to clarify the contribution of soil fertility to observed differences in species richness. This analysis was conducted in two contrasting settings.

The first setting was restricted to forest stands on Brunisolic and Luvisolic soils, in view of reported differences in calcium availability in these soils (Hoffman and Acton1974, Gillespie and Acton 1981). Soils with free calcium carbonate in the upper 15 cm of the soil profile (positive reaction

to 0.1N HCl) were excluded from this analysis in order to standardize samples with respect to exchangeable calcium. Exchangeable calcium in these soils ranged from 0.7 to 13.1 cmol/kg.

The results of this analysis are summarized in Figure 4.5. Differences in sugar maple abundance explained 63.2 % of the variance in species richness in 10m x 10m quadrats, when expressed as the percentage of live stems (>1m) that were sugar maple, and 50.0 % of variance in species richness in 10m x10m quadrats, when expressed as the number of live stems (>1m) that were sugar maple.

Exchangeable calcium, in turn, explained 11.1 % of the variance in sugar maple abundance (p=0.054), when expressed as the percentage of live stems (>1m) sugar maple, and 2.9 % of the variance in sugar maple abundance (p=0.200), when expressed as the number of live stems sugar maple. Exchangeable calcium, *sensu stricto*, explained 6.6 % of the variance in species richness (p=0.109) on these soils. Exchangeable calcium is a significant predictor of sugar maple abundance for selected size classes, however, and explains 13% to 19% of the variance in the percentage of live stems (> 1m) sugar maple in the 0-4 cm, 4-10 cm, and 10-30 cm, dbh size class (Figure 2.7).

The second setting was restricted to forest stands on Brunisolic soils in order to standardize samples for soil parent material (calcareous till), soil order (Orthic Melanic Brunisol), soil series (Otonabee loam), soil moisture (mesic), forest composition (Cover Type 2, 3), and recent site disturbance (no trails, canopy gaps, regenerating fields). Soils with free calcium carbonate in the upper 15 cm of the soil profile were included in the analysis in order to standardize samples for available calcium (free calcium carbonate + exchangeable calcium) in the upper 15 cm of the soil profile. The gradient in available calcium on these soils ranged from 0.3 cmol/kg to 20.2 cmol/kg. Soils with free calcium carbonate contained significantly higher levels of available calcium than non-reactive soils (16.6 cmol/kg versus 4.1 cmol/kg, respectively)(Wilcoxon rank sum test, not shown).

The results of this analysis are presented in Figure 4.6. Available calcium explained 62.8 % of the variance in sugar maple abundance, when expressed as the percentage of live stems (>1m) that were sugar maple, and, 45.9% of the variance in sugar maple abundance, when expressed as the number of live stems (>1 m) that were sugar maple. However, in contrast, to the first setting, differences in

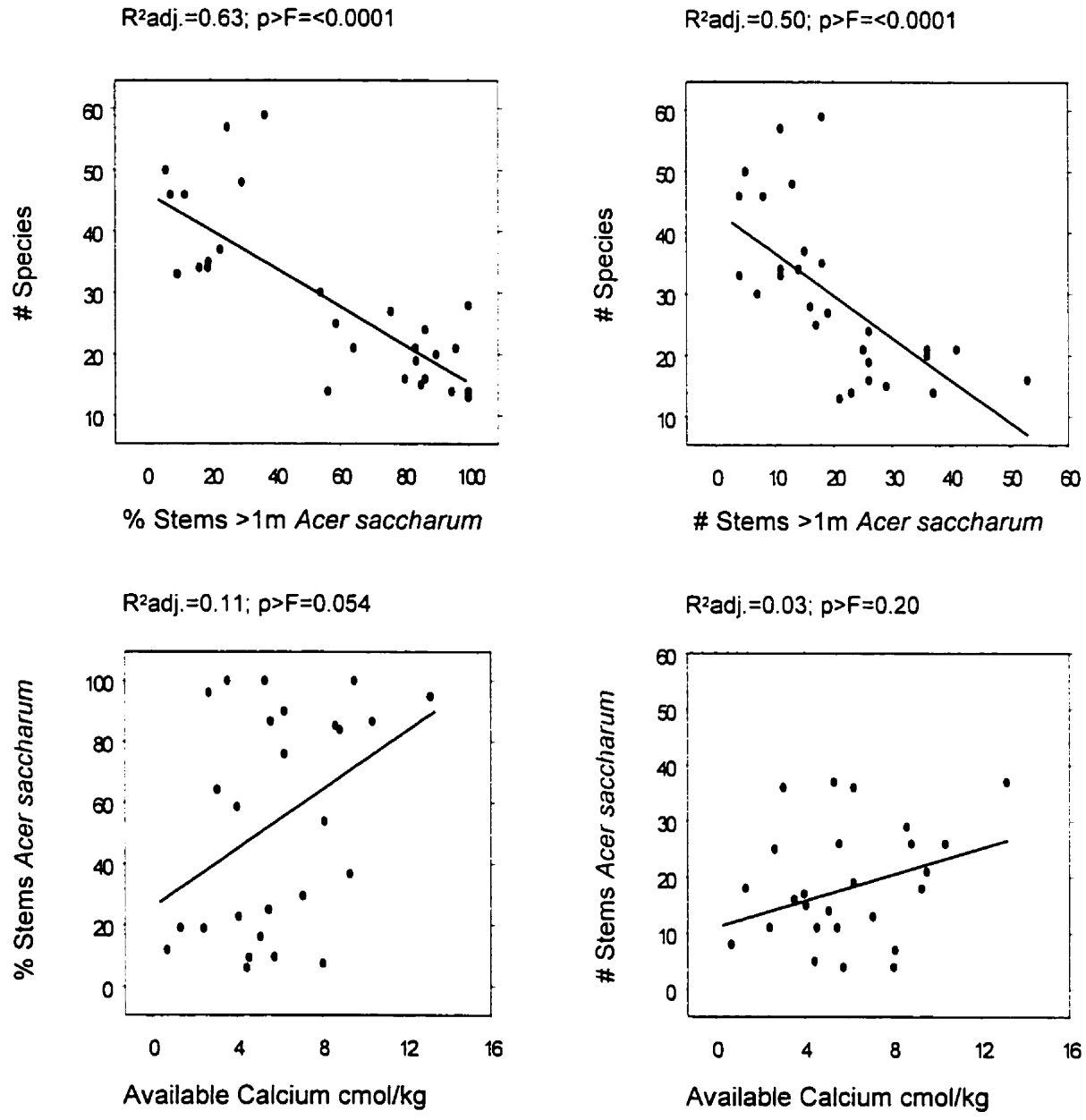

Figure 4.5. Species richness, sugar maple abundance, and available calcium, in 10m x 10m quadrats on Brunisolic and Luvisolic soils overlying calcareous till. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis (see text). Quadrats with apparent human disturbance excluded from analysis. Forest cover = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no red or white oak, no wet-mesic, wet, species). Regression statistics based on transformed data. Available calcium explains 6.6% of variance (p=0.11) in species richness (not shown). N=29 quadrats in 7 forest patches.

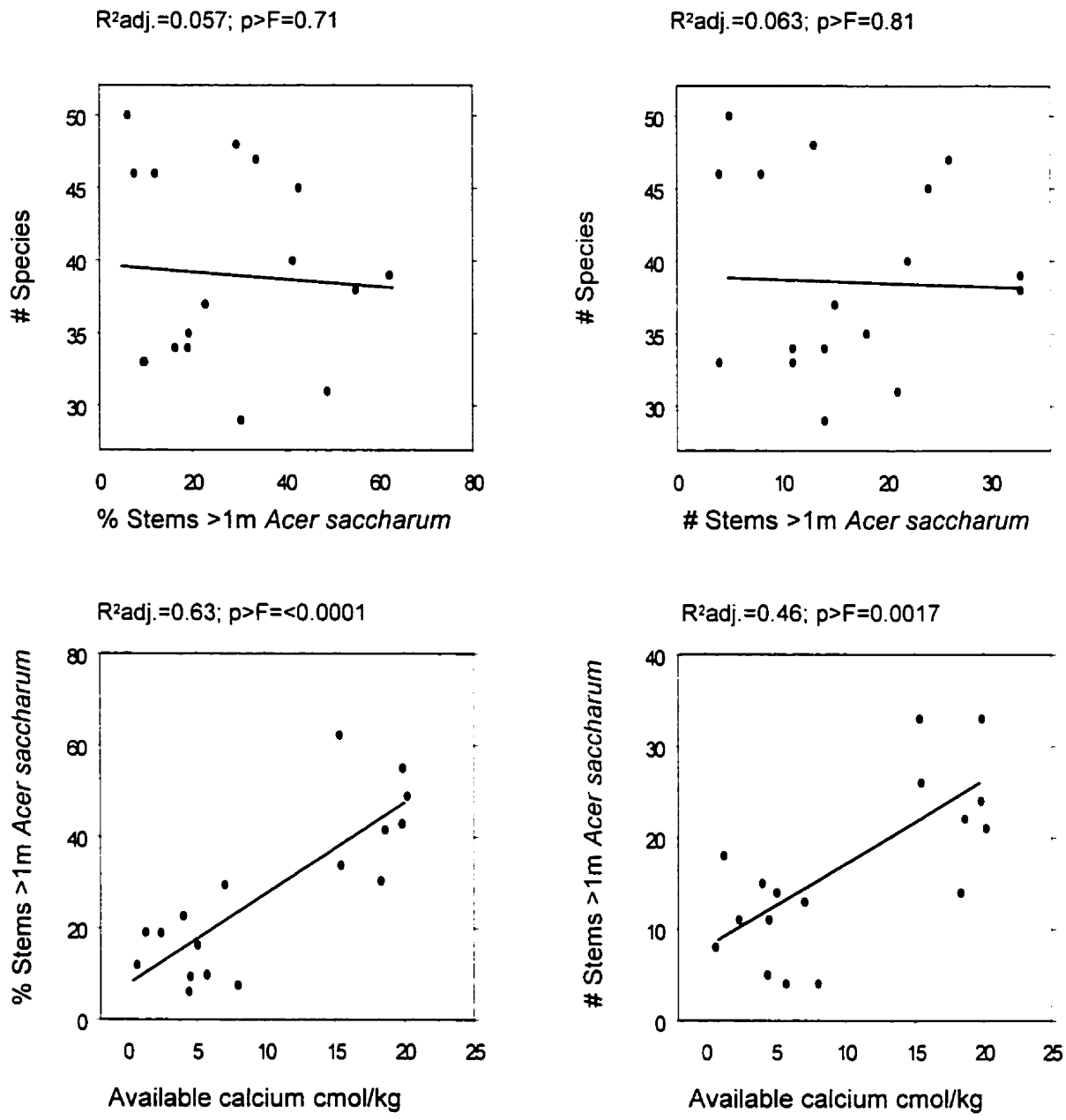

Figure 4.6. Species richness, sugar maple abundance, and available calcium, in 10m x 10m quadrats on Brunisolic soils overlying calcareous till. Soils with free calcium carbonate in upper 15 cm of soil profile included in analysis. Quadrats with apparent human disturbance excluded from analysis. Forest cover = cover type 2 (sugar maple + red or white oak) and cover type 3 (sugar maple, no oak, no wet-mesic, wet species). N=17 quadrats in 3 forest patches. Available calcium explains 6.0% of variance in species richness (p=0.76).

sugar maple abundance do not explain observed differences in species richness (p=0.71). As in the first setting, available calcium does not explain species richness on these soils (p=0.76).

The preceding results reveal that differences in exchangeable and available calcium do not explain observed differences in species richness. Or at least, not directly. The degree to which species richness is explained by differences in sugar maple abundance, and the degree to which sugar maple abundance is explained by differences in calcium availability in the upper 15 cm of the soil profile, depends on the setting in which the analysis is conducted and on the measure of sugar maple abundance that is used.

Available light, stand structure, and edaphic factors were examined further to reveal potential mechanisms that may explain the preceding results. The results of this analysis are summarized in Figures 4.7, 4.8, and 4.9.

The mean number of species, percent stems sugar maple, percent taxa shade tolerant herbs, and percent shade intolerant herbs, are compared in Figure 4.7. The mean number of species, and the mean percentage of taxa that were shade intolerant herbs, were significantly higher on Brunisolic soils whereas the mean percentage of live stems that were sugar maple, and the mean percentage of taxa that were shade tolerant herbs, were significantly higher on Luvisolic soils. This pattern suggests that more light is available in forest stands on Brunisolic soils than on Luvisolic soils, and, that the difference in species richness on these soils is due in part to the deep shade cast by maple saplings and trees. Observed differences in canopy closure were not significant (mean % canopy closure: 89.0% on Brunisolic soils versus 91.1% on Luvisolic soils, p=0.93, Wilcoxon rank sum test, not shown).

The abundance of sugar maple in selected size classes is presented in Figure 4.8. The data reveal that the number of sugar maple stems in a 10m x 10m quadrat is consistently higher on Luvisolic soils than on Brunisolic soils. The data also reveal that stands on Brunisolic soils have significantly fewer stems in the 10-30 cm dbh size class and no stems in the >30 cm size class. The most likely explanation for the latter patterns is that stands on Brunisolic soils were more intensively, or more

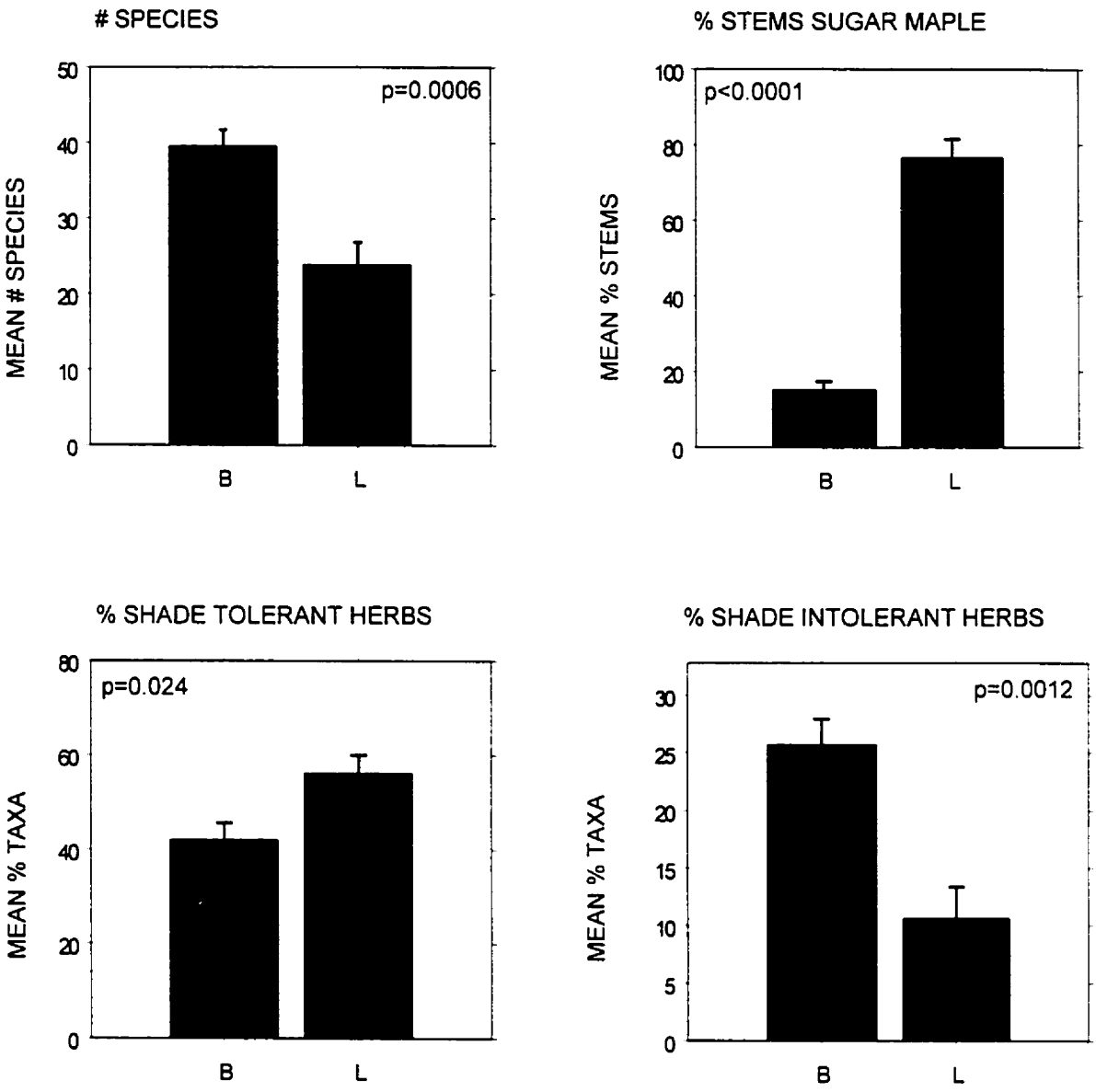

Figure 4.7. Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility I. Legend: B = Brunisolic soils, L = Luvisolic soils, overlying calcareous till. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis. Quadrats with apparent human disturbance excluded from analysis. N = 29 quadrats in 7 forest patches. Error bars: one standard error mean. Means: # SPECIES: B=39.6, L=23.9; % STEMS SUGAR MAPLE: B=15.1, L=76.7; % TAXA SHADE TOLERANT HERBS: B=42.1, L=56.1; % TAXA SHADE INTOLERANT HERBS: B=25.7, L=10.6. P-value: Wilcoxon rank sum test.

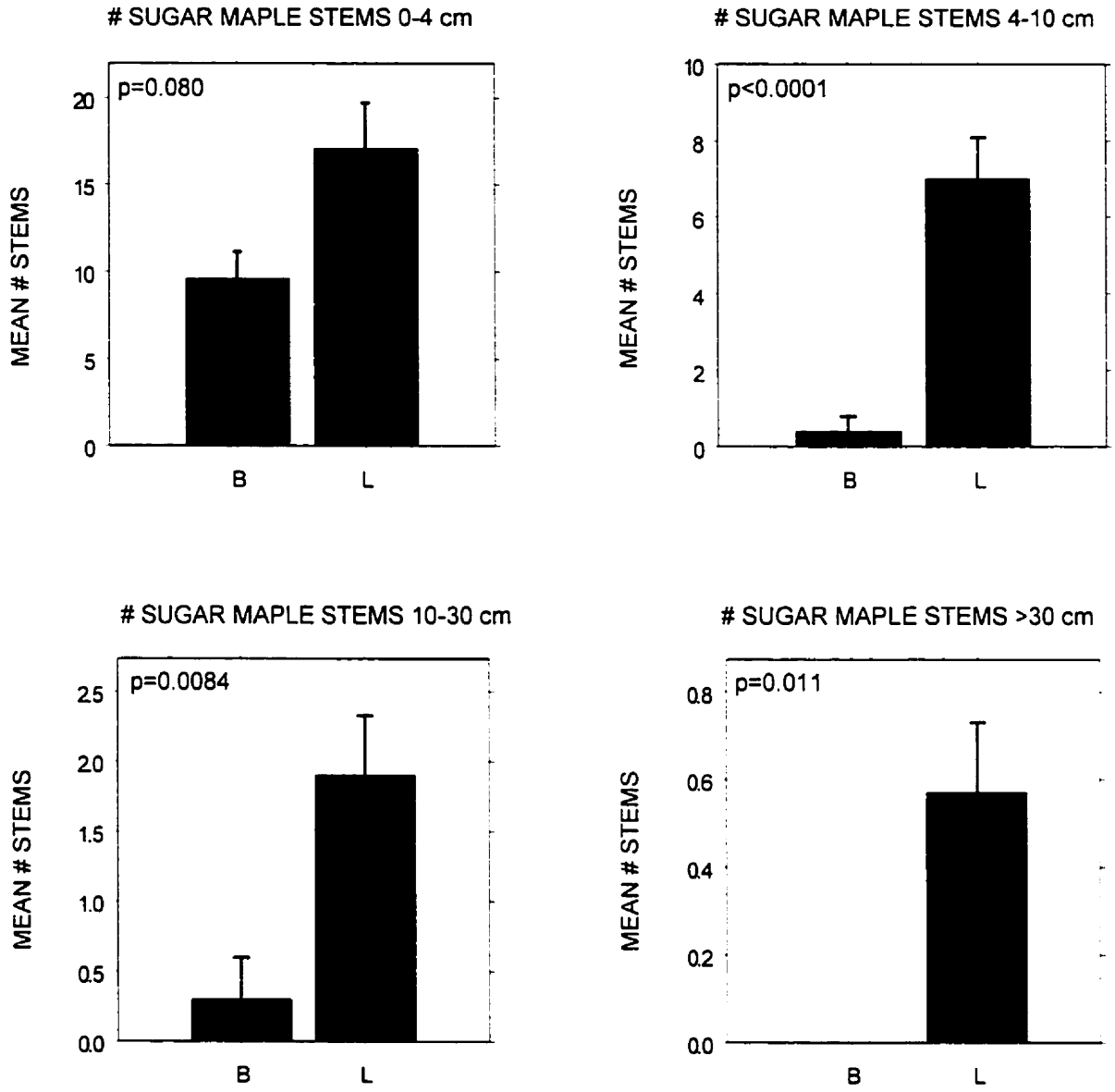

Figure 4.8. Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility II. Legend: B = Brunisolic soils, L = Luvisolic soils, overlying calcareous till. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis. Quadrats with apparent human disturbance excluded from analysis. N = 29 quadrats in 7 forest patches. Error bars: one standard error mean. Means: # SUGAR MAPLE STEMS 0-4 cm: B=9.6, L=17.1; # SUGAR MAPLE STEMS 4-10 cm: B=0.4, L=7.0; # SUGAR MAPLE STEMS 10-30 cm: B=0.3; L=1.9; # SUGAR MAPLE STEMS >30 cm: B=0.0, L=0.6. P-value: Wilcoxon rank sum test.

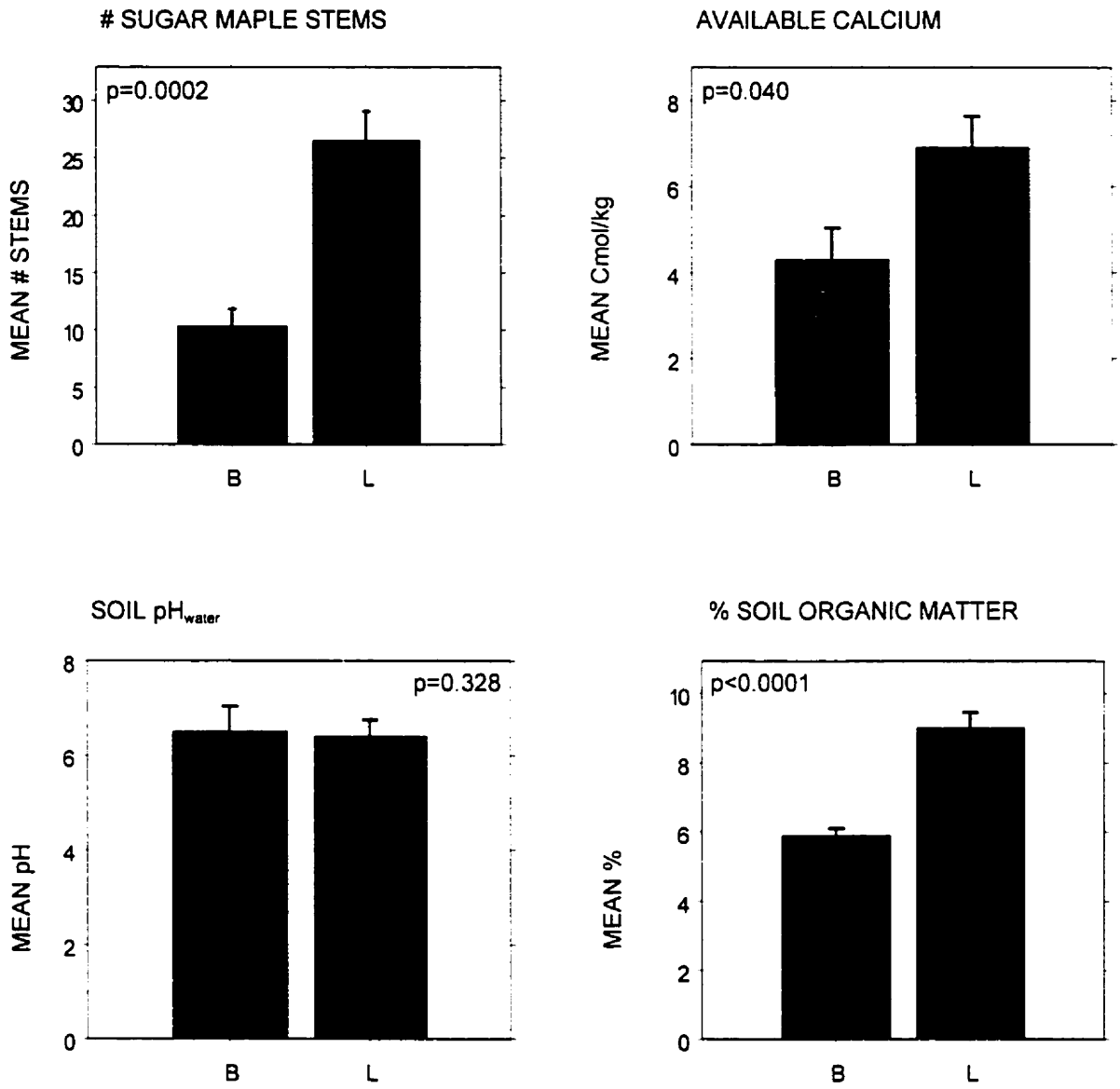

Figure 4.9. Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility III. Legend: B = Brunisolic, L = Luvisolic soils, overlying calcareous till. Soils with free calcium carbonate in upper 15 cm of soil profile excluded from analysis. Quadrats with apparent human disturbance excluded from analysis. N = 29 quadrats in 7 forest patches. Error bars: one standard error mean. Means: # SUGAR MAPLE STEMS: B=10.3, L=26.5; AVAILABLE CALCIUM: B=4.3, L=6.9; pH_{water}: B=6.5, L=6.4; % SOIL ORGANIC MATTER: B=5.9, L=9.0. P-value: Wilcoxon rank sum test.

recently, logged than stands on Luvisolic soils. While such a difference in stand history may explain the relative scarcity of large diameter stems on Brunisolic soils, it does not readily explain the greater number of species, and the greater number of shade intolerant herbs, since the canopy in each stand in this analysis was intact. A more likely explanation, therefore, is that the number of sugar maple stems in stands on Brunisolic soils was not sufficient to cast a deep shade over the entire 10m x 10m quadrat. This explanation is in keeping with the relative and absolute difference in mean sugar maple abundance, and, with the difference in the mean percentage of taxa that were shade intolerant herbs (Figures 4.7 and 4.9). It also provides an explanation for the non-significant relationship between sugar maple abundance and species richness reported in Figure 4.6.

Selected soil properties and the mean number of sugar maple stems are presented in Figure 4.9. The mean number of sugar maple stems, the mean concentration of available calcium, and the mean percent soil organic matter, were significantly higher on Luvisolic soils than on Brunisolic soils. The difference in mean pH_{water} was not significant. The correspondence between available calcium and absolute sugar maple abundance on these soils is consistent with the calcium - mortality hypothesis proposed by Kobe *et al.* (1995) and Kobe (1996) (see Section 2.4, element iii). Other factors may contribute to the observed difference in sugar maple abundance on these soils, however, since the strength of the relationship between available calcium and sugar maple abundance depends on the parameters included in the analysis (non-significant when the analysis includes stands on both Luvisolic and Brunsiolic soils, Figure 4.5; significant when the analysis is restricted to Brunisolic soils, Figure 4.6).

Soil organic matter was positively and significantly correlated with the number of sugar maple stems in both analytical settings ($p=0.042$ when the analysis includes Brunisolic and Luvisolic soils; $p=0.0007$ when the analysis was restricted to Brunisolic soils) (supplementary correlation analysis not shown). The most apparent reason for this association is the high cation exchange capacity of soil organic matter (Brady 1990). In keeping with this property, the relationship between percent soil organic matter and available calcium on these soils was linear, positive, and strong ($r^2adj.=0.45$ when the analysis includes Brunisolic and Luvisolic soils; $r^2adj.=0.68$ when the analysis is restricted to Brunisolic soils). Soil organic matter may therefore contribute to differences in sugar maple

abundance by making calcium differentially available to surface roots.

Soil organic matter also facilitates the retention of soil moisture (Brady 1990) and thus may contribute to differences in sugar maple abundance by facilitating the germination, establishment, and persistence of sugar maple seedlings. The moisture retention hypothesis is not supported by data, however, since the relationship between percent soil organic matter and the mean cover class of sugar maple seedlings (<1m) was negative in both analytical settings (supplementary linear regression analyses not shown).

The relationship between percent soil organic matter and species richness was marginally significant (p=0.062) and negative when the analysis included both Brunisolic and Luvisolic soils, and, markedly non-significant (p=0.605) and positive when the analysis was restricted to Brunisolic soils (supplementary correlation analyses not shown). Differences in soil organic matter content, therefore, do not appear to have contributed to observed differences in species richness.

4.3.1.4 Contribution of Patch Isolation and Patch Size

The contribution of patch isolation and patch size to differences in species richness was evaluated by multiple linear regression (Table 4.1). Patch isolation, when expressed as the percent forest cover within a 5 km x 5km square centered on the study site, explained 6.6 % of the variance in species richness. In general, the species richness in a given 10m x 10m quadrat declined as the percent forest cover in the surrounding landscape increased (Figure 4.4). Patch isolation, when expressed as the mean distance to the nearest eight woodlots, measured in 45^0 arcs, was markedly non-significant (p=0.32). Significant pair-wise interactions were detected between patch isolation and selected edaphic, stand structure, and disturbance variables. Interactions with important, and complex, explanatory variables such as soil order, and forest cover type, suggest that patch isolation, *per se*, does not make an independent contribution to species richness in this study.

Patch size, when expressed as the area of the forest patch in which the study site was situated, explained 1.9% of the variance in species richness. In general, the species richness in given quadrat

declined as the size of the forest patch increased. Significant pair-wise interactions were detected between selected edaphic, stand structure, and landscape variables. The interaction with soil parent material, soil order and forest cover type, in particular, suggest that patch size, *per se*, does make an independent contribution to species richness in this study.

4.3.1.5 Contribution of Microhabitats

The contribution of microhabitats to observed differences in species richness was evaluated at the quadrat (Table 4.4), forest patch (Table 4.5), and landscape (Table 4.6) spatial scale. The objective of this analysis was to determine the degree to which a given microhabitat contained species that did not occur elsewhere in the sampled area.

The microhabitats that contributed maximally to species richness at the quadrat scale were open lane/roads (mean # unique species = 24.3); open regenerating fields (mean # unique species = 19.33); closed, seasonally dry, forest floors (mean # unique species = 16.60); open riparian meadows (mean # unique species = 15.33); and, closed, seasonally moist forest floors (mean # unique species = 15.30 species) (Table 4.4). Microhabitats that occasionally contributed additional species were open and closed tree pits (mean # unique species = 0.50 and 0.54, respectively); open and closed stumps (mean # unique species = 0.43 and 0.90, respectively); open and closed logs (mean # unique species = 0.83 and 1.87, respectively). Only two of twenty-three evaluated microhabitats did not make a significant contribution to species richness at the quadrat spatial scale (open tree pits, all moisture classes; and, open stumps). Seventeen microhabitats were not evaluated (minimum sample size criterion for Wilcoxon signed rank sum test not satisfied).

The microhabitats that contributed maximally to species richness at the patch scale were closed, seasonally dry, forest floors (mean # unique species = 17.05), open regenerating fields (mean # unique species = 12.5), and open lanes/roads (mean # unique species = 9.00) (Table 4.5). Microhabitats that contributed a modest but significant number of species at the patch scale were closed, seasonally moist, forest floors (mean # unique species = 6.13); open, seasonally dry, canopy gaps (mean # unique species = 4.40); closed, seasonally wet, forest depressions (mean # unique

Table 4.4. Contribution of microhabitats to species richness in 10m x 10m quadrats. Legend: %SA = % of sampled area (19.200 m^2). # Quads: number of quadrats in analysis; Mean difference = mean difference in species richness: (# species in quadrat) - (# species in quadrat - # species unique to microhabitat); paired t-tests when distribution of differences normal; Wilcoxon signed rank sum tests otherwise. NT = not tested (see text). Quadrats in which microhabitat is the only microhabitat excluded from analysis.

Microhabitat	% SA	# Quads	Mean Difference	p>|t|
seasonally dry forest floor-cc	54.3	102	16.60	0.0001
seasonally dry forest floor-oc	6.8	23	11.30	0.0001
seasonally moist forest floors-cc	3.0	21	15.30	0.0001
seasonally moist forest floors-oc	3.0	9	9.67	0.0028
seasonally moist forest depressions-cc	4.1	20	5.35	0.0001
seasonally moist forest depressions-oc	0.2	2	4.00	NT
seasonally wet forest floors-cc	0.6	3	5.33	NT
seasonally wet forest floors-oc	1.0	4	5.75	0.0431
seasonally wet forest depressions-cc	4.0	17	5.47	0.0001
seasonally wet forest depressions-oc	1.0	4	4.50	NT
seep-cc	0.9	3	4.67	NT
seep-oc	0.3	1	12.00	NT
seasonally dry gap-cc	2.2	3	9.00	NT
seasonally moist gap-cc	0.5	2	5.00	NT
pit/mound complexes-cc	5.6	64	3.66	0.0001
pit/mound complexes-oc	0.6	7	6.30	0.0378
mound-cc	3.6	60	3.12	0.0001
mound-oc	0.4	5	5.20	0.0466
pits-cc (all moisture classes)	1.8	46	0.54	0.0001
pits-oc (all moisture classes)	0.2	6	0.50	1.0000
seasonally dry pit-cc	1.5	41	0.38	0.0040
seasonally dry pit-oc	0.1	4	0.75	NT
seasonally moist pit-cc	0.3	2	0.50	NT

Table 4.4. Contribution of microhabitats to species richness in 10m x 10m quadrats (cont'd).

Microhabitat	% SA	# Quads	Mean Difference	p>|t|
seasonally wet pit-cc	0.2	3	1.33	NT
seasonally wet pit-oc	0.1	1	0.00	NT
log-cc	0.5	45	1.87	0.0001
log-oc	0.2	12	0.83	0.0310
stump-cc	0.2	30	0.90	0.0001
stump-oc	0.1	7	0.43	0.0781
raised root mat-cc	1.3	28	3.79	0.0001
raised root mat-oc	0.6	12	4.25	0.0040
stone-cc	<0.1	1	4.00	NT
lane/road-cc	2.3	11	6.18	0.0003
lane/road-oc	1.3	8	24.13	0.0107
ditch-cc	0.3	4	5.00	NT
ditch-oc	<0.1	2	2.50	NT
regenerating field-cc	1.3	5	14.20	0.0351
regenerating field-oc	1.3	6	19.33	0.0014
riparian meadow-oc	0.7	3	15.33	NT
riparian marsh-oc	0.4	3	2.33	NT
riparian thicket-oc	0.1	1	2.00	NT

Table 4.5. Contribution of microhabitats to species richness in surveyed forest patches. Legend: %SA = % of sampled area (19,200 m^2). # Patches: number of forest patches in analysis; Mean difference = mean difference in species richness: (# species in patch) - (# species in patch - # species unique to microhabitat); paired t-tests when distribution of differences normal; Wilcoxon signed rank sum tests otherwise. NT = not tested (see text). Patches in which microhabitat is the only microhabitat excluded from analysis.

Microhabitat	% SA	# Patches	Mean Difference	p>|t|
seasonally dry forest floor-cc	54.3	21	17.05	0.0001
seasonally dry forest floor-oc	6.8	14	4.40	0.0010
seasonally moist forest floors-cc	3.0	8	6.13	0.0040
seasonally moist forest floors-oc	3.0	6	1.83	0.2500
seasonally moist forest depressions-cc	4.1	6	1.12	0.2500
seasonally moist forest depressions-oc	0.2	1	2.00	NT
seasonally wet forest floors-cc	0.6	2	2.50	NT
seasonally wet forest floors-oc	1.0	2	1.00	NT
seasonally wet forest depressions-cc	4.0	7	3.00	0.0167
seasonally wet forest depressions-oc	1.0	2	2.00	NT
seep-cc	0.9	2	2.50	NT
seep-oc	0.3	1	7.00	NT
seasonally dry gap-cc	2.2	3	1.00	NT
seasonally moist gap-cc	0.5	1	2.00	NT
pit/mound complexes-cc	5.6	20	2.30	0.0001
pit/mound complexes-oc	0.6	5	1.40	0.0400
mound-cc	3.6	20	1.35	0.0001
mound-oc	0.4	5	1.20	0.1250
pits-cc (all moisture classes)	1.8	15	0.33	0.1250
pits-oc (all moisture classes)	0.2	5	0.20	0.5000
seasonally dry pit-cc	1.5	15	0.27	0.5000
seasonally dry pit-oc	0.1	4	0.50	NT

Table 4.5. Contribution of microhabitats to species richness in surveyed patches (cont'd).

Microhabitat	% SA	# Patches	Mean Difference	p>|t|
seasonally moist pit-cc	0.3	2	0.00	NT
seasonally wet pit-cc	0.2	2	0.00	NT
seasonally wet pit-oc	0.1	1	0.00	NT
log-cc	0.5	14	0.93	0.0310
log-oc	0.2	7	0.71	1.1250
stump-cc	0.2	10	0.400	0.2500
stump-oc	0.1	4	0.00	NT
raised root mat-cc	1.3	9	1.68	0.0630
raised root mat-oc	0.6	6	2.33	0.1250
stone-cc	<0.1	1	0.00	NT
lane/road-cc	2.3	6	1.33	0.0606
lane/road-oc	1.3	5	9.00	0.0390
ditch-cc	0.3	2	0.50	NT
ditch-oc	<0.1	2	1.00	NT
regenerating field-cc	1.3	2	5.00	NT
regenerating field-oc	1.3	2	12.5	NT
riparian meadow-oc	0.7	1	0.00	NT
riparian marsh-oc	0.4	1	3.00	NT
riparian thicket-oc	0.1	1	3.00	NT

Table 4.6. Contribution of microhabitats to species richness at the landscape scale. Legend: % SA = percent total surveyed area (19,200 m^2)

Microhabitat	% SA	# Species Restricted to Habitat
seasonally dry forest floors-cc[1]	54.3	16
seasonally dry forest floors-oc[2]	6.8	6
seasonally moist forest floors-cc[3]	3.0	5
seasonally wet forest floors-cc[4]	0.6	1
seasonally wet forest depressions-cc[5]	4.0	3
seep-oc[6]	0.3	1
mound-cc[7]	3.6	1
log-cc[8]	0.5	1
raised root mat-oc[9]	1.3	1
lane/road-oc[10]	1.3	6
regenerating field-cc[11]	1.3	1
regenerating field-oc[12]	1.3	8
riparian marsh-oc[13]	0.4	1

Notes:

1. *Botrychium multifidum*, *Carex communis*, *Carex platyphylla*, *Carex woodii*, *Chimaphila umbellata*, *Crataegus* species #1, *Crataegus* species #2, *Geum allepicum*, *Hieracium aurantiacum*, *Lonicera hirsuta*, *Monotropa hypopithys*, *Panax quinquefolium*, *Rhamnus alnifolia*, *Sanicula trifoliata*, *Veronica officinalis*, *Viola rostrata*.
2. *Calystegia sepium*, *Carduus acanthoides*, *Lobelia inflata*, *Nepeta cataria*, *Panicum capillare*, *Triosteum aurantiacum*.
3. *Amelanchier arborea*, *Cypripedium calceolus*, *Phegopteris connectilis*, *Stellaria longifolia*, *Typha latifolia*.
4. *Aster umbellatus*.
5. *Carex pseudo-cyperus*, *Cicuta bulbifera*, *Osmunda regalis*.
6. *Carex crinita*.
7. *Monarda fistulosa*.
8. *Echinocystis lobata*.
9. *Sicyos angulatus*.
10. *Ambrosia artemisiifolia*, *Carduus nutans*, *Festuca pratensis*, *Potentilla norvegica*, *Verbena hastata*, *Verbena urticifolia*.
11. *Rudbeckia hirta*.
12. *Antennaria neglecta*, *Aster ericoides*, *Carex prairea*, *Festuca arundinacea*, *Festuca rubra*, *Lycopodium tristachyum*, *Rhus typhina*, *Salix petiolaris*.
13. *Rumex orbiculatus*.

species = 3.00); closed pit/mound complexes (mean # unique species = 2.30); open pit/mound complexes (mean # unique species = 1.40); closed tip-up mounds (mean # unique species = 1.35); and, closed logs (mean # unique species = 0.93 species). Only nine of twenty evaluated habitats made a significant contribution to species richness at the patch scale. Twenty-one microhabitats were not evaluated (minimum sample size criterion for Wilcoxon signed rank sum test not satisfied).

Thirteen microhabitats contributed to species richness at the landscape scale (i.e. contained species that were not recorded in any other habitat)(Table 4.6). The habitat that contributed the greatest number of species was closed seasonally dry forest floor (16 species). Habitats that contributed an intermediate number of species were open regenerating fields (8 species); open lanes/roads (6 species);open, seasonally dry, forest floors (open canopy gaps)(6 species); and, closed seasonally moist forest floors (5 species). Habitats that contributed a minor number of unique species at the landscape scale were closed, seasonally wet, forest depressions (3 species); closed, seasonally wet, forest floors (1 species); open seeps (1 species); closed mounds (1 species); closed logs (1 species); open raised root mats (1 species); closed regenerating fields (1 species); and, open riparian marsh (1 species).

Taken together, these results suggest that light is more limiting than moisture for many plants in these forests. Open disturbed habitats were particularly strong contributors to species richness at the quadrat scale, whereas, closed dry forest floors were the strongest contributors to species richness at the patch and landscape spatial scale. While closed seasonally moist forest floors and seeps were important contributors to species richness at the quadrat scale, moist and wet habitats were modest to weak contributors to species richness at larger spatial scales. Habitats created by natural disturbance (tip-up mounds, tree pits, logs, stumps, raised root mats) were typically weak contributors to species richness at all spatial scales.

These results may depend in part on differences in sampled area. Habitats in these forests were typically closed and seasonally dry (Table 4.7). Open microhabitats occupied 16.5 % of the sampled area and were typically dry, whereas, seasonally moist or wet habitats occupied 21.3% of the

Table 4.7. Comparison of microhabitats by moisture and canopy closure class. Legend: % SA = % of total surveyed area (19,200 m^2).

Microhabitat	# Quadrats Present	Mean Area (m^2) per Quadrat When Present	Total Area	
			m^2	% SA
I. MOISTURE STATUS				
Dry Habitats	188	80.3	15,105	78.7
closed canopy	170	76.8	13,051	68.0
open canopy	43	47.8	2,054	10.7
Moist/Wet Habitats	71	57.7	4,095	21.3
closed canopy	58	51.5	2,986	15.6
open canopy	19	58.4	1,109	5.8
II. LIGHT STATUS				
Closed Habitats	174	92.2	16,037	83.5
dry habitats	170	76.8	13,051	68.0
moist/wet habitats	58	51.5	2,986	15.6
Open Habitats	47	67.3	3,163	16.5
dry habitats	43	47.8	2,054	10.7
moist/wet habitats	19	58.4	1,109	5.8

sampled area and were typically closed. These patterns increase the probability of recording restricted species in both closed - dry and closed - moist habitats. Passive sampling effects, however, cannot account for the tendency for open lane/roads and open regenerating fields to contribute more to species richness than their closed counterparts, since the open phase of these habitats occupied an equal or smaller percentage of the total sampled area than the closed phase, at each spatial scale. Nor, for similar reasons, can passive sampling account for the tendency for open seeps, open pit/mound complexes, and open raised root mats, to contribute more to species richness than their closed counterparts at the quadrat spatial scale. Nor, for similar reasons, can passive sampling account for the tendency for closed seasonally moist floors to consistently contribute more to species richness than the open phase.

4.3.2 Plant Trait Correlates of Species Richness

4.3.2.1 Generalized Linear Regression Models

Plant trait correlates of species richness in 10m x 10m quadrats are reported in Table 4.8, in relation to the following groupings: mode of dispersal, life history, provenance, life form, habitat affinity, shade tolerance, moisture affinity, and, overall model. Scatter plots of the most influential dispersal correlates are presented in Figures 4.10 and 4.11.

i) Mode of Dispersal

Modes of dispersal that maximally explained observed differences in species richness in 10m x 10m quadrats were dispersal by animal ingestion (r^2adj.=0.397), dispersal by wind (r^2adj.=0.334), dispersal by unassisted means (r^2adj.=0.317), and, dispersal by multiple modes (r^2adj.=0.246)(Table 4.8). Modes with intermediate explanatory power were dispersal by prolonged dormancy (r^2adj.=0.199), dispersal by ants (r^2adj.=0.152), and, dispersal by animal adhesion (r^2adj.=0.114). Modes with minimal explanatory power were dispersal by mechanical expulsion (r^2adj.=0.060) and dispersal by vegetative expansion (r^2adj.=0.050).

Species richness was positively correlated with dispersal by animal adhesion, wind, prolonged dormancy, unassisted means, and multiple modes, and, negatively correlated with dispersal by

Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats. Generalized linear regression (GLM) models, by row. Predictor variables = % taxa in quadrat with designated attribute. See notes for interactions among predictor variables; see Chapter 3.2.1.1 for description of dispersal modes. All models parsimonious based on Mallow's Cp criterion.

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
1. MODE OF DISPERSAL[2]						
animal ingestion[4,8,9,10,15,17,18,19,22,23,25,29,33,34,36,43]	sqrt # spp	126.67	0.0001	0.3969	0.81	negative
animal adhesion[3,6,7,10,11,15,16,17,18,19,24,28,31,35,36,37,39]	sqrt # spp	25.65	0.0001	0.1143	0.22	positive
ants[7,8,11,15,17,25,28,29,34,35,36,37,42,43]	sqrt # spp	35.23	0.0001	0.1520	0.57	negative
wind[4,10,15,16,17,21,24,31,36,37,41,42,43]	sqrt # spp	96.76	0.0001	0.3339	0.79	positive
prolonged dormancy[4,5,8,9,15,16,17,18,19,24,26,31,37,43]	sqrt # spp	38.56	0.0001	0.1992	0.80	positive
mechanical expulsion[4,5,7,11,15,16,17,18,19,28,31,39,40,42,43]	ln sqrt # spp	9.41	0.0026	0.0603	0.23	negative
unassisted means[3,7,24,25,33]	sqrt # spp	89.69	0.0001	0.3171	0.37	positive
multiple modes[3,4,6,11,15,16,17,18,19,20,22,24,28,31,37,39,40,41,42,43]	sqrt # spp	63.37	0.0001	0.2462	0.82	positive
vegetative expansion[4,5,8,10,15,17,26,28,29,39,41,42,43]	sqrt # spp	10.94	0.0011	0.0495	0.59	negative
MODEL 1 (HERBS)[12]: unassisted means + prolonged dormancy + ant + animal ingestion	# spp	61.35	0.0001	0.5583	0.95	
MODEL 2 (ALL LIFE FORMS)[13]: unassisted means + animal conveyance (ants + seed caching by birds and mammals) + prolonged dormancy	# spp	83.61	0.0001	0.5647	0.67	

Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
2. LIFE HISTORY[14]						
annual[3,4,5,6,7,8,16,17,18,19,22,23,24,25,28,29,33,35,39,40,41,42,43]	sqrt # spp	9.52	0.0023	0.0427	0.80	positive
biennial[4,6,7,8,10,15,17,18,19,20,21,22,24,31,36,37]	sqrt # spp	35.63	0.0001	0.1535	0.03	positive
perennial[3,4,5,6,7,8,10,11,15,16,18,19,21,23,24,28,29,31,35,37,39,40,41,42,43]	sqrt # spp	29.91	0.0001	0.1315	0.51	negative
MODEL: % taxa perennial	sqrt # spp	29.91	0.0001	0.1315	0.51	negative
3. PROVENANCE[14]						
native[3,4,7,8,10,15,16,17,21,23,24,25,29,30,31,33,36]	# spp	70.82	0.0001	0.2677	0.67	negative
alien[3,4,7,8,10,15,16,19,21,23,24,25,29,30,31,33,36]	# spp	66.54	0.0001	0.2555	0.36	positive
MODEL: % taxa native	# spp	70.82	0.0001	0.2677	0.67	positive
4. LIFE FORM[14]						
tree[10,15,16,23,24,25,28,30,31,33,36]	sqrt # spp	69.23	0.0001	0.2632	0.76	negative
shrub[6,15,16,17,18,19,24,29,30,33,36]	sqrt # spp	7.03	0.0087	0.0306	0.14	negative
vine[3,10,15,16,28,29,30,33,36,39,41,42,43]	sqrt # spp	32.91	0.0001	0.1783	0.04	positive
fern[3,15,17,18,19,20,28,34,35,43]	sqrt # spp	11.40	0.0009	0.0549	0.03	negative
fern ally[4,6,7,9,10,15,15,17,18,19,20,21,26,34,35,39,40,41,42,43]	ln sqrt # spp	3.10	0.0800	0.0109	0.003	positive
grass[3,5,9,15,18,19,20,26,28,35]	sqrt # spp	72.72	0.0001	0.2730	0.33	positive

Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
herb[7,11,24,25,30,31,33,36,39,42]	sqrt # spp	31.37	0.0001	0.1372	0.73	positive
MODEL (ALL TAXA)[27]: % tree+%vine	# spp	38.41	0.0001	0.3373	0.56	
5. HABITAT AFFINITY[14]						
forest[4,5,8,10,11,15,17,20 22,23,25,29,30,33,34,36]	# spp	68.63	0.0001	0.2615	0.45	negative
forest + open[3,5,11,15,17,18,19,21,22,28,30,31,35,39,40,42,43]	sqrt # spp	16.04	0.0001	0.0730	0.07	negative
open + forest (sqrt % "open + forest")[18,19,20,21,22,28,29,34,35]	sqrt # spp	47.06	0.0001	0.1943	0.10	positive
open[4,6,7,8,10,16,17,18,19,20,26,29,34,37,43]	# spp	121.85	0.0001	0.3875	0.04	positive
MODEL (ALL TAXA)[32]: % open + % forest	#spp	68.56	0.0001	0.4143	0.03	
6. SHADE TOLERANCE[11]						
shade tolerance class 1 (very shade tolerant)[3,9,15,18,19,20,21,22,26,28,34,35,41]	sqrt # spp	53.02	0.0001	0.2140	0.14	negative
shade tolerance class 2[3,5,23,24,28,30,31,33,36]	sqrt # spp	40.18	0.0001	0.1702	0.28	negative
shade tolerance class 3[4,5,15,17,23,24,25,29,30,33,36,37]	sqrt # spp	5.20	0.0237	0.0215	0.19	negative
shade tolerance class 4[3,4,5,6,16,18,19,20,21,22,26,28,34,35,37]	sqrt # spp	20.19	0.0001	0.0913	0.01	positive
shade tolerance class 5 (very shade intolerant)[4,5,6,7,10,16,17,31,35,36]	sqrt # spp	80.27	0.0001	0.2933	0.46	positive

Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	relationship
MODEL (ALL TAXA)[38]: % shade tolerance class 5 + % shade tolerance class 1	sqrt # spp	46.92	0.0001	0.3247	0.47	
7. MOISTURE AFFINITY[14]						
obligate upland[4,15,17,22,24,26,29,40,42,43]	sqrt # spp	66.52	0.0001	0.2554	0.77	negative
facultative upland[4,8,10,15,17,24,29,39,41,42,43]	sqrt # spp	71.35	0.0001	0.2692	0.65	negative
facultative[6,10,11,15,17,22,24,33,40,42,43]	sqrt # spp	0.06	0.8730	0.0051	0.02	-
facultative wetland[4,5,6,8,10,11,15,17,22,24,26,39,40,41,43]	sqrt # spp	83.38	0.0001	0.3014	0.83	positive
obligate wetland[3,4,5,6,7,8,10,11,15,17,22,23,24,39,40,41,42]	sqrt # spp	52.92	0.0001	0.2137	0.34	positive
MODEL: % taxa facultative wetland	sqrt # spp	83.38	0.0001	0.3014	0.83	positive
8. OVERALL MODEL: PLANT ATTRIBUTES[14]						
% taxa herbs dispersed by unassisted means + % taxa herbs dispersed by prolonged dormancy + % taxa herbs dispersed by ants + % taxa herbs dispersed by animal ingestion[12]	# spp	61.35	0.0001	0.5583	0.95	

Notes:

1. Shapiro-Wilk W test for normality of residuals (residuals normal when $p \geq 0.05$).
2. Predictor variables are the percentage of taxa in a given 10m x 10m quadrat that are herbs dispersed by designated mode. Percentages for prolonged dormancy and mechanical expulsion were transformed (ln p/q) to achieve normal residuals.
3. Significant interaction with % taxa that are herbs dispersed by animal ingestion.
4. Significant interaction with % taxa that are herbs dispersed by animal adhesion.

Notes (cont'd):

5. Significant interaction with % taxa that are herbs dispersed by ants.
6. Significant interaction with % taxa that are herbs dispersed by wind.
7. Significant interaction with ln (p/q) taxa that are herbs dispersed by prolonged dormancy.
8. Significant interaction with ln (p/q) taxa that are herbs dispersed by mechanical expulsion.
9. Significant interaction with % taxa that are herbs dispersed by unassisted means
10. Significant interaction with % taxa dispersed by multiple modes.
11. Significant interaction with % taxa dispersed by vegetative expansion.
12. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.05$. Partial F statistics: % unassisted means: F=32.06; % prolonged dormancy: F=25.17; % ant: F=14.44; % animal ingestion: F=6.16.
13. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.05$. Partial F statistics: % unassisted means: F=43.59; % animal conveyance (i.e., dispersal by ants or by seed caching): F=29.12; % prolonged dormancy: F=24.25.
14. Predictor variables are the percentage of taxa in a given 10m x 10m quadrat with the specified attribute.
15. Significant interaction with % taxa with an annual life history.
16. Significant interaction with % taxa with a biennial life history.
17. Significant interaction with % taxa with a perennial life history.
18. Significant interaction with % taxa native.
19. Significant interaction with % taxa alien.
20. Significant interaction with % taxa trees.
21. Significant interaction with % taxa shrubs.
22. Significant interaction with % taxa vines.
23. Significant interaction with % taxa ferns.
24. Significant interaction with % taxa fern allies (lnp/q).
25. Significant interaction with % taxa grasses.
26. Significant interaction with % taxa herbs.
27. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.05$. Partial F statistics: % trees: F=37.94; ln p/q vines: F=19.84.
28. Significant interaction with % taxa with an affinity for "forest" habitats.
29. Significant interaction with % taxa with an affinity for "forest + open" habitats.
30. Significant interaction with % taxa with an affinity for "open + forest" habitats.

Notes (cont'd):

31. Significant interaction with % taxa with an affinity for "open" habitats.
32. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.05$. Partial F statistics: % affinity for "open" habitats: $F=50.57$; % affinity for "forest" habitats: $F=9.69$.
33. Significant interaction with % taxa with shade tolerance class 1.
34. Significant interaction with % taxa with shade tolerance class 2.
35. Significant interaction with % taxa with shade tolerance class 3.
36. Significant interaction with % taxa with shade tolerance class 4.
37. Significant interaction with % taxa with shade tolerance class 5.
38. Variables in model presented in descending rank order, based on partial F statistics; interactions among variables not significant; all elements in model significant, $p<0.05$. Partial F statistics: % shade tolerance class 5 (sqrt transformed): $F=32.14$; % shade tolerance class 1: $F=9.84$.
39. Significant interaction with % taxa with an obligate upland affinity.
40. Significant interaction with % taxa with a facultative upland affinity.
41. Significant interaction with % taxa with a facultative moisture affinity.
42. Significant interaction with % taxa with a facultative wetland affinity.
43. Significant interaction with % taxa with an obligate wetland affinity.

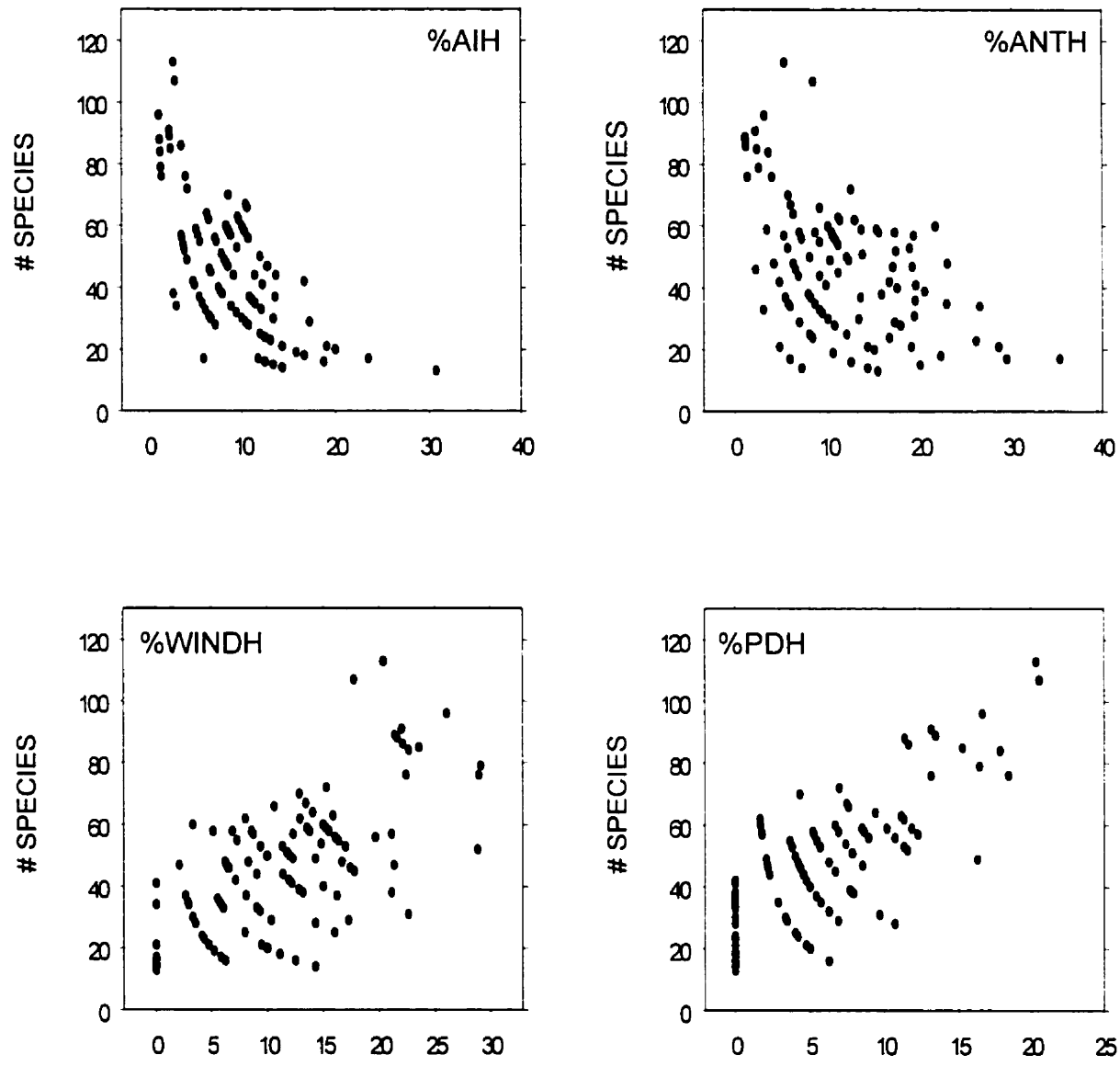

Figure 4.10. Scatter plots of dispersal correlates of species richness in 10m x 10m quadrats I. Legend: %AIH = % taxa herbs dispersed by animal ingestion; %ANTH = % taxa herbs dispersed by ants; %WINDH = % taxa herbs dispersed by wind; %PDH = % taxa herbs dispersed by prolonged dormancy.

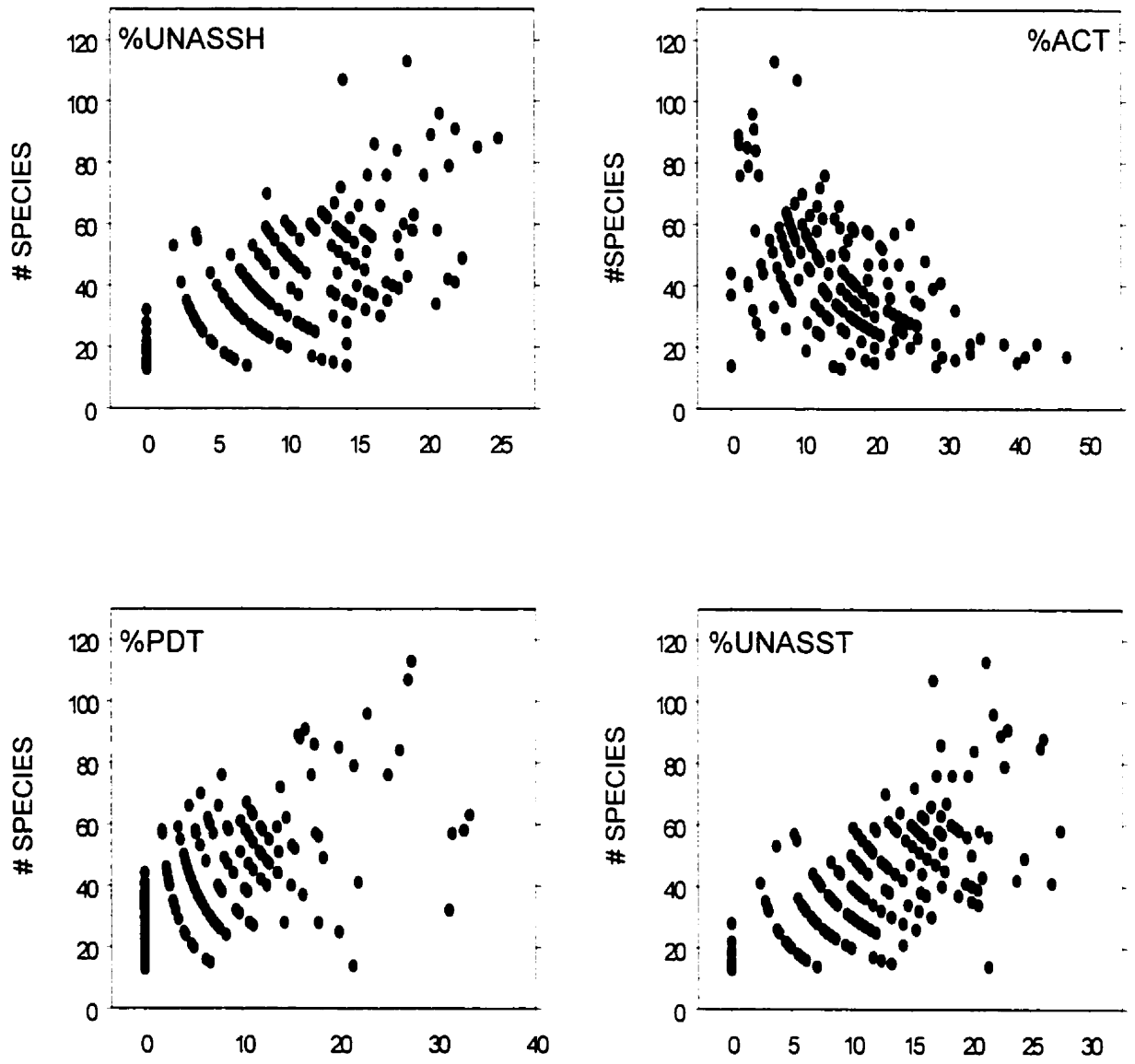

Figure 4.11. Scatter plots of selected correlates of species richness in 10m x 10m quadrats II. Legend: %UNASSH = % taxa herbs dispersed by unassisted means; %ACT = % taxa dispersed by animal conveyance (ants, or, seed caching by birds or mammals), all life forms; %PDT = % taxa dispersed by prolonged dormancy, all life forms; %UNASST = % taxa dispersed by uanssisted means, all life forms.

animal ingestion, ants, mechanical expulsion, and vegetative expansion.

The percentage of taxa that were herbs dispersed by unassisted means, prolonged dormancy, ants, and animal ingestion, explained 55.8 % of the variance in species richness in 10m x 10m quadrats. The percentage of taxa dispersed by unassisted means, animal conveyance (ants + seed caching by birds and mammals), and prolonged dormancy (all life forms), explained 56.5 % of the variance in species richness in 10m x 10m quadrats. The former model represents a better statistical fit ($p<W = 0.95$ versus $p<W = 0.67$) and is considered to be the superior model for dispersal variables.

Pair-wise interactions were common among dispersal variables (superscript 3-11), and between mode of dispersal and life history (superscript 15-17), habitat affinity (superscript 28-31), and moisture affinity (superscript 39-43) (Table 4.8). Less common were interactions between mode of dispersal and provenance (superscript 18-19), life form (superscript 20-26), shade tolerance (superscript 33-37).

ii) Life History

Life history variables that maximally explained observed differences in species richness in 10m x 10m quadrats were the percentage of taxa that possessed a biennial ($r^2adj.=0.154$) or perennial ($r^2adj.=0.132$) life history (Table 4.8). The latter model is considered to be the superior model for life history variables in view of its superior statistical fit. The percentage of taxa that possessed an annual life history explained a significant but small fraction of the observed variance in species richness ($r^2adj.=0.043$).

Species richness was positively correlated with the percentage of taxa with an annual or biennial life history, and, negatively correlated with the percentage of taxa that possessed a perennial life history.

Pair-wise interactions were common among life history variables (superscript 15-17) and between life history variables and mode of dispersal (superscript 3-11), provenance (superscript 18-19), life form (superscript 20-26), habitat affinity (superscript 28-31), and shade tolerance (superscript 33-37). Plants with an annual or perennial life history interacted with moisture affinity (superscript 39-

43) whereas plants with a biennial life history did not.

iii) Provenance

The percentage of taxa that were native species explained marginally more variance in species richness than the percentage that were not (r^2adj.= 0.268 versus 0.256, respectively) (Table 4.8). The former model is considered to be the superior model for provenance variables in view of its superior statistical fit and explanation of variance.

Species richness was positively correlated with the percentage of taxa that were alien species, and, negatively correlated with the percentage of taxa that were native.

Pair-wise interactions were common between provenance variables and mode of dispersal (superscript 3-11), life history (superscript 15-17), life form (superscript 19-26), habitat affinity (superscript 28-31), and shade tolerance (superscript 33-37). Provenance variables did not interact with moisture affinity (superscript 39-43).

iv) Life Form

Life form variables that maximally explained observed differences in species richness in 10m x 10m quadrats were the percentage of taxa that were grasses (r^2adj.= 0.273) and trees (r^2adj.= 0.263) (Table 4.8). Variables with intermediate explanatory power were the percentage of taxa that were vines (r^2adj.= 0.178) and herbs (r^2adj.= 0.137). The percentage of taxa that were ferns (r^2adj.= 0.055) and shrubs (r^2adj.= 0.031) explained a significant but minor fraction of variance in species richness. The percentage of taxa that were fern allies did not explain observed differences in species richness ($p>F=0.08$).

The percentage of taxa that were trees and vines collectively explained 32.5 % of the variance in species richness in 10m x 10m quadrats.

Species richness was positively correlated with the percentage of taxa that were vines, fern allies, grasses, and herbs, and, negatively correlated with the percentage of taxa that were trees, shrubs, and

ferns.

Pair-wise interactions between life form and life history (superscript 15-17) were more common than interactions among life forms and between life form and other plant traits. The percentage of taxa that were trees, shrubs, and grasses did not interact with moisture affinity (superscript 39-43).

v) Habitat Affinity

Habitat affinity variables that maximally explained observed differences in species richness in 10m x 10m quadrats were the percentage of taxa with an affinity for open (r^2adj.= 0.388) and forested (r^2adj.= 0.214) habitats (Table 4.8). The percentage of taxa with an affinity for "open + forest" habitats (r^2adj.= 0.194) explained more than twice as much variance in species richness as taxa with an affinity for "forest + open" habitats (r^2adj.= 0.073).

The percentage of taxa with an affinity for "open" and "forest" habitats collectively explained 41.4% of the variance in species richness in 10m x10m quadrats.

Species richness was positively associated with the percentage of taxa with an affinity for "open + forest" and "open" habitats, and, negatively correlated with the percentage of taxa with an affinity for "forest" and "forest + open" habitats.

Pair-wise interactions were common among habitat affinity variables (superscript 28-31), and, between habitat affinity variables and mode of dispersal (superscript 3-11), life history (superscript 15-17), provenance (superscript 18-19), life form (superscript 20-26), shade tolerance (superscript 33-37). Only the interactions between moisture affinity and the percentage of taxa with an affinity for "forest + open" and "open" habitats were significant.

vi) Shade Tolerance

Shade tolerance variables that maximally explained observed differences in species richness in 10m x 10m quadrats were the percentage of taxa classified as shade tolerance class 5 (r^2adj.= 0.293), shade tolerance class 1 (r^2adj.= 0.214), and, shade tolerance class 2 (r^2adj.= 0.170) (Table 4.8). The

percentage of taxa classified as shade tolerance 4 (r^2adj.= 0.091) explained more variance than taxa classified as shade tolerance class 3 (r^2adj.= 0.024).

The percentage of taxa classified as shade tolerance class 5. and shade tolerance class 1. collectively explained 32.5 % of the variance in species richness in 10m x 10m quadrats.

Species richness was positively correlated with the percentage of taxa classified as shade tolerance class 4 and 5. and. negatively correlated with the percentage of taxa classified as shade tolerance class 1 and 2.

Pair-wise interactions were common among shade tolerance classes (superscript 33-37). and. between shade tolerance classes and mode of dispersal (superscript 3-11). life history (superscript 15-17). life form (superscript 20-27). Shade tolerance class interacted infrequently with provenance (superscript 18-19) and moisture affinity (superscript 39-43).

vii) Moisture Affinity

Moisture affinity variables that maximally explained observed differences in species richness in 10m x 10m quadrats were the percentage of taxa that were facultative wetland species (r^2adj.= 0.301). facultative upland species (r^2adj.= 0.269). obligate upland species (r^2adj.= 0.255). and obligate wetland species (r^2adj.= 0.214) (Table 4.8). The percentage of taxa with a facultative affinity for moisture did not explain observed differences in species richness (p>F=0.87).

The percentage of taxa that were facultative wetland species was considered to be the superior model for moisture affinity variables in view of its superior statistical fit and explanation of variance.

Species richness was positively correlated with the percentage of taxa classified as facultative wetland. and obligate wetland. species. and. negatively correlated with the percentage of taxa classified as facultative upland. and obligate upland. species.

Pair-wise interactions were common among moisture affinity variables (superscript 39-43). and.

between moisture affinity variables and mode of dispersal (superscript 3-11), life history (superscript 15-17), and, life form (superscript 20-26). Moisture affinity variables interacted infrequently with habitat affinity (superscript 28-31) and shade tolerance (superscript 33-37) and did not interact with provenance (superscript 18-19).

viii) Overall Model

The combination of plant attributes that maximally explained observed differences in species richness in 10m x10m quadrats was the percentage of taxa that were herbs dispersed by unassisted means, prolonged dormancy, ants, and animal ingestion. This model, which explains 55.8 % of the observed variance in species richness, was considered superior to all other models because of superior statistical fit and strong explanation of variance. An alternative model (composed of the percentage of taxa dispersed by unassisted means, animal conveyance and prolonged dormancy) explained marginally more variance in species richness (56.5 % versus 55.8%) but was a weaker statistical fit ($p<W = 0.67$ versus $p<W = 0.95$).

4.3.3 Comparison of Alternative Models of Species Richness

4.3.3.1 Generalized Linear Regression Models

The combinations of variables that maximally explain differences in species richness in 10m x 10m quadrats are presented in Table 4.9. Models E1 and E2 summarize the optimum combination of environmental variables; models D1 and D2 summarize the optimum combination of dispersal variables; models M1 through M5 summarize the optimum combination of environmental, dispersal, and life form variables. One outlier, quadrat #160, was removed from each model to improve the statistical fit (see Section 4.2.2.3).

Models D1, D2, and M4 were considered inferior models in view of the comparatively weak statistical fit ($p<W = 0.33, 0.11, 0.22$, respectively). Models M1, M3, and M5 were considered superior models in view of the excellent statistical fit ($p<W = 0.88, 0.95, 0.89$, respectively) and strong explanation of variance ($r^2adj. = 0.659, 0.712, 0.642$, respectively). Interactions among model elements prevented an overall statistical evaluation of superior and inferior models (see Section

Table 4.9. Comparison of selected GLM models of species richness. Model elements presented in descending rank order, based on partial F statistics. Response variable: sqrt # species; MSE = mean square error; p<W = Shapiro-Wilk W test for normality of residuals (residuals normal when p>0.05); % taxa = % taxa (all life forms) in 10m x 10m quadrats. All models parsimonious based on Mallow's Cp criterion. One outlier (quadrat #160) removed from each model.

Model	Model Attribute			
	F	r^2adj	MSE	p<W
I. ENVIRONMENTAL VARIABLES				
MODEL E1: ln # tree species (>1 m) + % canopy closure (ln p/q) + forest cover type + open microhabitats (cut or snag gap, lane regenerating field, seep, riparian meadow, riparian thicket, riparian marsh)[1]	39.00	0.5833	0.8491	0.70
MODEL E2: % canopy closure (ln p/q) + sqrt # stems 0-4 cm dbh + soil moisture class + soil parent material[2]	33.93	0.5482	0.9207	0.69
II. DISPERSAL VARIABLES				
MODEL D1 (ALL LIFE FORMS): % taxa dispersed by unassisted means + % taxa dispersed by animal conveyance (ants + seed caching by birds and mammals) + % taxa dispersed by prolonged dormancy[3]	83.61	0.6285	0.7571	0.33
MODEL D2 (HERBS ONLY): % taxa dispersed by unassisted means + % taxa dispersed by prolonged dormancy + % taxa dispersed by ants + % taxa dispersed by animal ingestion[4]	74.10	0.6061	0.82026	0.11
III. MIXED VARIABLES				
MODEL M1. % stems sugar maple + % taxa herbs dispersed by unassisted means + % taxa dispersed by prolonged dormancy (all life forms)[5]	123.54	0.6593	0.6943	0.88

Table 4.9. Comparison of selected GLM models of species richness (cont'd).

Model	Model Attribute			
	F	r^2adj	MSE	p<W
III. MIXED VARIABLES (cont'd)				
MODEL M2: ln # tree species (>1 m) + % canopy closure (ln p/q) + forest cover type + % taxa dispersed by unassisted means (all life forms)[6]	56.51	0.6716	0.6692	0.61
MODEL M3: sqrt # stems 0-4 cm dbh + % taxa grasses + % taxa herbs dispersed by prolonged dormancy + % taxa herbs dispersed by animal ingestion + % canopy closure (ln p/q) + forest cover type[7]	53.18	0.7119	0.5870	0.95
MODEL M4: sqrt # stems 0-4 cm dbh + % taxa herbs dispersed by prolonged dormancy + % taxa dispersed by animal conveyance (ants or seed caching by birds and mammals) + % canopy closure (ln p/q) + soil order + open regenerating fields[8]	44.89	0.6732	0.6660	0.22
MODEL M5: % taxa herbs dispersed by wind + sqrt # stems 0-4 cm dbh + soil moisture class + % canopy closure (ln p/q) + soil parent material[9]	43.63	0.6422	0.7291	0.89

Notes:

1. Model E1. Partial F statistics: ln # tree species: F=66.16; % canopy closure (ln p/q): F=18.29; forest cover type: F=17.96; open microhabitats: F=15.09.
2. Model E2. Partial F statistics: % canopy closure (ln p/q): F=43.19; sqrt # live stems 0-4 cm dhb: 31.08; soil moisture class: F=22.85; soil parent material: F=8.10.
3. Model D1. Partial F statistics: % taxa dispersed by unassisted means (all life forms): F=59.36; % taxa dispersed by animal conveyance (all life forms): F=46.15; % taxa dispersed by prolonged dormancy (all life forms): F=25.92.
4. Model D2. Partial F statistics: % taxa herbs dispersed by unassisted means: F=32.63: % taxa herbs dispersed by prolonged dormancy: F=22.39; % taxa herbs dispersed by ants: F=19.99; % taxa herbs dispersed by animal ingestion: F=14.38.
5. Model M1. Partial F statistics: % live stems sugar maple: F=92.35; % taxa herbs dispersed by unassisted means: F=58.19; % taxa dispersed by

Notes (cont'd):

5. prolonged dormancy (all life forms): F=57.99.
6. Model M2. Partial F statistics: number tree species >1m: F=79.51; % canopy closure (ln p/q): F=20.33; forest cover type: F=4.29; % taxa dispersed by unassisted means (all life forms): F=69.64.
7. Model M3. Partial F statistics: sqrt # live stems 0-4 cm dbh: F=48.79; % taxa grasses: F=34.58; % taxa herbs dispersed by prolonged dormancy: F=18.00; % taxa herbs dispersed by animal ingestion: F=15.64; % canopy closure (ln p/q): F=9.02; forest cover type: F=6.99.
8. Model M4. Partial F statistics: sqrt # live stems 0-4 cm dbh: F=36.40; % taxa herbs dispersed by prolonged dormancy: F=31.46; % taxa dispersed by animal conveyance: F=22.66; % canopy closure (ln p/q): F=8.51; soil order: F=5.08; open regenerating fields: F=4.53.
9. Model M5. Partial F statistics: % taxa herbs dispersed by wind: F=49.10; sqrt # live stems 0-4 cm dbh: F=29.75; soil moisture class: F=17.34; % canopy closure (ln p/q): F=17.34; soil parent material: F=7.28.

4.2.2.3). In general, dispersal models explained more variance in species richness than did environmental models, and, mixed models explained more variance than either dispersal or environmental models, *sensu stricto*. Model M3, which included environment, life form and dispersal variables, explained 29.9% more variance in species richness than model E2, which included only environment variables.

4.3.3.2 Graphical Evaluation of Alternative Models of Species Richness

The degree to which elements in alternative models explained similar properties of the underlying environment was evaluated graphically by submitting the elements of each model to detrended correspondence analysis (DCA) and using the resulting "species" scores to construct a polygon in ordination space (see Section 4.2.2.3). The ordination space enclosed by each polygon was interpreted to represent the portion of sample space maximally explained by each model. Regression models that overlapped in ordination space were considered less distinctive than models that did not.

The results of this analysis are summarized in Table 4.10; representative graphical solutions are presented in Figure 4.12. The most distinctive model contrasts were between regression models E2 and M1 (no overlap in ordination space), E1 and D2 (minor overlap), and, M1 and M2 (minor overlap). All other models overlapped moderately or strongly in ordination space. Individual elements occupied distinct regions in ordination space when evaluated in contrasts with selected regression models: e.g. elements E14 (open microhabitats) and D12 (dispersal by animal conveyance) when present with elements in model D1 (Figure 4.12); element M34 (dispersal by animal ingestion) when present with elements in model M1 (Figure 4.13); element M53 (soil moisture) when present with elements in model M1 (Figure 4.13); and element M33 (dispersal by prolonged dormancy) when present with elements in model M5 (Figure 4.13). However, dispersal and environmental elements typically occupied proximate positions when present with elements in the superior models of species richness: M1, M3 and M5 (Figure 4.13). These results suggest that while each model addresses unique regions in ordination space, the models in this study primarily represent alternative ways of explaining underlying causal factors.

Table 4.10. Summary of graphical evaluation of leading models of species richness. Legend: E = environmental model, D = dispersal model, M = mixed model. Minor overlap: <10% area of smaller polygon; moderate overlap:10-50% area of smaller polygon: major overlap: >50% of area of smaller polygon.

Model	DCA Ordination Space	Degree of Overlap
E1 vs E2	overlap	moderate
D1 vs D2	overlap	major
M1 vs M2	overlap	minor
M1 vs M3	overlap	moderate
M1 vs M4	overlap	moderate
M1 vs M5	overlap	moderate
M2 vs M3	overlap	major
M2 vs M4	overlap	moderate
M2 vs M5	overlap	major
M3 vs M4	overlap	major
M3 vs M5	overlap	major
M4 vs M5	overlap	major
E1 vs D1	overlap	moderate
E1 vs D2	overlap	major
E1 vs M1	overlap	major
E1 vs M2	overlap	moderate
E1 vs M3	overlap	major
E1 vs M4	overlap	moderate
E1 vs M5	overlap	moderate
E2 vs D1	overlap	minor
E2 vs D2	overlap	minor
E2 vs M1	separate	none
E2 vs M2	overlap	moderate
E2 vs M3	overlap	major

Table 4.10. Summary of graphical evaluation of leading models of species richness (cont'd).

Model	DCA Ordination Space	Degree of Overlap
E2 vs M4	overlap	moderate
E2 vs M5	overlap	moderate
D1 vs M1	overlap	major
D1 vs M2	overlap	minor
D1 vs M3	overlap	moderate
D1 vs M4	overlap	moderate
D1 vs M5	overlap	moderate
D2 vs M1	overlap	major
D2 vs M2	overlap	moderate
D2 vs M3	overlap	moderate
D2 vs M4	overlap	moderate
D2 vs M5	overlap	moderate

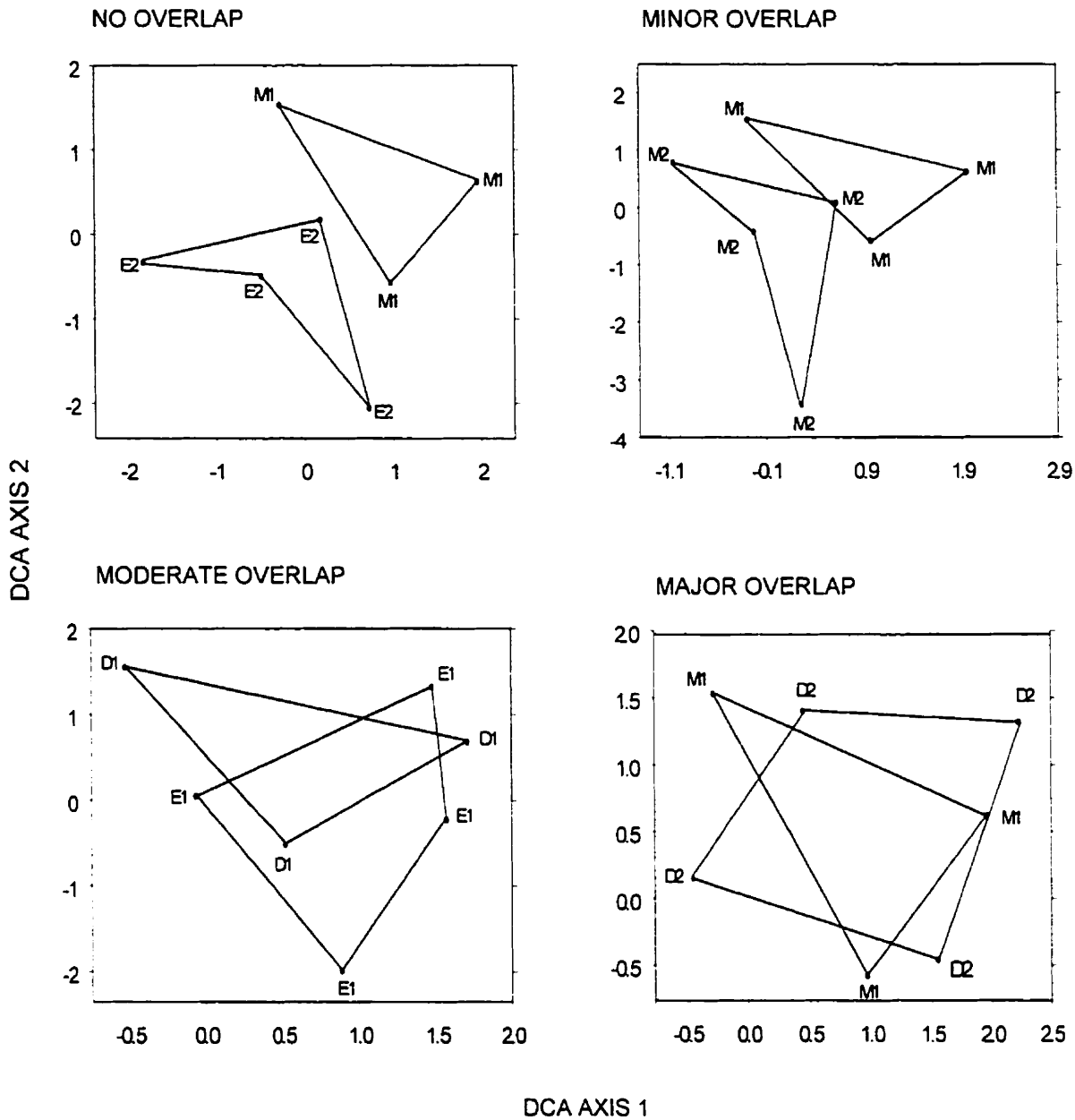

Figure 4.12. Representative results from graphical evaluation of leading GLM models of species richness. Legend: Minor Overlap: <10% area of smaller polygon; Moderate Overlap: 10% - 50% area of smaller polygon; Major Overlap: >50% area of smaller polygon. See Table 4.14 for description of regression models.

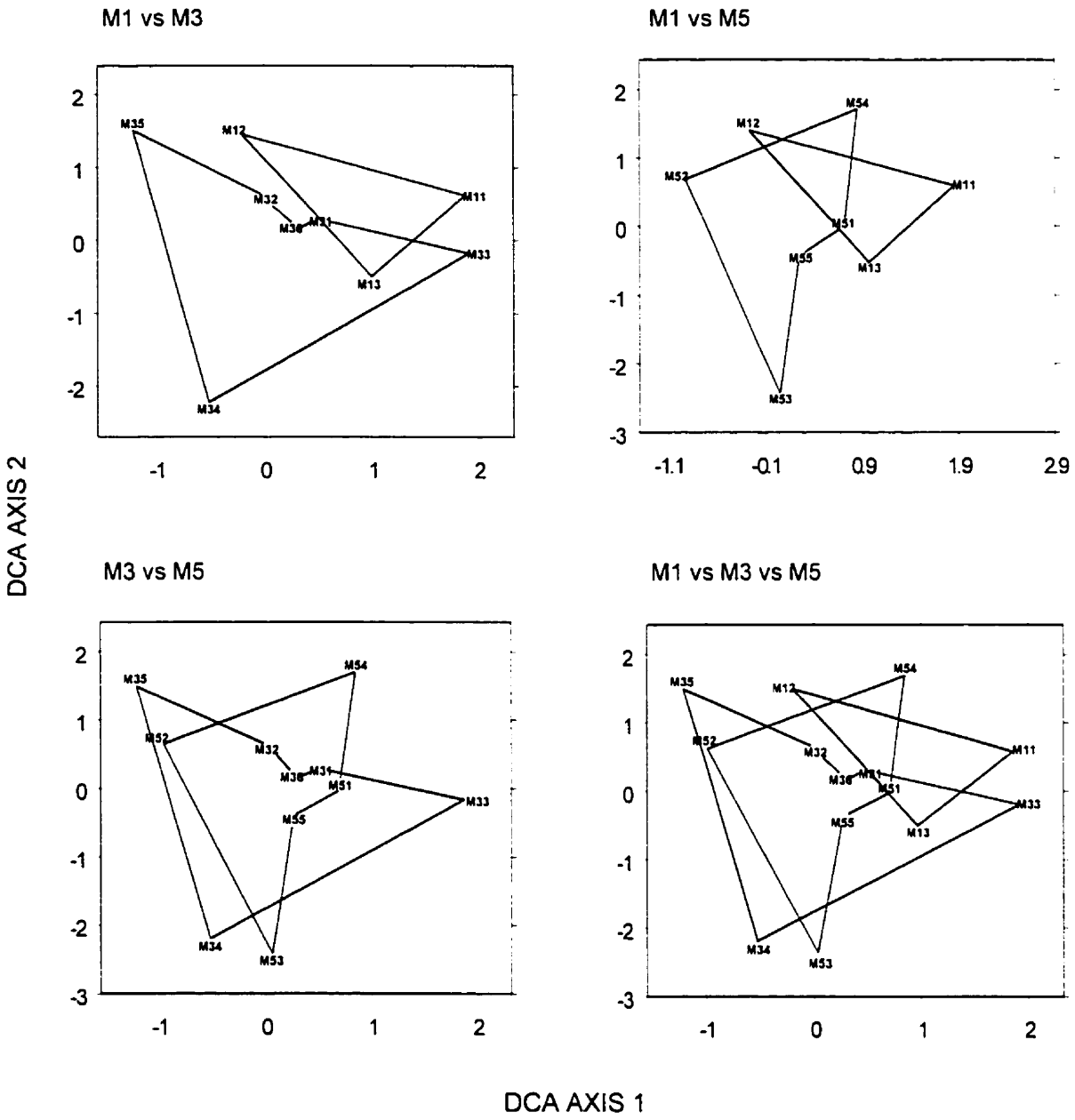

Figure 4.13. Graphical evaluation of superior GLM models of species richness. Legend: M11 = mixed model, number 1, element 1. See Table 4.14 for description of elements and models. DCA = Detrended Correspondence Analysis (ter Braak 1987).

The results of the graphical evaluation of the "superior" models of species richness are presented in Figure 4.13. Model 1 was the most distinct, based on the degree of overlap in ordination space, whereas models M3 and M5 were the most similar. The portion of ordination space shared by all three models was very small.

Shared elements among models have presumably contributed to overlaps in ordination space when present (e.g. D2 vs M1, M3 vs M5). The contribution of shared elements to similarities in the fraction of variance explained by each model, however, is more difficult to discern, owing to the degree to which the elements in a given model co-vary. Inspection of the partial F statistics for each model (Table 4.11) reveals that the contribution of variables-in-common is largely context dependent.

4.3.4 Contribution of Phylogeny

The variables that explain species richness in a given linear regression model may depend in part on the taxonomic rank at which the relationships are examined. Variables that are significant, and non-interacting, at one taxonomic rank may not retain this status at more inclusive ranks owing to a reduction in the number of degrees of freedom. The regression models reported in Table 4.9 were re-evaluated at the ranks of genus, family and order to determine their dependence on taxonomic rank. The results of the analysis for the superior models are reported in Table 4.12.

As expected, the variance explained by a given model, and the quality of the statistical fit, declined with taxonomic rank. The number of interacting elements typically increased with taxonomic rank and, depending on the model, peaked at the rank of genus, family or order. The relative importance of variables often depended on the taxonomic rank of the analysis and elements in selected models did not retain their significance at the more inclusive ranks. The mean number of taxa in a given 10m x 10m quadrat was 42.5 species, 33.4 genera, 23.2 families, and 19.0 orders.

The most apparent cause of the interactions reported in Table 4.12 is the progressive inclusion of plant attributes at the higher taxonomic ranks (Table 4.13). This tendency is most strongly expressed at the rank of order, where more than 50 % of the orders included more than one mode of dispersal,

Table 4.11. Explanatory variables included in leading models of species richness (Table 4.9). Legend: E = environmental model, D = dispersal model, M = mixed model, ALF = all life forms, H = herb life form. See Table 4.9 for descriptions of models and summary statistics.

Variable	Model(s)	Partial F	p>F
# tree species	E1	66.16	<0.0001
	M2	75.51	<0.0001
% canopy closure	E1	18.29	<0.0001
	E2	43.19	<0.0001
	M2	20.33	<0.0001
	M3	9.02	0.0030
	M4	8.51	0.0040
	M5	12.64	<0.0001
forest cover type	E1	17.96	<0.0001
	M2	4.29	0.0024
	M3	6.99	<0.0001
open microhabitats	E1	15.09	0.0001
# stems 0-4 cm dbh	E2	31.08	<0.0001
	M3	48.79	<0.0001
	M4	36.40	<0.0001
	M5	29.75	<0.0001
soil moisture class	E2	22.85	<0.0001
	M5	22.41	<0.0001
soil parent material	E2	8.10	<0.0001
	M5	7.28	0.0001
% unassisted means(ALF)	D1	59.36	<0.0001
	M2	69.64	<0.0001
% animal conveyance (ALF)	D1	46.15	<0.0001
	M4	22.66	<0.0001
% prolonged dormancy (ALF)	D1	25.29	<0.0001
	M1	57.99	<0.0001
% unassisted means (H)	D2	32.63	<0.0001
	M1	58.19	<0.0001
% prolonged dormancy (H)	D2	22.39	<0.0001
	M3	18.00	<0.0001
	M4	31.46	<0.0001
% ants (H)	D2	19.99	<0.0001

Table 4.11. Explanatory variables included in leading models of species richness (cont'd).

Variable	Model(s)	Partial F	p>F
% animal ingestion (H)	D2 M3	14.38 15.65	0.0002 0.0001
% stems sugar maple	M1	92.36	<0.0001
% grasses	M3	34.58	<0.0001
soil order	M4	5.08	0.0007
open regenerating fields	M4	4.53	0.0347
% wind (H)	M5	49.10	<0.0001

Table 4.12. Contribution of phylogeny to superior models of species richness. Generalized linear regression (GLM) models, by row. Predictor variables are the percentage of species, genera, families, or, orders, in 10m x 10m quadrats, with the specified attribute. Sqrt = square root; ln p/q = ln [(proportion)÷(1-proportion)]; n.s. = not significant ($p>0.05$); AI = % taxa herbs dispersed by animal ingestion; ASACC = % live stems >1m *Acer saccharum*; CC = % canopy closure; GRASS = % taxa grasses; MC = soil moisture class; PDH = % taxa herbs dispersed by prolonged dormancy; PDT = % taxa dispersed by prolonged dormancy (all life forms); SPM = soil parent material; WIND = % taxa herbs dispersed by wind; UNASS = % taxa herbs dispersed by unassisted means; 0-4 cm dbh = sqrt # stems 0-4 cm dbh. One outlier, quadrat # 160, removed from each model.

Model	Response Variable	F Statistic	p-Value	r^2 adj.	$p<W$[1]	Interaction
MODEL M1 - SPECIES: % stems sugar maple + % taxa herbs dispersed by unassisted means + % taxa dispersed by prolonged dormancy (all life forms)[1]	sqrt # spp	123.54	0.0001	0.6593	0.88	no
MODEL M1 - GENUS: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means[2]	# genera	94.68	0.0001	0.5996	0.42	no
MODEL M1 - FAMILY: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means[3]	# families	63.77	0.0001	0.4977	0.002	ASACC x PDT ASACC x UNASS
MODEL M1 - ORDER: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means[4]	# orders	59.16	0.0001	0.4787	0.06	ASACC x PDT
MODEL M3 - SPECIES: sqrt # stems 0-4 cm dbh + % taxa grasses + % taxa herbs dispersed by prolonged dormancy + % herbs dispersed by animal ingestion + % canopy closure + forest cover type[5]	sqrt # spp	53.18	0.0001	0.7119	0.95	no

Table 4.12. Contribution of phylogeny to superior models of species richness (cont'd).

Model	Response Variable	F Statistic	p-Value	r^2 adj.	p<W[1]	Interaction
MODEL M3 - GENUS: sqrt # stems 0-4 cm dbh +% taxa herbs dispersed by prolonged dormancy + % taxa grasses + % herbs dispersed by animal ingestion + % canopy closure + forest cover type[6]	# genera	47.07	0.0001	0.6857	0.77	PDH x GRASS
MODEL M3 - FAMILY: sqrt # stems 0-4 cm dbh +% taxa herbs dispersed by prolonged dormancy + forest cover type + % canopy closure + % taxa herbs dispersed by animal ingestion + % taxa grasses (n.s.)[7]	# families	25.65	0.0001	0.5387	0.26	PDH x 0-4 cm dbh CC x 0-4 cm dbh PDH x GRASS PD x AI
MODEL M3 - ORDER: sqrt # stems 0-4 cm dbh +% taxa herbs dispersed by prolonged dormancy + % taxa herbs dispersed by animal ingestion + forest cover type + % canopy closure + % taxa grasses (n.s.)[8]	# orders	23.58	0.0001	0.5168	0.81	CC x 0-4 cm dbh PDH x GRASS AI x GRASS
MODEL M5 - SPECIES: % taxa herbs dispersed by wind + sqrt # stems 0-4 cm dbh + soil moisture class + canopy closure (ln p/q) + soil parent material[9]	sqrt # spp	43.63	0.0001	0.6422	0.89	no
MODEL M5 - GENUS: % taxa herbs dispersed by wind +canopy closure (ln p/q) + sqrt # stems 0-4 cm dbh + moisture class + soil parent material[10]	# genera	36.00	0.0001	0.5957	0.12	MC x 0-4 cm dbh CC x 0-4 cm dbh
MODEL M5 - FAMILY: canopy closure (ln p/q) + moisture class + sqrt # stems 0-4 cm dbh + soil parent material + % taxa herbs dispersed by wind (n.s.)[11]	# families	30.09	0.0001	0.5505	0.40	CC x 0-4 cm dbh

Table 4.12. Contribution of phylogeny to superior models of species richness (cont'd).

Model	Response Variable	F	p-Value	r^2 adj.	p<W[1]	Interaction
MODEL M5 - ORDER: soil parent material + sqrt # stems 0-4 cm dbh + canopy closure (ln p/q) + moisture class + % taxa herbs dispersed by wind (n.s.)[12]	# orders	32.06	0.0001	0.5667	0.07	SPM x WIND SPM x CC CC x 0-4 cm dbh

Notes:

1. MODEL M1: SPECIES: Partial F statistics: % live stems sugar maple: F=92.35; % taxa herbs dispersed by unassisted means: F=58.19; % taxa dispersed by prolonged dormancy (all life forms): F=57.99.
2. MODEL M1: GENUS: Partial F statistics: % taxa dispersed by prolonged dormancy (all life forms): F=115.12; % live stems sugar maple: F=48.18; % taxa herbs dispersed by unassisted means: F=11.42.
3. MODEL M1: FAMILY: Partial F statistics: % taxa dispersed by prolonged dormancy (all life forms): F=69.21; % live stems sugar maple: F=31.62; % taxa herbs dispersed by unassisted means: F=8.07.
4. MODEL M1: ORDER: Partial F statistics: % taxa dispersed by prolonged dormancy (all life forms): F=69.72; % live stems sugar maple: F=16.21; % taxa herbs dispersed by unassisted means: F=9.69.
5. MODEL M3: SPECIES: Partial F statistics: sqrt # live stems 0-4 cm dbh: F=48.79; % taxa grasses: F=34.58; % taxa herbs dispersed by prolonged dormancy: F=18.00; % taxa herbs dispersed by animal ingestion: F=15.64; % canopy closure (ln p/q): F=9.02; forest cover type: F=6.99.
6. MODEL M3: GENUS: Partial F statistics: sqrt # stems 0-4 cm dbh: F=38.08; % taxa herbs dispersed by prolonged dormancy: F=30.20; % taxa grasses: F=24.91; % herbs dispersed by animal ingestion: F=9.41; % canopy closure: F=8.80; forest cover type: F=5.48.
7. MODEL M3: FAMILY: Partial F statistics: sqrt # stems 0-4 cm dbh: F=28.57; % taxa herbs dispersed by prolonged dormancy: F=25.16; forest cover type: F=10.16; % canopy closure: F=6.53; % taxa herbs dispersed by animal ingestion: F=6.41; % taxa grasses: F=0.001 (n.s.).
8. MODEL M3: ORDER: Partial F statistics: sqrt # stems 0-4 cm dbh: F=30.68; % taxa herbs dispersed by prolonged dormancy: F=25.85; % taxa herbs dispersed by animal ingestion: F=10.80; forest cover type: F=6.42; % canopy closure: F=6.14; % taxa grasses: F=0.64 (n.s.).
9. MODEL M5: SPECIES: Partial F statistics: % taxa herbs dispersed by wind: F=49.10; sqrt # live stems 0-4 cm dbh: F=29.75; soil moisture class: F=17.34; % canopy closure (ln p/q): F=17.34; soil parent material: F=7.28.
10. MODEL M5: GENUS: Partial F statistics: % taxa herbs dispersed by wind: F=41.86; % canopy closure (ln p/q): F=20.42; sqrt # stems 0-4 cm dbh: F=18.86; moisture class: F=16.62; soil parent material: F=7.68.
11. MODEL M5: FAMILY: Partial F statistics: soil moisture class: F=22.15; canopy closure (ln p/q): F=21.37; sqrt # stems 0-4 cm dbh: F=21.08; soil parent material: F=15.65; % taxa herbs dispersed by wind: F=0.95 (n.s.).
12. MODEL M5: ORDER: Partial F statistics: soil parent material: F=23.21; sqrt # stems 0-4 cm dbh: F=22.21; canopy closure (ln p/q): F=21.78; moisture class: F=15.27; % taxa herbs dispersed by wind: F=1.36 (n.s.).

Table 4.13. Proportion of taxa with selected plant attributes at progressively more inclusive taxonomic ranks. Categories: Moisture Affinity: obligate upland, facultative upland, facultative, facultative wetland, obligate wetland; Light Affinity: Shade tolerance class 1 (very shade tolerant) - class 5 (very shade intolerant); Mode of Dispersal: animal ingestion, animal adhesion, animal conveyance, wind, prolonged dormancy, mechanical expulsion, unassisted means. Cell entries = % classified taxa with specified number of attribute categories.

Taxonomic Rank	# classified taxa	# Attribute Categories					
		1	2	3	4	5	>1
MOISTURE AFFINITY							
Species	387	100	0	0	0	0	0
Genus	204	74.5	17.2	4.4	2.5	1.5	25.5
Family	76	46.1	22.4	17.1	3.9	10.5	53.9
Order	45	28.9	17.8	26.7	11.1	15.6	71.1
LIGHT AFFINITY							
Species	266	100	0	0	0	0	0
Genus	171	81.3	12.9	5.3	0.6	0	18.7
Family	62	56.5	17.7	16.1	9.7	0	43.5
Order	45	26.7	17.8	31.1	11.1	13.3	73.3
MODE OF DISPERSAL							
Species	413	88.1	11.1	0.5	0.2	0	11.9
Genus	208	86.5	12.5	1.0	0	0	13.5
Family	77	66.2	14.3	11.7	2.6	5.2	33.8
Order	45	42.2	20.0	22.2	4.4	11.1	57.8

and, where more than 70 % of the orders included more than one moisture or light affinity.

Taken together, these results reveal the models of species richness developed for this study are sensitive to the taxonomic rank at which they are assessed. This provides indirect evidence that phylogeny has contributed to the number of taxa recorded in 10m x 10 m quadrats in this study.

4.4 Discussion

i) Environmental Heterogeneity

Environmental heterogeneity, in this study, is spatial and temporal variation in conditions that govern the germination, establishment, growth and reproduction of plants. When measured in relation to traditional environmental variables, heterogeneity in the availability of moisture, nutrients and light explains up to 58.3% of the variance in species richness in 10m x 10m quadrats (Table 4.9). When measured in relation to microhabitats, heterogeneity in site conditions at the landscape scale has facilitated the germination and establishment of 38.3% of the sampled flora (158 species) that was not recorded on closed, seasonally dry, forest floors, *sensu stricto* (Appendix 5).

The contribution of microhabitats to species richness was strongly scale dependent. Whereas 21 of 23 evaluated microhabitats contributed to differences in species richness at the quadrat scale (Table 4.4), only 9 of 20 evaluated microhabitats contributed to differences in species richness at the patch scale (Table 4.5). In contrast, whereas 38 of 39 habitats contained at least one unique species at the quadrat scale (Table 4.4), only 13 of 39 microhabitats contained at least one unique species at the landscape scale, and only five of these contained five or more species not recorded elsewhere in the forest understory (Table 4.6).

One apparent reason for this pattern is that the distribution of species has been constrained by opportunities for germination, establishment and persistence. In a spatially variable environment, differences in plant traits are expected to lead to pattern in the distribution of species and in the composition of local plant assemblages. In this analytical setting, the probability of encountering a new species scales with the size of the sampled area and with the scale of heterogeneity in the local

environment. The observed decline in the number of species restricted to a given habitat is consistent with this scaling relationship, and, with the passive sampling effects associated with an increasing sample size. This suggests that an increasing proportion of the species capable of occupying a given habitat were recorded as the size of the sampled area increased from quadrat to patch to landscape. The sharp decline in the number of contributing habitats in the transition from quadrat to patch suggests that much of the regional variance in environmental heterogeneity was captured at the scale of the forest patch.

Additional factors that may have contributed to this pattern of scale dependence include: the degree of habitat specialization in the sampled flora: the thresholds used to differentiate continuous environmental states into discrete habitat types; the decision to evaluate the relationship at the habitat level, and not in relation to more generalized categories; the sampling decision to locate all eight 10m x 10m quadrats within a 35 metre radius of a fixed sampling point within each forest patch; and, plant dispersal.

The contribution of dispersal to observed differences in the distribution and composition of plant assemblages is less transparent, given the decision to sample plants rather than propagules in this study. Nevertheless, the repeated observation that most propagules land in close proximity of the maternal plant (Appendix 11) suggests that dispersal may rarely limit the availability of propagules within 10m x 10m quadrats, on ecological time scales. This suggests, in turn, that pattern in the distribution of species at this spatial scale is controlled primarily by factors that govern germination, establishment and persistence. Dispersal on the order of decimetres to metres may also be sufficient to sample all habitats with a given forest patch, on most ecological time scales, since all eight quadrats were located within a 35 metre radius of a fixed sampling point.

Dispersal to nearby forest patches currently requires a mean dispersal reach of 41m to1378m, depending on the degree of forest cover in the landscape. Dispersal over this distance should not pose an absolute constraint for taxa dispersed by birds and large mammals (38.5% of the sampled flora) and for taxa dispersed by spores or winged and plumed seeds of low mass (proportion of wind-dispersed taxa, 30.5% of the sampled flora, unknown). Such distances will be beyond the normal

reach of species dispersed by other means, however, and, except for rare long-distance dispersal events, the propagules of these species will remain within the current patch. Dispersal beyond these distances is presumably a low-probability event for even the most mobile of species and thus plant migration, rather than dispersal, is the more relevant consideration when evaluating the distribution of plants at the landscape scale.

Taken together, this reasoning suggests that the distribution and richness of plant assemblages in these forests has been not been constrained by dispersal, given the length of time available, post-glacially, for the dispersal and migration of less mobile taxa. The number of species restricted to a particular habitat, therefore, has been influenced primarily by the spatial and temporal scale of heterogeneity in the local environment and by the spatial scale of the analysis.

Heterogeneity, when measured as the number of microhabitats in a given 10m x10m quadrat, was a significant but weak contributor to species richness ($p=0.0007$, $r^2adj = 0.054$, Table 4.1). The mean number of habitats per 10m x 10m quadrat was 3.01 and ranged from one to ten habitats (supplementary analysis not shown). The weak explanation of variance suggests that diversity in the number of habitats is less important at this spatial scale than the attributes, and area, of the habitats that are present.

The habitats that contributed maximally to species richness, at every spatial scale, were closed seasonally dry forest floors, open regenerating fields, and, open lanes/roads (Tables 4.4,4.5,4.6). These habitats stand in contrast to one another, with respect to available light, habitat structure and site history; and, to related habitats in the forest understory, with respect to available moisture, substrate, transience, and sampled area. Seasonally dry forest floors were more species rich than open lanes/roads and open regenerating fields with respect to total species richness (255 species, 181 species, and 147 species, respectively, Appendix 11) but were far less species rich with respect to mean-richness-when-present (31.1 species, 50.7 species, and 58.0 species, respectively; supplementary analysis not shown). When differences in habitat transience and area are taken into account, open lanes/roads and open regenerating fields are markedly species rich, by any measure, since the latter habitats are transient in time and individually occupied only 1.3% of the total sampled area

(Table 4.4), whereas, closed seasonally dry forest floors persist for the life span of the canopy and occupied 54.3% of the total sampled area.

One apparent reason for the large number of restricted species in these habitats is the suite of adaptations required to germinate, establish, and persist in low and high light environments. One plant trait that has been differentially favored in these habitats is mode of dispersal. Herbs recorded on closed, seasonally dry forest floors were disproportionately dispersed by animal ingestion whereas herbs recorded on open lanes/roads were disproportionately dispersed by prolonged dormancy (Table 3.11). In contrast, herbs recorded in open regenerating fields were disproportionately dispersed by the wind. It may not be coincidental that herbs dispersed by these modes are the most mobile taxa in these forests (Appendix 11), since the seed rain from mobile taxa is more likely to include a greater proportion of species from the surrounding landscape with the capacity to establish in such habitats.

One habitat factor that presumably contributes to this pattern is available light at the soil surface. Establishment in dense shade, for example, has been shown to be facilitated by seed reserves that enable seedlings to survive to the cotyledon stage (Saverimuttu and Westoby 1996). This enables plants with large seeds to specialize on shaded conditions and to avoid the reduction in mean annual fitness that arises when dormancy constrains the number of seeds produced in favorable years (Venable and Brown 1988). Selection pressure for the evolution of dormancy is therefore expected to be weak in closed forest habitats. In contrast, dormancy is expected to be favored in open habitats where the capacity for delayed germination enables plants to avoid unfavorable conditions and to specialize on conditions that maximize reproductive success (Brown and Venable 1986, Cohen and Levin 1987). Selection pressure for the evolution of dormancy in these environments is expected to be greatest in small-seeded annual and biennial plants since the cost of reproductive failure is extirpation. In keeping with these expectations, the number of herbs in this study dispersed by prolonged dormancy increased with increasing light availability and no herbs with an apparent affinity for forested habitats were dispersed by prolonged dormancy (Table 3.7).

The tendency for herbs dispersed by prolonged dormancy to occur more frequently on open lanes

than in open regenerating fields may also be due to differences in available light since leaf litter was absent on the traveled portion of lanes but present in regenerating fields (personal observation). The periodic breakage of stems by passing vehicles and equipment, and the crushing of plants by tires, may also be important since on lanes and access roads the mean height of plants dispersed by prolonged dormancy was significantly lower than plants dispersed by wind or by both wind and dormancy (mean minimum height = 17.3 cm, 32.3cm and 32.3, respectively, $p>\chi^2 = 0.0097$; mean maximum height = 76.6 cm, 133.2cm, and 146.4 cm, respectively, $p>\chi^2 = 0.0001$; supplementary Wilcoxon rank sum tests, based on data on stem heights presented in Gleason and Cronquist 1991, not shown). The mean heights of plants dispersed by prolonged dormancy was also lower on open lanes than in open fields, but not significantly so. In general, however, herbs dispersed by prolonged dormancy were significantly shorter than herbs dispersed by wind or by both wind and dormancy (mean minimum height = 23.0 cm, 31.2 cm and 30.0 cm, respectively, $p>\chi^2 = 0.0333$; mean maximum height = 81.4 cm, 121.7 cm, and 139.5 cm, respectively, $p>\chi^2 = <0.0001$). Taken together, these results suggest that habitat conditions in lanes and fields have favored the persistence of plants with contrasting traits that are causally or passively correlated with mode of dispersal.

ii) Environmental vs Plant Correlates of Species Richness

Overall, plant attributes in this study explained more variance in species richness in 10m x 10m quadrats that did physical attributes of the environment (r^2 adj. = 0.6285, Model D1, versus r^2 adj. = 0.5833, Model E1, Table 4.9). Plant attributes that maximally explained differences in species richness were mode of dispersal (r^2 adj. = 0.5583), habitat affinity (r^2 adj. = 0.4143), life form (r^2 adj. = 0.3373), shade tolerance (r^2 adj. = 0.3247) and moisture affinity (r^2 adj. = 0.3014) (Table 4.8). In contrast, environmental attributes that maximally explained differences in species richness were stand structure (r^2 adj. = 0.5485) and soils (r^2 adj. = 0.3557) (Table 4.1). Significant but weak predictors of species richness were life history (r^2 adj. = 0.1315), human disturbance (r^2 adj. = 0.1280), landscape variables (r^2 adj. = 0.0658) and environmental heterogeneity (r^2 adj. = 0.0537) (Tables 4.1 and 4.8).

The tendency for plant attributes to explain more variance than physical attributes of the environment was not unexpected. Plants in the forest understory sample spatial differences on the

scale of centimetres and temporal differences over the course of a life span, whereas, apparent differences in moisture, nutrients and light were measured or characterized on the scale of decimetres to metres and over the course of one field season. The similarities in explained variance suggests that the scale of the environmental data was appropriate for the scale of heterogeneity in the environment. The overall fraction of explained variance, however, suggests that important factors may have been weakly characterized or overlooked.

Among plant attributes, mode of dispersal explained far more variance than life form, shade tolerance or moisture affinity. One apparent reason for this pattern is that the moisture affinity and shade tolerance of taxa both varied in relation to mode of dispersal ($p>\chi^2$ = 0.02, and <0.0001, respectively, supplementary log likelihood ratio tests, not shown). In contrast, only the shade tolerance of taxa varied with life form ($p>\chi^2$ =<0.0001); the moisture affinity and shade tolerance of classified species were not associated ($p>\chi^2$ = 0.42). Differences in moisture and light availability are thus more likely to be accounted for by modes of dispersal than by life form, or by moisture and light affinity alone.

Mode of dispersal also explained more variance than habitat affinity (r^2 adj. = 0.5583 versus 0.4143, respectively, Table 4.8). The most apparent explanation for this pattern is that mode of dispersal was also strongly correlated with calcium availability in the upper 15 cm of the soil profile whereas habitat affinity was not. Thus differences in moisture, nutrients and light are more likely to be correlated with mode of dispersal than with habitat affinity alone.

The degree to which dispersal has contributed to differences in species richness was not resolved. While there is indirect evidence of directed dispersal by birds in former canopy gaps, and by birds, mammals and ants on disturbance features associated with former canopy gaps (tip-up mounds, tree pits, logs, stumps, closed lanes), most propagules appear to be dispersed at random and in close proximity to the maternal plant (Chapter 3). This suggests that the distribution of plants in a given 10m x 10m quadrat has been determined primarily by factors that govern germination, establishment and persistence.

However, the number of species with a particular attribute in a given quadrat may be influenced by dispersal since the seed rain from mobile taxa is more likely to reflect the diversity of species in the surrounding region that are capable of establishing there. In keeping with this line of reasoning, the mean percentage of plants dispersed by animal ingestion in 10m x 10m quadrats was significantly greater than the proportion in the flora as a whole (herbs:10.1 % vs 6.7 %, $p>|z| = 0.0001$; all life forms: 27.6 % vs 16.9 %, $p>|z| = 0.0000$). This pattern was also apparent in plants dispersed by animal conveyance (all life forms: 15.8% vs 9.7%, $p>|z| = 0.0000$). These taxa are typically shade tolerant and thus may be less constrained by understory conditions that species with an affinity for open habitats. Approximately 80% of the taxa dispersed by animal ingestion were recorded on closed, seasonally dry, forest floors.

The reverse pattern, however, was observed in plants dispersed by the wind (herbs: 10.1% vs 25.4%, $p>|z| = 0.0000$; all life forms: 29.69 % vs 30.5 %, $p>|z| = 0.1054$). This result was not expected and may reflect differences in the dispersal reach of seeds relative to spores, since the proportion of wind dispersed taxa approached their proportion in the sampled flora when ferns and fern allies were included in the analysis. This pattern may also reflect a greater diversity in germination and establishment requirements among wind than animal dispersed taxa, since only 67.6% of the species dispersed by wind were found in canopy openings and only 49.2% were recorded in apparently favorable habitats such as open roads and open regenerating fields (Appendix 11).

On balance, these results suggest that long-distance dispersal has enriched the proportion of species dispersed by animal ingestion and animal conveyance. Overall species richness has been governed by additional factors, however, since dispersal by animal ingestion was strongly associated with low species richness in 10m x 10m quadrats whereas dispersal by wind was strongly associated with high species richness (Table 3.16).

The degree to which dispersal and environmental factors accounted for a unique fraction of the variance in species richness was evaluated indirectly by detrended correspondence analysis (DCA). The results of this analysis suggest that while certain combinations of dispersal and environmental variables may occupy distinct regions in ordination space, they primarily represent alternative ways

of explaining the proximate mechanisms of causation. Modes of dispersal are thus strongly correlated with the habitat factors and plant traits that govern germination, establishment and persistence. Environmental variables, in turn, are correlated with modes of dispersal that determine the composition and size of the seed rain, the initial conditions that seeds and seedlings must confront, and, therefore, who interacts with whom and with what intensity.

In these models (Figures 4.12, 4.13), dispersal by animal ingestion was associated with soil moisture, whereas, dispersal by the wind was associated with the number of tree stems in the 0-4 cm dbh class, forest cover type, and soil parent material. In contrast, dispersal by prolonged dormancy was associated with sugar maple abundance and dispersal by the wind, whereas dispersal by unassisted means was associated with percent canopy closure.

Factors that may contribute to the correlation of environmental and dispersal variables include: i) the predominance of short-distance dispersal in plant communities (Portnoy and Willson 1993, Hughes *et al.* 1994); ii) a convergence of germination and dispersal biology, owing to the necessity for prior germination and reproductive success for the transmission of dispersal alleles from parent to offspring (Venable and Lawlor 1980, Olivieri and Berger 1985, Venable *et al.* 1995, Cody and Overton 1996); iii) the presence of habitat factors that favor dispersal by some modes but not others (Cohen and Levin 1987, Venable and Brown 1988, 1993); and, iv) heterogeneity in local conditions governing germination, establishment and persistence (Fowler and Antonovics 1981, Robertson *et al.* 1988, Lechowicz and Bell 1991, Palmer 1990).

These factors suggest that the contribution of dispersal to species richness is both fundamental and pervasive. The failure to find strong evidence of this contribution, therefore, may be due more to the choice of methodology than to the importance of dispersal, *per se*.

iii) Forest Stand Structure

In this study, the environmental variables that maximally explained species richness were attributes of forest stand structure: forest cover type (r^2 adj. = 0.2765), number of tree species (r^2 adj. = 0.2682), and, the relative abundance of sugar maple (r^2 adj. = 0.2555) (Table 4.1). Stand structure

variables explained more than 50% of the variance in species richness in 10m x 10m quadrats (Table 4.1) and were important elements in the superior models of species richness (Table 4.9).

The capacity of forest stand structure to account for species richness is due in part to the fact that measured attributes both respond to, and alter, the spatial and temporal availability of moisture, nutrients and light on the forest floor. As "consequence", stand structure reflects the past influence of physical and ecological processes that govern the distribution and abundance of plants in the forest understory. As "cause", stand structure controls the spatial and temporal availability of light within the forest canopy and on the forest floor (Minkler and Woerhiede 1965, Horn 1971, 1975, Messier and Bellefleur 1988, Canham *et al.* 1990, Canham *et al.* 1994, Brewer 1980); moderates the availability of nutrients and moisture in the rooting zone of forest soils (Aber *et al.* 1991, Pastor and Post 1986, Zinke 1962, Crozier and Boerner 1984,1986, Leininger and Winner 1988, Boerner and Koslowsky 1989); determines the quantity and quality of coarse woody debris on the forest floor (Harmon *et al.* 1986, Hale and Pastor 1998); influences the probability and size of tree pits created during wind-throw events (Putz *et al.* 1983); and, influences the timing and size of gaps in the forest canopy (Lorimer *et al.* 1988, Lorimer 1989, Frelich and Lorimer 1991).

As a causal factor, stand structure contributes to species richness by providing spatial and temporal heterogeneity in the form of logs, stumps, tree pits, tip-up mounds, raised root mats, and gaps in the forest canopy. These features provide novel resources for the germination, establishment and persistence of new species and for the co-existence of species already established on the forest floor. The results of this study suggest that contribution to coexistence may be far more important than the contribution to richness *per se*.

At small spatial scales, habitat features created by the death of canopy trees provide novel and alternative settings for the germination of propagules from nearby plants, and, the number of local species is substantially enriched (Table 4.4). At larger spatial and temporal scales, these features increasingly represent alternative rather than novel habitat, owing to the apparent tolerance of plants to conditions created by the death of a canopy tree (Figure 2.9), and, the number of new species recorded on these features declines (Tables 4.5 and 4.6). When viewed from the perspective of the

forest patch, or regional landscape, the contribution of habitats created by the death of canopy trees to species richness is strikingly modest relative to the contribution of the forest floor.

The predominance of short-distance dispersal in plant communities, however, suggests that the appropriate spatial scale for this analysis is on the order of metres to tens of metres. At this spatial scale, the availability of alternative habitat is expected to promote species coexistence by increasing the probability that there will be some place, or time, where competitors perform poorly or do not survive and where populations of low abundance species may expand (Hutchinson 1961, Levin 1974, Warner and Chesson 1985, Comins and Noble 1985, Hurt and Pacala 1995). In keeping with this expectation, more species in this study were recorded in canopy gaps (282) than on tip-up mounds (180), logs (120), pits (97) or stumps (64) (Appendix 11). This suggests that species in the understory of these forests differ in their capacity to colonize or persist on these features, and, that the principal contribution of habitats created by the death or removal of canopy trees may be the maintenance, rather than generation, of species richness.

The principal mechanism by which stand structure contributes to differences in species richness, however, is by altering the spatial and temporal availability of light within the forest canopy and on the forest floor. For plants in these settings, the composition of the canopy matters, owing to differences among species in the arrangement of leaves and stems (Horn 1971, Brown and Parker 1994), the transmission of light (Canham *et al.* 1994), the seasonal pattern of leaf expansion and senescence (Brewer 1980), the shade tolerance of seedlings and young saplings (Kobe *et al.* 1995, Lusk and Reich 2000), and, life span (Lorimer 1989). In the forests examined in this study, the species that exerted the greatest control was sugar maple (supplementary correlation analysis not shown: % stems *Acer saccharum*, % stems *Fagus grandifolia*, % stems *Tsuga canadensis*, % stems shade intolerant and very shade intolerant trees, % stems wet-mesic or wet trees, % taxa in shade tolerance class 1, class 2, class 4, class 5). Although capable of casting a deeper shade than sugar maple (Canham *et al.* 1994), beech and hemlock exerted little influence over the availability of light, owing to their low density in the forest canopy.

In keeping with these patterns, the number of species in 10m by 10m quadrats was strongly and

negatively correlated with the absolute and relative abundance of sugar maple. Sugar maple abundance explained 25.6% of the overall variance in species richness (Table 4.1) and up to 63.0% of the variance in species richness in undisturbed quadrats on Brunisolic and Luvisolic soils overlying calcareous till (Figure 4.5). The diversity of trees in the forest canopy, a strong correlate of overall species richness in these forests, and in forests elsewhere in glaciated eastern North America (Braun 1950, Curtis 1959, Whittaker 1965), declined sharply in the presence of sugar maple (Table 4.3), and was up to 50% lower in stands on mesic soils (Table 2.11).

Sugar maple achieved its highest abundance on mesic soils that were high in available calcium (Figures 4.5, 4.6, 4.7 and 4.9). This pattern is commonly observed in southern Ontario (Farrar 1995), where sugar maple abundance is strongly associated with lime rich soils; in the mesic forests of southern Wisconsin (Curtis 1959), where sugar maple dominance and low canopy diversity are associated with high levels of exchangeable calcium in the A_1 layer (36 to 64 cmol/kg); and, in mesic forests elsewhere in the Beech-Maple and Maple-Basswood forest regions (Braun 1950), where sugar maple dominance is strongly associated with glaciated soils that possess an argillic B horizon (Braun 1950, Brady 1990). The correlation between sugar maple abundance and calcium rich soils has also been observed in selected northern hardwood stands in northwestern Connecticut, where the mortality of sugar maple seedlings and young trees is sharply lower than on nearby acidic soils (Kobe *et al.* 1995, Kobe 1996).

This pattern contrasts sharply with abundance of sugar maple elsewhere in its range, where it is typically only one of several trees in the forest canopy. This is particularly true of the rich cove forests of the Mixed Mesophytic, and Oak-Chestnut, forest regions which typically contain up to 30 or more canopy trees (Braun 1950) and an exceptionally species rich understory (Whittaker 1965). The availability of base cations in these forests varies. Reported mean values for exchangeable calcium range from 3.3 cmol/kg in old growth stands in eastern Kentucky (Muller 1982) to 1.95 cmol/kg in mesic eutrophic cove forests on the North Carolina Piedmont (Peet and Christensen 1980). These values are substantially lower than the mean concentration of available calcium in sugar maple dominated quadrats in this study (8.9 cmol/kg) and the mean concentrations reported by Curtis (1950) for exchangeable calcium in the A_1 horizon of sugar maple dominated forests in

southern Wisconsin (32 to 64 cmol/kg).

Exchangeable base cations have been identified as a potential contributing factor to species richness in forests on the North Carolina piedmont (Peet and Christensen 1980). In an analysis of 105 hardwood forest stands on soils of contrasting moisture and fertility, total exchangeable base cations (calcium + magnesium + potassium) explained 85% of the variance in species richness in 0.1 ha plots. In mesic eutrophic cove forests, the most species rich community, the mean concentration of total base cations in the upper 10 cm of the soil profile was 1043 ppm. Calcium ions accounted for 75.0 % of this total. In keeping with cove forests elsewhere in the Oak-Chestnut forest region, the stand with the highest species richness contained 29 species of trees.

In contrast, total base cations in this study explained only 2.5% of the overall variance in species richness ($p>F=0.02$) and did not explain the variance in species richness in undisturbed maple stands on mesic soils overlying calcareous till. When two strong outliers were excluded from the analysis, soil order explained 71.8% of the variance in species richness in these stands and 86.2% of the variance in sugar maple abundance (measured as percent stems sugar maple). Sugar maple abundance, in turn, explained 69.9% of the variance in species richness. In keeping with cove forests, species richness was significantly higher in the quadrats with high tree diversity (mean # tree species per quadrat: 9.4 species on Brunisolic soils versus 4.2 species on Luvisolic soils) and with low sugar maple abundance (mean % stems sugar maple per quadrat: 15.1% on Brunisolic soils versus 76.7% on Luvisolic soils). In contrast to the cove forests, high concentrations of total base cations and exchangeable calcium in the upper 15 cm of the soil profile were associated with low rather than high species richness.

Taken together, these results suggest that species richness on mesic soils in the Peterborough area is governed primarily by soil order and by the percentage of sugar maple stems (>1 m) in the forest canopy. In contrast to the cove forests, calcium availability in Ontario stands is strongly correlated with sugar maple dominance which in turn sharply limits the availability of light within the canopy and on the forest floor. The mean concentration of base cations at which the transition to sugar maple dominance and low species richness may occur is not known, but in these forests, it appears

to lie between 4.3 and 6.8 cmol/kg for available calcium, and between 1795 and 2780 ppm for total base cations. These values are substantially above those reported by Peet and Christensen (1980) for cove forests on the North Carolina piedmont.

The capacity of soil order to explain observed differences in species richness and sugar maple abundance requires further study, since the degree to which soil order stands for available calcium in the preceding analysis is not known. A narrow reading would suggest that properties other than available calcium may be involved since soil order in this analysis explained far more variance in species richness and sugar maple abundance than available calcium (71.8% vs 20.7%, species richness; 86.2% vs 14.2%, sugar maple abundance; supplementary regression analysis not shown). Caution and further analysis are required, however, since available calcium explained 63.0% of the variance in sugar maple abundance when the analysis was restricted to undisturbed second-growth stands on Brunisolic soils (Figure 4.6).

Taken together, however, these results suggest sugar maple abundance, mediated by differences in the availability of calcium, and potentially by unmeasured properties of differentially weathered soils, is the principal contributor to species richness in closed-canopied forests on mesic soils. The proximate mechanism by which this influence is exerted is primarily by control of the spatial and temporal availability of light within the forest canopy and on the forest floor.

iv) Forest Fragmentation

The observation that larger areas, in general, contain more species than smaller areas has recently, and critically, been explained in relation to three hypotheses:

i) the "habitat diversity" hypothesis (Williams 1943,1964), which argues that species number is governed primarily by environmental factors and thus larger areas typically have more species because they have more habitats;

ii) the "passive sampling" hypothesis (Connor and McCoy 1979, Coleman 1981), which argues that species number is controlled primarily by passive sampling of the species pool and thus

larger areas typically contain more species because they represent larger samples;

iii) the "area *per se*" hypothesis (Preston 1960, 1962; MacArthur and Wilson 1963, 1967), which argues that when distance to the propagule pool is held constant, species number will be governed primarily by extinction rates; since these rates are inversely proportional to population size, the number of species in a given sample will be proportional to its area.

The fixed-area sampling design applied in this study provides a suitable context for an indirect test (Gilbert 1980) of the area *per se* hypothesis. The passive sampling and habitat diversity hypotheses each predict that no correlation should be found between patch area and species richness, whereas, the area *per se* hypothesis predicts that a positive correlation should be found (Kelly *et al.* 1989). The mechanisms underlying the passive sampling and habitat diversity hypothesis cannot be distinguished by this test, however, since diverse rather than uniform habitats were sampled in this study (Connor and McCoy 1979). Evidence of a negative relationship between extinction processes and area, however, would provide indirect support for the habitat diversity hypothesis since no relation should be found if passive sampling were the principal or only causal factor involved (Connor and McCoy 1979).

The results of this study were not consistent with the predictions of the area *per se* hypothesis. Species richness in 10m x 10m quadrats was negatively (rather than positively) correlated with patch area (Spearman Rho: -0.2208, $p>|Rho| = 0.0021$) and explained less than 2% of the variance in species richness in linear regression (Table 4.1). In keeping with the habitat diversity hypothesis, the number of microhabitats in 10m x 10m quadrats was positively correlated with species richness (Spearman Rho: 0.2460, $p>|Rho| = 0.0006$) and environmental variables in multiple linear regression explained 58.2% of the variance in species richness in 10m x10m quadrats (Table 4.1). In keeping with the habitat diversity hypothesis, the number of taxa recorded primarily or exclusively in forested habitats ("Forest" and "Forest + Open", *sensu* section 2.2.3.4) was negatively correlated with patch area (Spearman Rho: - 0.2803, $p>|Rho| < 0.0001$). These species are more likely to persist in the forest understory than species of open habitats and thus provide an indirect measure of post-settlement extinction rates in these forests. The negative correlation of apparent

extinction and patch area is contrary to the prediction of both the area *per se* and passive sampling hypotheses. In contrast to the predictions of the habitat diversity hypothesis, however, the number of habitats in 10m x 10m quadrats did not increase with patch area (Spearman Rho: - 0.1949, $p>|Rho| = 0.0068$).

One apparent explanation for the failure of the area *per se* hypothesis in this study is the ameliorating effect of dispersal on local extinction rates (Brown and Kodrik-Brown 1977, Holt 1992). Given the predominance of short-distance dispersal in plant communities (Portnoy and Willson 1993, Hughes *et al.* 1994, Appendix 11), dispersal is expected to be a non-limiting process at the scale of centimetres to metres. In the presence of spatial and temporal heterogeneity, and non-limiting dispersal, differences in plant traits should facilitate persistence by ensuring that there will be some place or time where competitors perform poorly or do not survive and where populations of low abundance may expand (Hutchinson 1961, Levin 1974, Warner and Chesson 1985, Comins and Noble 1985, Hurt and Pacala 1995). Moreover, given that the distance over which plants compete is on the order of centimetres to metres (Harper 1977, Pacala and Silander 1985, 1987, Venable and Brown 1993), the spatial aggregation of conspecifics resulting from short-distance dispersal should sharply diminish the potential for competitive displacement by ensuring that most interactions in a competing plant assemblage occur between individuals of the same species (Schmida and Ellner 1984, Pacala 1986, Lavorel *et al.* 1994, Rees *et al.* 1996). Under these conditions, extinction processes in the forest understory should proceed slowly. And, since both immigration and extinction operate primarily at the micro spatial scale, on ecological time scales, there is no apparent reason why extinction processes should proceed more rapidly in forest patches of smaller size.

The failure to detect a positive correlation between species richness and patch area is consistent with the few studies that have controlled for passive sampling (Harner and Harper 1976, Westman 1983, Kelly *et al.* 1989, Holt 1992, Fukamachi *et al.* 1996, and Scariot 1999). These studies encompass a wide variety of habitats: pinyon-juniper communities in Utah and New Mexico; xeric shrublands of the inner Channel Islands, California; beech forest and manuka scrub on islands in Lake Manpouri, New Zealand; a successional field in Kansas; old growth forest reserves in the cool temperate zone of Japan; and, palm communities in isolated forest fragments in central Amazonia.

respectively. The study by Kelly *et al.* (1989) is perhaps the most convincing demonstration of the contribution of passive sampling effects to species-area relations, since it was conducted on islands on which the entire flora had been systematically sampled by proportional sampling (Quinn *et al.* 1987). The percentage of variation in species richness explained by island area declined from 92% with proportional sampling to 17% (beech forest) and 10% (manuka scrub) with fixed-area samples. The latter results were statistically non-significant.

The negative correlation between habitat diversity and patch area in my study was unexpected and may be due to the fixed-area sampling design. For example, whereas the number of habitats at both the quadrat and patch scale declined with area, the increase in the mean number of habitats from quadrat to patch was highly significant ($p>|t| = 0.0000$: Wilcoxon signed rank sum test). This result conforms to the more traditional pattern when a proportional sampling design has been used.

On balance, the evidence from this study supports the view that the positive correlation that has traditionally been found between patch area and species richness is due primarily to passive sampling effects and to environmental heterogeneity.

4.5 Principal Findings

1. Edaphic variables explained 35.6% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were soil order (r^2adj. = 0.253), soil moisture (r^2adj. = 0.247), and soil parent material (r^2adj. = 0.220).

2. Stand structure variables explained 54.9% of the variance in species richness in 10m x10m quadrats. The variables that maximally explained differences in richness were forest cover type (r^2adj. = 0.277), # tree species >1m (r^2adj. = 0.268), % stems sugar maple (r^2adj. = 0.256), % stems sugar maple 0-4 cm dbh (r^2adj. = 0.254), # wet-mesic, wet tree species >1m (r^2adj. = 0.224), and, # live tree stems 0-4 cm dbh (r^2adj. = 0.196).

   The variance in species richness explained by sugar maple abundance was substantially higher in undisturbed quadrats on Luvisolic or Brunisolic soils overlying calcareous till. In

these settings, the percentage of tree stems (>1m) that were sugar maple explained 63.0 % of the variance in species richness in 10m x 10m quadrats.

3. Human disturbance (lanes, roads, ditches, regenerating fields) explained 12.8% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were disturbed microhabitats (r^2adj. = 0.089), open trails (r^2adj. = 0.089), and open regenerating fields (r^2adj. = 0.079).

4. Environmental heterogeneity, when measured as the number of recorded microhabitats, explained 5.4% of the variance in species richness in 10m x 10m quadrats.

5. Environmental heterogeneity, when measured as the contribution to species richness by individual microhabitats, explained the presence of 38.3% of the sampled flora that did not occur on closed, seasonally dry, forest floors, *sensu stricto*.

Microhabitats that contributed maximally to species richness at the quadrat scale, when present, were open lanes/roads (mean # unique species = 24.3); open regenerating fields (mean # unique species = 19.3); closed, seasonally dry, forest floors (mean # unique species = 16.6), open riparian meadows (mean # unique species = 15.3), and, closed, seasonally moist forest floors (mean # unique species = 15.3)

Microhabitats that contributed maximally to species richness at the patch scale, when present, were closed, seasonally dry, forest floors (mean # unique species = 17.1), open regenerating fields (mean # unique species = 12.5), and open lanes/roads (mean # unique species = 9.0).

Thirteen microhabitats contributed to species richness at the landscape scale (i.e. contained species that were not recorded in any other habitat). Microhabitats that contributed the greatest number of species were closed, seasonally dry, floors (17 species), open regenerating fields (8 species), open lanes/roads (6 species), open canopy gaps on seasonally dry forest

floors (6 species), and, closed, seasonally moist, forest floors (5 species).

6. Patch size was negatively correlated with species richness and explained 1.9% of the variance in species richness in 10m x 10m quadrats. This pattern, and significant interactions with important explanatory variables such as soil parent material, soil order, and forest cover type, were interpreted as evidence that patch size, *per se*, did not make an independent contribution to species richness in this study.

   The most apparent reasons for the failure of the area *per se* hypothesis to explain differences in species richness were the use of a fixed-area sampling design to control for the effects of passive sampling, and, the spatial scale at which extinction processes operate on ecological time scales.

7. Patch isolation, when measured as the mean distance to the nearest 8 forest patches, measured in 45^0 arcs, was negatively correlated with species richness and non-significant. When measured as the percentage of forest cover within a 5 km by 5 km square centred on the study site, path isolation was significantly and negatively correlated with species and explained 6.6% of the variance in species richness. The latter pattern was not regarded as supporting evidence for the MacArthur-Wilson hypothesis, owing to the strongly non-significant relationship for the more direct test of the immigration hypothesis, and, to significant pair-wise interactions between percent forest cover in the landscape and important explanatory variables such as soil order and forest cover type.

8. Dispersal explained 55.8% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were the percentage of taxa that were herbs dispersed by animal ingestion (r^2adj. = 0.397), ants (r^2adj. = 0.333), and the wind (r^2adj. = 0.317).

9. Life history explained 13.2 % of the variance in species richness in 10m x 10m quadrats. The variable that maximally explained differences in richness was percentage of taxa that were

perennial herbs (r^2adj. = 0.132).

10. Provenance explained 26.8% of the variance in species richness in 10m x 10m quadrats. The variable that maximally explained differences in richness was the percentage of taxa that were native herbs (r^2adj. = 0.268).

11. Life form explained 33.7% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were the percentage of taxa that were grasses (r^2adj. = 0.273) and trees (r^2adj. = 0.263).

12. Habitat affinity explained 41.4 % of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in species richness were the percentage of taxa classified as having an affinity for "open" and "forest" habitats (r^2adj. = 0.388 and 0.262, respectively).

13. Shade tolerance explained 32.5% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were the percentage of taxa classified as being very intolerant, and very tolerant, of shade (r^2adj. = 0.293 and 0.214, respectively).

14. Moisture affinity explained 30.1% of the variance in species richness in 10m x 10m quadrats. The variables that maximally explained differences in richness were the percentage of taxa classified as having a facultative affinity for wetland habitats (r^2adj. = 0.301), and the percentages of taxa classified as having a facultative or obligate affinity for upland habitats (r^2adj. = 0.269 and 255, respectively).

15. In general, linear regression models composed of dispersal and environmental variables explained more variance than models composed of dispersal or environmental variables alone. For example, mixed model M3 explained 71.2% of the variance in species richness in 10m x 10m quadrats, whereas dispersal model D1 and environmental model E1,

respectively, explained 62.9% and 58.3% of the variance in richness.

A graphical evaluation of alternative models of species richness revealed that while individual variables and models may occupy distinct regions in DCA ordination space, dispersal and environmental variables primarily represent alternative ways of explaining underlying causal factors. The most apparent reason for this convergence is that dispersal is a non-limiting process at the scale of centimetres to metres. A further contributing factor may the tendency for the dispersal and germination biology of plants to converge, owing to the necessity of prior germination success for the transmission of alleles for dispersal.

16. The linear regression models of species richness in this study are sensitive to the taxonomic rank at which they are assessed. The variance in richness explained by a given model, and the quality of the statistical fit, declined at progressively more inclusive ranks. The number of interacting elements typically increased with taxonomic rank, and, depending on the model, peaked at the rank of genus, family or order.

The most apparent cause of the interactions was the progressive inclusion of plant traits at the higher taxonomic ranks. This tendency was most strongly expressed at the rank of order, where more than 50% of the orders in the analysis included more than one mode of dispersal, and where more than 70% of the orders included more than one moisture or light affinity. Taken together, these patterns were interpreted as indirect evidence that phylogeny has contributed to the diversity of taxa recorded in these forests.

5.0 GENERAL CONCLUSIONS

The principal findings and conclusions of the thesis are summarized below. Specific findings related to the distribution of species, and to modes of dispersal, in relation to environmental variables are reported in Chapters 2.5 and 3.5 respectively. Specific findings related to the capacity of environmental variables and plant traits to explain observed differences in species richness are reported in Chapter 4.5.

1. Herbs, unlike other life forms, were dispersed by every mode of dispersal recorded in these forests. The reasons for this pattern are beyond the scope of this thesis but suggest in part that the outer integuments that evolved to protect the developing ovule in the angiosperms have been responsive to selection pressure when subsequent modifications facilitated dispersal by various means (Stebbins 1974). The capacity to disperse by one or by many modes, however, did not influence the number of habitats colonized by a given life form.

2. The mode by which a given herb dispersed was often associated with the type of fruit it possessed. Achenes, for example, were more likely to be dispersed by the wind than by other modes, whereas, berries and drupes were more likely to be dispersed by animal ingestion. Seeds in capsules were more likely to be dispersed by mechanical expulsion and by animal conveyance, whereas, schizocarps were more likely to be dispersed by adhesion to animals. Nutlets were more likely to be dispersed by unassisted means and by prolonged dormancy in the soil, whereas seeds in capsular fruits were more likely to be dispersed by prolonged dormancy in the soil and by animal conveyance.

   The degree to which mode of dispersal was predetermined by the type of fruit a herb possessed was less clear. The berry, drupe, and silique were over-represented in herbs with an affinity for forest habitats whereas the legume was over-represented in herbs with an affinity for open habitats. This tendency is consistent with some measure of control by fruit type. However, the colonization pattern for fleshy fruits may also be explained, in part, by the tendency of seeds of fruits ingested by birds to be excreted in tree-fall gaps and the adjacent forest (Hoppes 1988, Malmborg and Willson 1988).

Evidence consistent with marginal or no control by fruit type among herbs was more pervasive. First, in contrast to the previous pattern, the majority of fruit types in this study (achene, capsular, capsule, follicle, nutlet, schizocarp) were *not* associated with the habitats in which they are typically found. Second, most fruits of herbs in this study were dispersed by several modes. The apparent exceptions were the drupe, which was dispersed by animal ingestion; the silique, which was dispersed by unassisted means; and, the berry, which was dispersed by animal ingestion and by animal conveyance. In contrast, the achene and the capsule were each dispersed by every mode save one (mechanical expulsion and animal ingestion, respectively). The latter fruit types were possessed by 70% of the herbs recorded in this study.

Third, the tendency for certain modes of dispersal to be more frequent in some habitats than others appears to be related more to germination constraints than to fruit type. For example, the tendency for wind-dispersed herbs to be over-represented in open habitats, and under-represented but present in forest habitats, may be explained in part by the differential germination success of large versus small seeds in deep shade (Salisbury 1942, 1974; Baker 1972, Luftensteiner 1979, Mazer 1990, Saverimutto and Westoby 1996). In keeping with this hypothesis, the reported seed mass for congeners of wind-dispersed herbs in this study was consistently heavier for herbs with an affinity for closed versus open habitats (*sensu lato*). The statistical significance of this trend could not established owing to the small sample size. In a similar fashion, the tendency for herbs dispersed by prolonged dormancy to be associated with an affinity for open habitats may also be explained by differential germination success in open versus closed habitats (Brown and Venable 1986, Cohen and Levin 1987, Venable and Brown 1988).

Taken together, the evidence from this study suggests that fruit type exerts little or no control over the mode of dispersal of herbs in the forest understory. Further study of the understory flora in the Great Lakes - St. Lawrence Forest Region (Rowe 1972) is necessary, however, in view of modest sample size (n=234 herbs) associated with this study. This pattern, if widespread, is keeping with the finding by Westoby *et al.* (1992) that mode of dispersal is

rarely constrained by seed size. Taken together, these findings suggest that the habitats in which plants establish will rarely be constrained by the way in which they disperse. This greatly increases the range of solutions (to ecological problems) available to plants.

3. The composition of herb assemblages in sampled patches has apparently not been constrained by the *mode* of dispersal, or at least, has not been constrained absolutely. Each mode of dispersal was represented on each portion of the environmental gradients examined, and, with few exceptions, in each type of microhabitat. The exceptions were 7 rare habitats with moist or wet soil conditions: closed seeps; open seeps; closed, seasonally moist tree pits; open, seasonally wet tree pits; open riparian marsh; open riparian thicket. Although most modes were absent from at least one 10m x 10m quadrat, each mode of dispersal was present in all but one of twenty-four sampled patches. These patterns reveal that at least some seeds from each functional group were able to reach most patches and to germinate in the conditions recorded there.

4. The habitats in which a given herb was found, however, were associated with the mode by which it dispersed. This suggests that certain modes of dispersal, or traits correlated with dispersal, may be favored in some habitats but not others. Herbs dispersed by animal ingestion, for example, were strongly over-represented (relative to their proportion in the sampled flora) in closed seasonally dry canopy gaps, on open tip-up mounds, and in closed seasonally dry tree pits. In contrast, herbs dispersed by the wind were over-represented in regenerating fields, and, herbs dispersed by prolonged dormancy were over-represented on open lanes and access roads. Herbs dispersed by animal adhesion, ants, mechanical expulsion, unassisted means, and vegetative expansion were over-represented in at least one of the habitats in which they were found.

The degree to which these patterns of association were caused by dispersal, or by plant traits correlated with dispersal, could not be answered with the sampling design applied in this study. However, the habitats in which certain herbs were typically over-represented were consistent with a distribution pattern that had been mediated by dispersal. The indirect

evidence for directed dispersal was strongest for herbs dispersed by birds and mammals: i) patterns of colonization that were consistent with the foraging and seed-processing patterns of frugivorous birds (Thompson and Willson 1978, Willson *et al.* 1982, Malmborg and Willson 1988, Hoppes 1988); ii) patterns of colonization that provided little evidence of differential germination or persistence; e.g., all fleshy-fruited herbs recorded in tree pits or on tip-up mounds, logs, and stumps were observed on forest floors, and, all but two fleshy-fruited herbs recorded on forest floors were present in tree pits or on tip-up mounds, logs and stumps; and, iii) patterns of distribution which revealed that the over-representation of fleshy-fruited herbs on these features was due to the greater number of fleshy-fruited species rather than to a greater proportion of taxa that were able to colonize such habitats.

The degree to which dispersal has contributed to the distribution pattern of herbs dispersed by other means is less certain. Herbs dispersed by the wind, for example, were consistently associated with open microhabitats and with human disturbance. While propagules with wings and plumes may travel farther in these habitats than under a closed forest canopy (Hughes *et al.* 1994), the tendency for wind-dispersed herbs to be poorly represented in forest habitats is equally or more likely to be caused by differential germination success arising from differences in seed weight (Salisbury 1942, 1974, Baker 1972, Luftensteiner 1979, Mazer 1990, Saverimuttu and Westoby 1996). In keeping with this line of reasoning, wind-dispersed herbs with an affinity for "forest" habitats were recorded in significantly more quadrats than were wind-dispersed herbs with an affinity for "open" habitats. This pattern suggests that the distribution of wind-dispersed herbs in the forest understory is constrained more by germination, establishment and persistence than by dispersal.

A similar case can be made for herbs dispersed by prolonged dormancy in the soil. In keeping with recent models of the evolution of dormancy (Venable and Lawlor 1980, Brown and Venable 1986, Cohen and Levin 1987, 1991, Venable and Brown 1988, 1993, Rees 1996), more than 90% of the seed-pooling herbs in this study were species with an affinity for "open" or "open + forest" habitats, and, none of the herbs with an apparent affinity for "forest" habitats was classified as a seed-banking species. Taken together, these patterns

suggest that in forested habitats dispersal in time may be restricted to fugitive species and to sites of recent canopy disturbance. In keeping with this line of reasoning, herbs with the capacity for dormancy were significantly over-represented in the trace cover class (1-5 individuals) and under-represented in the higher cover classes. Herbs with the capacity for prolonged dormancy were found in a wide variety of habitats, however, including closed forest floors. This suggests that these herbs may persist in the understory of second-growth forests for many years. For these herbs, the conditions required for germination and establishment appear to be more limiting than the conditions required for persistence (Grubb 1977, 1988; Grime 1997).

The colonization pattern of herbs dispersed by other modes was consistent with non-directed dispersal and factors governing germination, establishment and persistence. Longer distance dispersal of herbs dispersed by mechanical expulsion and by unassisted means is presumably facilitated by animal ingestion since each species has a sizeable North American range. However, pattern resulting from such dispersal events was not detectable by the sampling design applied in this study.

Taken together, the indirect evidence from this study suggests that distribution of herbs in the forest understory is governed more by differential germination, establishment and persistence than by dispersal. The apparent exceptions are plants dispersed by animal ingestion and by ants. The tendency in this study for modes of dispersal to be associated with particular habitats appears to be due more to plant traits that are correlated with dispersal than to the dispersal process *per se*.

5. The number and composition of plants in the forest understory was strongly influenced by the abundance of sugar maple. Mean species richness (all life forms) in undisturbed 10m x 10m quadrats declined from 46.0 species in quadrats with ≤25 % stems (>1 m) sugar maple to 27.1 species in quadrats with ≥75% stems (>1 m) sugar maple. Associated with this 41.1% decline in mean richness was a marked rise in the proportion of prevalent species (≥20% frequency) that flowered before canopy closure (35.2% to 55.6%) and that were shade

tolerant (54.9% to 72.7%).

Curtis (1959) has argued that the forest floor is a demanding environment that requires specialized traits for success and that it is the limited set of species that possess those traits that has led to the striking uniformity in species composition in the mesic hardwood forests of eastern North America. In keeping with this hypothesis, 92.5% of the species that were prevalent in the understory of southern mesic forests in Wisconsin were present in maple dominated forests in this study. Traits that were prominent in each geographic region were early spring flowering and shade tolerance.

Early spring flowering is one of several plant traits that have been associated with deep shade in the forest understory. In herbs with low shade tolerance, early flowering is associated with an ephemeral (Sparling 1967) or winter annual (Rogers 1982) life history. Each facilitates net carbon gain by restricting the growth phase to periods when the canopy is leaf free. More commonly, however, the early flowering habit is associated with varying degrees of shade tolerance that enables shoots and leaves to persist until mid to late summer (Sparling 1967, Rogers 1982). The latter combination of characters was more common in the Peterborough area where only six of sixty-two early flowering species were spring ephemerals (*Allium tricoccum, Caulophyllum thalictroides, Claytonia caroliniana, Dicentra canadensis, Dicentra cucullaria, Erythronium americanum*); only one species (*Galium aparine*) was a known winter annual.

Related plant traits that may facilitate survival in deeply shaded habitats include winter-green leaves (Bierzychudek 1982) and the initiation of shoot growth (Taylor and Pearcy 1976) or flower initials (Bierzychudek 1982) in early autumn. The former trait greatly extends the period of carbon gain in species such as *Carex plantaginea, Hepatica acutiloba, Maianthemum canadense, Tiarella cordifolia, Trientalis borealis, Viola blanda,* and *Viola rostrata,* whereas the latter traits facilitate early spring growth and flowering in species such as *Allium tricoccum, Trillium grandiflorum, Arisaema triphyllum,* and *Geranium maculatum.*

The capacity of plants to tolerate deep shade has been attributed to a suite of traits that facilitate the capture and processing of light energy at the lowest net cost. Morphological characters associated with shade plants include: thin leaves with a large surface area (Grime 1965); a higher proportion of chlorophyll *b* relative to chlorophyll *a* (Boardman 1977); a chloroplast with large grana stacks oriented in more than one plane (Boardman 1977); a higher proportion of leaf nitrogen allocated to chlorophyll than to carboxylating enzymes and other proteins (Seeman *et al.* 1987, Niinemets 1997, Lusk and Reich 2000); a rapid stomatal response to changes in light intensity (Hicks and Cabot 1985); and leaves deployed in horizontal, non-overlapping layers (Grime 1965, Horn 1971). These traits facilitate the capture of energy in low light environments while minimizing the energetic cost to construct and maintain plant tissue. The latter is perceived to be especially important since it results in a lower leaf dark respiration rate and lowers the compensation point for net carbon gain (Grime 1965, Loach 1967, Lambers *et al.* 1983, Lusk and Reich 2000). These characters were not scored directly in this study owing to the lack of a suitable data set.

The foregoing traits, and a large seed (Saverimuttu and Westoby 1996), are expected to be among those essential for germination, growth and reproduction on the forest floor. It is more likely, therefore, that it is traits correlated with dispersal, rather than the dispersal process *per se*, that fundamentally govern the distribution of plants on the forest floor. One important reason for this may be the necessity of prior germination and reproductive success for the transmission of dispersal alleles from parent to offspring.

6. Sugar maple abundance on mesic soils was significantly correlated with available calcium (exchangeable calcium + free calcium carbonate) in the upper 15 cm of the soil profile. When differences in soil parent material, soil order, soil series, and site disturbance were standardized, available calcium explained 42.1% of the variance in the number of sugar maple stems (>1m) in 10m x 10m quadrats and 62.8% of the variance in the percentage of stems that were sugar maple. In keeping with the calcium - mortality hypothesis (Kobe *et al.* 1995, Kobe 1996), calcium availability explained observed differences in the number of sugar maple stems subject to shade stress and self-thinning. In undisturbed stands on

Brunisolic soils overlying calcareous till, differences in available calcium explained 70.9% of the variance in stem number in the 4-10 cm dbh size class and 22.3% of the variance in stem number in the 10-30 cm size class. The decline in explained variance with increasing stem size is consistent with the decline in shade stress experienced by stems as they reach the middle and upper layers of the forest canopy.

Unexpectedly, however, available calcium did not explain the variance in the number of sugar maple stems (>1m) in the 0-4 cm class. These stems are typically the most deeply shaded stems within the forest canopy, and therefore among the stems that would most benefit from a calcium-mediated reduction in leaf dark respiration rates. The soils in this analysis were particularly rich in magnesium, however, and may be causing nutrient stress owing to an imbalance in base cations. To avoid antagonism in the uptake of potassium and magnesium in sugar maple in the Quebec Appalachians, Ouimet and Camire (1995) concluded that the potassium:magnesium ratio in the B soil horizon should be >1. To avoid calcium deficiencies associated with crown die-back, the calcium:magnesium ratio should be > 4. In contrast, the potassium:magnesium ratio was <1 in approximately 50% of the quadrats in this analysis, whereas, the calcium:magnesium ratio was < 4 in approximately 60% of the quadrats. In keeping with a cation imbalance hypothesis, the number of sugar maple stems in the 0-4 cm dbh size class on these soils increased with increasing values of the calcium:magnesium, and magnesium:potassium, ratio, and, declined in the presence of increasing magnesium.

Taken together, these results suggest that the abundance of sugar maple in the forest understory may be limited by the availability, and ratio, of base cations in the soil. This constraint was most apparent on mesic soils and suggests that on the optimal portion of the moisture gradient sugar maple may be secondarily constrained by the availability of base cations.

7. The data from this study suggests that many plants in the forest understory may be responsive to differences in available calcium. Ephemeral spring herbs, for example,

typically occurred on more calcium rich soils (mean concentration = 6.9 cmol/kg) than plants with persistent shoots that flowered prior to, or after, canopy closure. Early spring flowering plants with persistent shoots typically occurred on more calcium rich soils than plants which flowered mid to late season (mean concentration = 5.7 and 5.4 cmol/kg, respectively), but not significantly so. The shade tolerant members of these functional groups, however, occurred on soils that were significantly more calcium rich than species with moderate and low shade tolerance. This pattern suggests that plants in these forests have partitioned the calcium availability gradient in relation to the degree of shade stress to which they were exposed.

The mechanism(s) by which understory plants benefit from calcium rich soils are presently unresolved. Recent studies of cold temperate trees have found an association between foliar calcium levels and dark respiration rates (McLaughlin *et al.* 1991, McLaughlin and Kohut 1992) and sharp reductions in the mortality of sugar maple saplings on calcium rich soils (Kobe *et al.* 1995, Kobe 1996). The greater availability of nitrogen on calcium rich soils (Dancer *et al.* 1973) may be equally or more important for some species, however, and studies have recently been initiated in the U.S. northeast to clarify the relative contribution of calcium and nitrogen to tree growth and mortality relations (Dr. A. Finzi, Department of Biology, Boston University, *pers. com.*; Dr. R.K. Kobe, Department of Forestry, Michigan State University, *pers. com.*).

The greater availability of nitrogen may be particularly important for ephemeral spring herbs since they typically complete their life cycle before the canopy closes (*Allium tricoccum*, the apparent exception, flowers mid to late summer). These species typically have a high light compensation point and a high saturation light intensity (Sparling 1967, Taylor and Pearcy 1976) and may therefore have a greater physiological requirement for nitrogen than more shade tolerant species. The reported affinity of ephemeral spring herbs for base rich, and particularly calcium rich, soils (Curtis 1959, Rogers 1982) may therefore be due in part to the greater availability of nitrogen on these soils.

For shade tolerant herbs, however, the principal mechanism may be a reduction in dark respiration rate. The morphology and physiology of these species typically emphasizes the conservation of reserves rather than photosynthetic performance (Went 1957, Grime 1965, Loach 1967) and thus may benefit more from a reduction in dark respiration rate than from a greater availability in nitrogen. Efficient use of high irradiance requires a high nitrogen investment in carboxylating enzymes and proteins responsible for photosynthetic electron transport (Niinemets 1997). Shade tolerant species, however, typically allocate proportionally more leaf nitrogen to chlorophyll than to carboxylation capacity (Seeman *et al.* 1987). This investment pattern is thought to be the primary reason why shade tolerant species have a lower respiration rate per unit of leaf N (Lusk and Reich 2000) and an intrinsically low photosynthetic plasticity (Niinemets 1997). In keeping with the latter finding, experimental transfers of plants between high and low light environments have shown that dark respiration rates can change much more rapidly than photosynthetic capacity (Azcon-Bieto and Osmond 1983, Sims and Pearcy 1991). Taken together, these findings suggest that shade tolerant plants on calcareous soils may benefit more from a reduction in dark respiration rate than from a greater availability in nitrogen.

8. The contribution of environmental heterogeneity to species richness was strongly scale dependent. Whereas 21 microhabitats contributed to a significant difference in species richness at the quadrat scale, only 9 microhabitats did so at the scale of the forest patch. In keeping with this pattern, 38 of 39 microhabitats contained at least one unique species when evaluated at the quadrat scale whereas only 13 of 39 microhabitats did so when evaluated at the landscape scale.

In a spatially and temporally variable environment, differences in plant traits are expected to lead to pattern in the distribution of species owing to differential germination, establishment and persistence. In this context, the probability of encountering new species should scale with the size of the sampled area and the scale of heterogeneity in the sampled environment. The observed decline in unique species at increasingly larger spatial scales is consistent with this scaling relationship and suggests that an increasing proportion of the

species capable of occupying a given habitat were recorded as the size of the sampled area increased from quadrat to patch to landscape. The sharp decline in the number of contributing habitats in the transition from quadrat to patch suggests that a large fraction of the regional variance in environmental heterogeneity was captured at the scale of the forest patch.

In this study, habitat features created by the death or removal of canopy trees were an important source of environmental heterogeneity at small spatial scales. Features such as logs, stumps, tree pits, tip-up mounds, raised root mats, and canopy openings provided novel resources for the germination and establishment of new species and alternative habitat for species already established on the forest floor. The latter process is expected to promote species coexistence by providing some place or time where competitors perform poorly or do not survive and where populations of low abundance may expand (Hutchinson 1961, Levin 1974, Warner and Chesson 1985, Comins and Noble 1985, Hurtt and Pacala 1995).

In keeping with this expectation, these habitats were colonized by 86% of species recorded on closed, seasonally dry, forest floors, 82% of species recorded in moist or wet habitats, and 78% of species recorded in habitats created by human disturbance. However, the capacity of species to colonize or persist on these features was not uniform: more species were recorded in canopy gaps (282) than on tip-up mounds (180), raised root mats (138), logs (120), tree pits (97), and stumps (64). In these forests, the provision of alternative habitat was far more prevalent than the provision of novel resources for new species since only 20% of the species recorded on these features were not found elsewhere on the forest floor.

Taken together, these results provide support for the hypothesis that heterogeneity facilitates the coexistence of species through the spatial and temporal segregation, and differential performance, of competing species (e.g. Levin 1974, Chesson and Warner 1981, Shmida and Ellner 1984, Comins and Noble 1985, Warner and Chesson 1985).

9. Dispersal variables explained more variance in species richness in 10m x 10m quadrats than

did environmental variables (r^2adj. = 0.6285, Model D1 versus r^2adj. = 0.5833, Model E1). The statistical significance of this difference could not be determined, however, owing to interactions among the explanatory variables. The degree to which modes of dispersal and physical attributes of the environment accounted for the same variance was subsequently evaluated indirectly by detrended correspondence analysis (DCA). The results of this analysis revealed that while certain combinations of dispersal and environmental variables may occupy distinct regions in ordination space, they primarily represent alternative ways of explaining the proximate mechanisms of causation. Modes of dispersal are thus strongly correlated with habitat factors and plant traits that govern germination, establishment and persistence. Environmental variables, in turn, are correlated with modes of dispersal that determine the composition and size of the seed rain, the initial conditions that seeds and seedlings must confront, and, therefore, who will interact with whom and with what intensity in competing plant assemblages.

The most apparent explanations for this correlation are: i) the predominance of short-distance dispersal in plant communities (Portnoy and Willson 1993, Hughes *et al.* 1994, Appendix 11); ii) a convergence of germination and dispersal biology, at local spatial scales, owing to the necessity of prior germination success for the transmission of dispersal alleles from parent to offspring (Venable and Lawlor 1980, Olivieri and Berger 1985, Venable *et al.* 1995, Cody and Overton 1996); iii) the presence of habitat factors that favor dispersal by some modes but not others (Cohen and Levin 1987, Venable and Brown 1988, 1993); and, iv) heterogeneity in local conditions governing germination, establishment and persistence (Fowler and Antonovics 1981, Robertson *et al.* 1988, Lechowicz and Bell 1991, Palmer 1990).

Under these conditions, dispersal in the forest understory is primarily a non-limiting process and pattern in the composition and distribution of plant assemblages is due primarily to factors governing germination, establishment and persistence.

10. Dispersal is expected to have profound consequences for populations and communities since it determines the size and composition of the seed rain (Clark and Yi 1995), determines the initial conditions that seeds and seedlings confront (Schupp and Fuentes 1995), determines who interacts with whom, with what intensity, and over what time scale (Atkinson and Shorrocks 1981, Schmida and Ellner 1984, Pacala and Silander 1985, Pacala 1986, 1987, Lavorel *et al.* 1994, Rees *et al.* 1996), influences local extinction rates by affecting the probability that declining or extirpated populations are rescued (Brown and Kodric-Brown1977), influences the rate at which plants colonize new habitat (Halpern *et al.* 1990, Matlack 1994, Kotanen 1997, Brunet and von Oheimb 1998) and the sequences in which they arrive (Drake 1991, Fastie 1995), and, influences the level of gene flow between populations and thus the degree to which neighboring plants are related (Williams and Guries 1994) and genetic variation is structured spatially (Levin 1981, Hamrick *et al.* 1993, Hamrick and Godt 1997).

This suggests that the contribution of dispersal to plant dynamics is both fundamental and pervasive. The failure to find strong evidence of this influence in the composition and distribution of herbs in the understory of sampled forests is therefore surprising. On reflection, this result reflects both the nature of the dispersal process and the choice of methodology for this study.

If most seeds of most plants land within a few metres of the maternal plant, then the principal contribution of dispersal to spatial pattern is the spatial aggregation of conspecifics and the randomization of neighbors in competing plant assemblages. Theory predicts that the former pattern should facilitate the coexistence of species by increasing the frequency of competitive interactions among conspecifics, whereas, the latter pattern should enable populations of low abundance to expand by increasing the probability of reversals in relative competitive strength (Hutchinson 1961, Atkinson and Shorrocks 1981, Chesson and Warner 1981, Shmida and Ellner 1984, Pacala and Silander 1985, Warner and Chesson 1985, Pacala 1986, Lavorel *et al.* 1994, Rees *et al.* 1996). The contribution of the latter mechanism is expected to increase with increasing dispersal distance from the maternal plant and to be influenced

by the scale of spatial and temporal heterogeneity in the local environment (Levin *et al.* 1984, Comins and Nobel 1985, Chesson 1986, Pacala 1987, Lavorel and Chesson 1995).

This suggests that the principal contribution of dispersal to spatial pattern may occur at the scale of the competing plant assemblage. The degree to which these micro-scale processes have influenced the spatial distribution of plants in the forest understory could not be answered with the methodology applied in this study. The decisions at the outset of this study to map plants rather than propagules, and to evaluate functional groups in relation to microhabitats and environmental gradients rather than individual species in relation to spatial aggregation and competing plant assemblages, precluded subsequent examination of these matters when their potential significance became apparent during preliminary analysis of the data.

The inference that pattern in the composition and distribution of plant assemblages is due primarily to differential germination, establishment and persistence, therefore, understates the contribution of dispersal to plant dynamics and persistence at the micro spatial scale.

Concluding Remarks

The patterns of colonization examined in this study suggest that the principal contribution of dispersal to the spatial distribution, composition, and coexistence of species is made at the scale of the competing plant assemblage and at the scales at which environmental heterogeneity enables populations of low abundance species to expand. If most seeds of most plants land within one to two canopy diameters of the maternal plant, as the current literature suggests, then the principal contributions of dispersal to the spatial distribution, and coexistence, of plants may be the spatial aggregation of conspecifics near the base of the maternal plant, and the randomization of neighbors in adjacent competing plant assemblages. Paradoxically, but perhaps necessarily, the primary contribution to species coexistence, and to reproductive assurance, is made at a spatial scale where differences in the dispersal reach of evolved dispersal morphologies are minimized.

In the forest understory, habitat features created by the death or removal of canopy trees are an important source of environmental heterogeneity at small spatial scales. Canopy openings, tree pits, tip-up mounds, raised root mats, logs and stumps were widespread on the forest floor and apparently well within the dispersal reach of even the least mobile species. Evidence from this study suggests that these features provide novel resources for new species and alternative habitat for species already established on the forest floor. The former contributes to species richness in the forest understory, whereas, the latter may promote species coexistence by providing some place or time where competitors perform poorly, or do not survive, and where populations of low abundance may expand. In this study, the provision of alternative habitat appeared to be the more important process, since only twenty percent of the species recorded on these features were not found elsewhere on the forest floor.

Heterogeneity in site conditions provided novel habitat for 38.3 percent of the sampled flora (158 species) that was not recorded on closed, seasonally dry, forest floors, *sensu stricto*. Habitats that were the most significant contributors to species richness were closed seasonally dry forest floors, habitats created by human disturbance, and, habitats with moist and wet soils. Conditions in these habitats contrast sharply with respect to relative availability of light, moisture, and substrate, and provide the most apparent explanation for the distinctive flora associated with each setting.

The degree to which dispersal has contributed to differences in species richness was not resolved. While there is indirect evidence of directed dispersal by birds in former canopy gaps, and by birds, mammals, and ants, on disturbance features associated with former canopy gaps (tip-up mounds, tree pits, logs, stumps, closed lanes), most propagules appear to be dispersed at random and in close proximity to the parent plant. This suggests that the distribution and richness of plants in a given 10m x 10m quadrat has been determined primarily by factors that govern germination, establishment and persistence.

The capacity for longer distance dispersal, however, may influence the composition of species with a particular set of traits since the seed rain from mobile taxa is more likely to reflect the diversity of species in the surrounding region that are capable of establishing there. The strongest evidence for

this source of influence was found in plants dispersed by animal ingestion and by ants. In each case, the mean proportion of plants in 10m x 10m quadrats dispersed by each mode was significantly higher than their proportion in the flora as a whole. These taxa are typically shade tolerant and thus inherently less constrained by understory conditions than species with an affinity for more open habitats. The low shade tolerance of species in open habitats may explain the failure to find a similar pattern in plants dispersed by the wind.

Overall species richness, however, has been governed by other factors, since dispersal by animal ingestion was strongly associated with low species richness whereas dispersal by wind and by prolonged dormancy was strongly associated with high species richness.

On balance, the principal contributors to differences in species richness have been the moisture and base cation status of forest soils. The relative availability of these limiting resources has strongly influenced the composition of the forest canopy and the consequent soil-vegetation complexes have mediated the composition and richness of species by controlling the spatial and temporal availability of light on the forest floor, and, the availability of alternative habitats where competitors may perform poorly or not survive and where populations of low abundance may expand.

On mesic soils, the most significant factor has been the absolute and relative abundance of sugar maple. The number of species in 10m x 10m quadrats was strongly and negatively correlated with each measure. Overall, sugar maple abundance explained 25.6 % of the variance in species richness and up to 63% of the variance in species richness on Brunisolic and Luvisolic soils overlying calcareous till. Mean species richness in undisturbed quadrats declined from 46.0 species in quadrats with $\leq$25% stems (>1m) sugar maple to 27.1 species in quadrats with $\geq$75 % stems (>1m) sugar maple. Associated with this sharp decline in species richness was a marked rise in the proportion of species that flowered before canopy closure and that were shade tolerant.

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APPENDICES

APPENDIX 1

LOCATION OF STUDY SITES

Appendix 1. Location of Study Sites.

Site	Quadrats	Region/County	Municipality/Township	UTM	NTS Sheet
LANDSCAPE I					
B1	1-8	Peterborough	South Monaghan	110E 966N	31D/1
M1	9-16	Peterborough	Otonabee	264E 082N	31D/8
N8	17-24	Peterborough	Asphodel	362E 132N	31D/8
O8	25-32	Peterborough	Asphodel	309E 141N	31D/8
O9	33-40	Peterborough	Asphodel	329E 118N	31D/8
P1	41-48	Peterborough	Otonabee	195E 005N	31D/1
P3	49-56	Peterborough	Otonabee	221E 037N	31D/1
P5	57-64	Peterborough	Otonabee	296E 037N	31D/8
Pi2	65-72	Peterborough	Otonabee	215E 961N	31D/1
Y1	73-80	Peterborough	Asphodel	357E 119N	31D/8
Y2	81-88	Peterborough	South Monaghan	124E 950N	31D/1
Y5	89-96	Peterborough	Asphodel	365E 134N	31D/8
LANDSCAPE II					
BB1	97-104	Durham Regional Municipality (R.M.)	Newcastle Town Municipality (T.M.)	833E 814N	31D/2
DD1	105-112	Victoria	Manvers	897E 975N	31D/2

Appendix 1. Location of study sites (cont'd).

Site	Quadrats	Region/County	Municipality/Township	UTM	NTS Sheet
LANDSCAPE II (cont'd)					
GG1	113-120	Durham R.M.	Newcastle T.M.	803E 804N	31D/2
GG2	121-128	Victoria	Manvers	835E 955N	31D/2
MM2	129-136	Victoria	Manvers	836E 907N	31D/2
MM8	137-144	Victoria	Manvers	891E 825N	31D/2
NN2	145-152	Durham R.M.	Scugog	784E 837N	31D/2
NN3	153-160	Durham R.M.	Scugog	796E 891N	31D/2
NN4	161-168	Durham R.M.	Scugog	789E 888N	31D/2
OO12	169-176	Victoria	Manvers	848E 834N	31D/2
PP1	177-184	Victoria	Manvers	841E 841N	31D/2
PP3	185-192	Victoria	Manvers	923E 955N	31D/2

APPENDIX 2

SUMMARY OF PLANT ATTRIBUTES BY SPECIES

Appendix 2. Summary of Plant Attributes by Species.

Legend: SPECIES: species code (see Appendix 3); **# Q:** number of quadrats (N=192); **LF:** life form: T= tree, S = shrub, V = vine, F= fern, FA =fern ally, G = grass, H = herb; **LH:** life history, A = annual, B = biennial, annual/biennial, P = perennial, annual/perennial, biennial/perennial; **P:** provenance, N = native, A = alien, U = unknown; **HA:** habitat affinity, F = forest, FO = forest + open, OF = open + forest, O = open; **FRUIT TYPE:** "arillate seed", "winged seed" (gymnosperms), "spore" (homosporous spores of ferns and fern allies) are regarded as fruit types in this classification; **DISPERSAL MODES: AI** = animal ingestion: FF = fleshy fruit; **AA** = animal adhesion: AD = adhesive fruit; **AC** = animal conveyance: EL = elaiosome bearing seed or fruit, NF = nut fruit; **PD** = prolonged dormancy: SP = long term persistent seed pool; **W** = wind; **ME** = mechanical expulsion: EM = explosive mechanism, WM = wind-push mechanism, SM = splash-cup mechanism; **U** = unassisted; **MM** = multiple modes; **VE** = vegetative expansion.

Sources: plant names and provenance: Morton and Venn 1990, Cody and Britton 1989; life form, life history and fruit type: Gleason and Cronquist 1991.

References: (1) Alex 1992, (2) Arditti 1992, (3) Beattie and Culver 1981, (4) Beattie and Lyons 1975, (5) Beattie *et al.* 1979, (6) Bell 1991, (7) Berg 1966, (8) Berg 1969, (9) Brodie 1955, (10) Bulow-Olsen 1984, (11) Burnside *et al.* 1996, (12) Cody and Britton 1989, (13) Corner 1976, (14) Crockett 1977, (15) Culver and Beattie 1978, (16) Darley-Hill and Johnson 1981, (17) Dore and McNeill 1980, (18) Elliott 1978, (19) Farrar 1995, (20) Fisher 1988, (21) Gaddy 1986, (22) Gates 1940, (23) Gates 1941, (24) Gleason 1952, (25) Gleason and Cronquist 1991, (26) Graber and Thompson 1978, (27) Gunther and Lanza 1989, (28) Handel 1976, (29) Handel 1978ab, (30) Handel *et al.* 1981, (31) Heithaus 1981, (32) Howard 1961, (33) Hitchcock 1971, (34) Livingston and Allessio 1968, (35) Martin *et al.* 1951, (36) McDonald *et al.* 1996, (37) McKay and Catling 1979, (38) Montgomery 1977, (39) Montgomery Collection Test 1997, (40) Pudlo *et al.* 1980, (40) Rasmussen 1995, (42) Ridley 1930, (43) Roberts and Vankat 1991, (44) Savile 1953, (45) Savile 1979, (46) Semple and Heard 1987, (47) Semple and Ringius 1983, (48) Sernander 1906, (49) Smith and Reichman 1984, (50) Smith *et al.* 1989, (51) Snow and Snow 1988, (52) Soper and Heimburger 1982, (53) Sorensen 1986, (54) Stamp and Lucas 1983, (55) Stiles 1980, (56) Stiles 1989, (57) Thompson 1980, (58) Thompson 1981, (59) Thompson and Willson 1979, (60) Thompson *et al.* 1997, (61) Trapp 1988, (62) Webb and Willson 1985, (63) Wein and Pickett 1989, (64) White and Stiles 1992, (65) Whitney 1986, (66)Williams and Guries, (67) Willson 1986. ST = see text Section 3.2.1.

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	FRUIT TYPE	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
ABIEBALS	Pinaceae	61	T	P	N	-	winged seed	-	-	-	-	W	-	-	-	-	19
ACERNEGU	Aceraceae	4	T	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACERRUBR	Aceraceae	86	T	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACERSACC	Aceraceae	175	T	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACERSACN	Aceraceae	22	T	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACERSANI	Aceraceae	7	T	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACERSPIC	Aceraceae	34	S	P	N	-	schizocarp	-	-	-	-	W	-	-	-	-	19
ACHIMILL	Asteraceae	10	H	P	A	OF	achene	-	-	-	SP	W	-	-	MM	VE	60; 42; 25
ACTAPACH	Ranunculaceae	29	H	P	N	F	berry	FF	-	-	-	-	-	-	-	-	67
ACTARUBR	Ranunculaceae	22	H	P	N	F	berry	FF	-	-	-	-	-	-	-	-	67
ACTA_SP	Ranunculaceae	40	H	P	N	F	berry	FF	-	-	-	-	-	-	-	-	67
ADIAPEDA	Adiantaceae	20	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
AGRIGRYP	Rosaceae	9	H	P	N	FO	achene	-	AD	-	-	-	-	-	-	VE	25, 38; 25
AGROGIGA	Poaceae	13	G	P	A	OF	caryopsis	-	-	-	SP	-	-	-	-	VE	60; 25
AGROSTOL	Poaceae	3	G	P	N	O	caryopsis	-	-	-	SP	-	-	-	-	VE	60; 25
ALLITRIC	Liliaceae	25	H	P	N	F	capsule	-	-	-	-	-	-	U	-	-	25
ALNUINCA	Betulaceae	1	S	P	N	O	samara	-	-	-	SP	W	-	-	MM	-	60; 19
AMBRARTE	Asteraceae	2	H	A	N	OF	achene	-	AD	-	SP	-	-	-	MM	-	24, 25; 60
AMELARBO	Rosaceae	1	S	P	N	OF	pome	FF	-	-	-	-	-	-	-	-	64

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	H	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
AMELINTE	Rosaceae	5	S	P	N	OF	pome	FF	-	-	-	-	-	-	-	-	64
AMEL__SP	Rosaceae	47	S	P	N	OF	pome	FF	-	-	-	-	-	-	-	-	64
AMPHBRAC	Fabaceae	11	H	A	N	FO	legume	-	-	-	-	-	EM	-	-	-	61
ANEMCANA	Ranunculaceae	4	H	P	N	O	achene	-	-	-	-	W	-	-	-	VE	37; 25
ANEMQUIN	Ranunculaceae	1	H	P	N	FO	achene	-	-	EL	-	-	-	-	-	VE	3, 31; 25
ANEMVIRG	Ranunculaceae	11	H	P	N	OF	achene	-	-	-	-	W	-	-	-	-	25, 38
ANTENEGL	Asteraceae	1	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	25, 38; 25
APOCANDR	Apocynaceae	16	H	P	N	OF	follicle	-	-	-	-	W	-	-	-	VE	14, 25; 25
AQUICANA	Ranunculaceae	13	H	P	N	OF	follicle	-	-	-	SP	-	WM	-	MM	VE	34; ST; 25
ARALNUDI	Araliaceae	40	H	P	N	F	berry-like-drupe	FF	-	-	-	-	-	-	-	VE	55, 64; 25
ARCTMINU	Asteraceae	9	H	B	A	O	achene	-	AD	-	SP	-	-	-	MM		20, 25; 64
ARISTRIP	Araceae	97	H	P	N	F	berry	FF	-	-	-	-	-	-	-	-	64
ASARCANA	Aristolochiaceae	38	H	P	N	F	capsular	-	-	EL	-	-	-	-	-	VE	3,7,27,31,40, 57; 25
ASCLINCA	Asclepiadaceae	2	H	P	N	OF	follicle	-	-	-	-	W	-	-	-	-	25
ASCLSYRI	Asclepiadaceae	17	H	P	N	O	follicle	-	-	-	SP	W	-	-	MM	-	11; 25
ASTECILI	Asteraceae	24	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTECORD	Asteraceae	13	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTEERIC	Asteraceae	1	H	P	N	O	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTELANC	Asteraceae	5	H	P	N	O	achene	-	-	-	-	W	-	-	-	VE	46; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
ASTELATE	Asteraceae	66	H	P	N	FO	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTEMACR	Asteraceae	7	H	P	N	F	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTENOVE	Asteraceae	18	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTEPUNI	Asteraceae	15	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	46; 25
ASTEUMBE	Asteraceae	1	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	46; 25
ATHYFILI	Aspleniaceae	64	F	P	N	OF	spore	-	-	-	-	W	-	-	-	VE	12
ATHYTHEL	Aspleniaceae	4	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
BETUALLE	Betulaceae	32	T	P	N	-	samara	-	-	-	-	W	-	-	-	-	19
BETUPAPY	Betulaceae	29	T	P	N	-	samara	-	-	-	SP	W	-	-	-	-	34; 19
BIDEFRON	Asteraceae	14	H	A	N	OF	achene	-	AD	-	SP	-	-	-	MM	-	20, 25; 60
BOEHCYLI	Urticaceae	28	H	P	N	F	achene	-	AD	-	-	W	-	-	MM	-	42; 25, 38
BOTRMATR	Ophioglossaceae	2	F	P	N	OF	spore	-	-	-	-	W	-	-	-	-	12
BOTRMULT	Ophioglossaceae	1	F	P	N	O	spore	-	-	-	-	W	-	-	-	-	12
BOTRVIRG	Ophioglossaceae	43	F	P	N	F	spore	-	-	-	-	W	-	-	-	-	12
BRACEREC	Poaceae	5	G	P	N	F	caryopsis	-	AD	-	-	-	-	-	-	VE	33, 39; 25
BROMINER	Poaceae	3	G	P	A	OF	caryopsis	-	-	-	-	-	-	U	-	VE	25
CALTPALU	Ranunculaceae	1	H	P	N	OF	follicle	-	-	-	SP	-	-	-	-	-	60
CALYSEPI	Convolvulaceae	1	H	P	N	O	capsular	-	-	-	SP	-	-	-	-	VE	60; 25
CARDACAN	Asteraceae	1	H	B	A	O	achene	-	AD	-	-	W	-	-	MM	-	25; 20
CARDDIPH	Brassicaceae	48	H	P	N	F	silique	-	-	-	-	-	-	U	-	VE	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
CARDNUTA	Asteraceae	1	H	B	A	O	achene	-	AD	EL	SP	W	-	-	MM	-	25; 48; 60; 20
CARDPENS	Brassicaceae	3	H	B	N	F	silique	-	-	-	-	-	-	U	-	-	25
CAREALBU	Cyperaceae	5	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREALOP	Cyperaceae	3	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREARCT	Cyperaceae	35	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREBACK	Cyperaceae	9	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREBEBB	Cyperaceae	8	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREBLAN	Cyperaceae	61	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CAREBREV	Cyperaceae	4	H	P	N	O	achene	-	-	-	-	-	-	U	-	-	25
CARECEPH	Cyperaceae	2	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CARECOMM	Cyperaceae	1	H	P	N	FO	achene	-	-	EL	-	-	-	-	-	-	28, 29b
CARECRIN	Cyperaceae	1	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CARECRIS	Cyperaceae	16	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CAREDEWE	Cyperaceae	82	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREDIGI	Cyperaceae	5	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREGRAC	Cyperaceae	63	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CAREGRAN	Cyperaceae	6	H	P	N	OF	achene	-	-	-	-	-	-	U	-	VE	25
CAREHIRT	Cyperaceae	6	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CAREHITC	Cyperaceae	3	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREINTU	Cyperaceae	28	H	P	N	FO	achene	-	-	-	-	W	-	-	-	-	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
CARELANU	Cyperaceae	7	H	P	N	OF	achene	-	-	-	-	-	-	U	-	VE	25
CARELAXI	Cyperaceae	14	H	P	N	FO	achene	-	-	EL	-	-	-	-	-	-	21
CAREPECK	Cyperaceae	2	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREPEDU	Cyperaceae	80	H	P	N	FO	achene	-	-	EL	-	-	-	-	-	VE	28, 29a, 30; 25
CAREPENS	Cyperaceae	120	H	P	N	OF	achene	-	-	EL	-	-	-	-	-	VE	ST; 25
CAREPLAN	Cyperaceae	19	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CAREPLAT	Cyperaceae	1	H	P	N	F	achene	-	-	EL	-	-	-	-	-	-	3
CAREPRAI	Cyperaceae	1	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREPROJ	Cyperaceae	4	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREPSEU	Cyperaceae	1	H	P	N	OF	achene	-	-	-	-	-	-	U	-	VE	25
CARERADI	Cyperaceae	50	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CARERETR	Cyperaceae	13	H	P	N	FO	achene	-	-	-	-	W	-	-	-	VE	25
CAREROSE	Cyperaceae	71	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CARESPAR	Cyperaceae	5	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
CARESTIP	Cyperaceae	16	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
CARETENE	Cyperaceae	15	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CARETRIB	Cyperaceae	6	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREVULP	Cyperaceae	9	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
CAREWOOD	Cyperaceae	1	H	P	N	F	achene	-	-	-	-	-	-	U	-	VE	25
CARE_719	Cyperaceae	2	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
CARE_868	Cyperaceae	2	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25
CARE_870	Cyperaceae	1	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25
CARE_879	Cyperaceae	1	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25
CARE_OV	Cyperaceae	5	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25
CARE_SP	Cyperaceae	6	H	P	N	-	achene	-	-	-	-	-	-	U	-	-	25
CARPCARO	Betulaceae	28	T	P	N	-	nutlet	-	-	-	-	W	-	-	-	-	19
CARYCORD	Juglandaceae	68	T	P	N	-	nut	-	-	NF	-	-	-	-	-	-	32
CAULTHAL	Berberidaceae	57	H	P	N	F	resembles-drupe	FF	-	-	-	-	-	-	-	-	59, 67
CEANAMER	Rhamnaceae	2	S	P	N	OF	capsule-like-drupe	-	-	-	-	-	-	U	-	-	25
CELASCAN	Celastraceae	33	V	P	N	OF	capsule	FF	-	-	-	-	-	-	-	-	55
CERAFONT	Caryophyllaceae	10	H	P	A	OF	capsule	-	-	-	SP	-	-	-	-	VE	60; 25
CHIMUMBE	Pyrolaceae	2	S	P	N	FO	capsule	-	-	-	-	-	-	U	-	VE	25
CHRYLEUC	Asteraceae	7	H	P	A	O	achene	-	-	-	SP	W	-	-	MM	VE	60; 42; 25
CICUBULB	Apiaceae	1	H	P	N	OF	schizocarp	-	-	-	-	-	-	U	-	VE	25
CICUMACU	Apiaceae	3	H	P	N	OF	schizocarp	-	-	-	-	-	-	U	-	-	25
CINNLATI	Poaceae	11	G	P	N	F	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
CIRCALPI	Onagraceae	36	H	P	N	F	capsule	-	AD	-	-	-	-	-	-	VE	25, 38; 25
CIRCLUTE	Onagraceae	95	H	P	N	F	capsule	-	AD	-	-	-	-	-	-	VE	25, 38; 25
CIRSARVE	Asteraceae	8	H	P	A	O	achene	-	AD	-	SP	W	-	-	MM	VE	25; 11; 60; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
CIRSVULG	Asteraceae	6	H	B	A	O	achene	-	AD	-	SP	W	-	-	MM	-	25; 60; 25
CLAYCARO	Portulacaceae	13	H	P	N	F	capsule	-	-	EL	-	-	-	-	-	-	35, ST
CLEMVIRG	Ranunculaceae	12	V	P	N	OF	achene	-	-	-	-	W	-	-	-	-	25, 38
CLINBORE	Liliaceae	2	H	P	N	FO	berry	FF	-	-	-	-	-	-	-	VE	67; 25
CONYCANA	Asteraceae	5	H	P	N	O	achene	-	-	-	SP	W	-	-	MM	-	60; 20, 25
CORNALTE	Cornaceae	90	S	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	64
CORNFOEM	Cornaceae	16	S	P	N	OF	drupe	FF	-	-	-	-	-	-	-	-	64
CORNRUGO	Cornaceae	29	S	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	55, 64
CORNSTOL	Cornaceae	22	S	P	N	OF	drupe	FF	-	-	-	-	-	-	-	VE	55, 64; 25
CORYCORN	Betulaceae	45	S	P	N	FO	nut	-	-	NF	-	-	-	-	-	-	25
CRAT_SP1	Roseaceae	3	S	P	N	O	pome	FF	-	-	-	-	-	-	-	-	64
CRAT_SP2	Roseaceae	1	S	P	N	O	pome	FF	-	-	-	-	-	-	-	-	64
CRAT_SP3	Roseaceae	1	S	P	N	O	pome	FF	-	-	-	-	-	-	-	-	64
CRAT__SP	Roseaceae	26	S	P	N	O	pome	FF	-	-	-	-	-	-	-	-	64
CRYPCANA	Apiaceae	2	H	P	N	F	schizocarp	-	-	-	-	-	-	U	-	-	25
CRYPCALC	Orchidaceae	2	H	P	N	FO	capsular	-	-	-	-	W	-	-	-	-	2, 41
CYSTBULB	Aspleniaceae	35	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
CYSTFRAG	Aspleniaceae	4	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
CYSTTENU	Aspleniaceae	2	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
DACTGLOM	Poaceae	6	G	P	A	OF	caryopsis	-	AD	-	SP	-	-	-	MM	-	33, 39; 60

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
DANTSPIC	Poaceae	4	G	P	N	OF	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
DAUCARO	Apiaceae	6	H	B	A	O	schizocarp	-	AD	-	SP	-	-	-	MM	-	38; 34
DESMGLUT	Fabaceae	7	H	P	N	FO	legume	-	AD	-	-	-	-	-	-	-	25, 38
DIANARME	Caryophyllaceae	2	H	B	A	O	capsule	-	-	-	-	-	WM	-	-	-	25
DICECANA	Fumariaceae	18	H	P	N	F	capsular	-	-	EL	-	-	-	-	-	VE	8, 58; 25
DICECUCU	Fumariaceae	4	H	P	N	F	capsular	-	-	EL	-	-	-	-	-	VE	8,30,57,58; 25
DIERLONI	Caprifoliaceae	12	S	P	N	FO	capsule	-	-	-	SP	-	-	-	-	-	34
DIRCPALU	Thymelaceae	9	S	P	N	F	drupe	FF	-	-	-	-	-	-	-	-	67
DRYOCART	Aspleniaceae	107	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12
DRYOCRIS	Aspleniaceae	23	F	P	N	OF	spore	-	-	-	-	W	-	-	-	VE	12
DRYOINTE	Aspleniaceae	71	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12
DRYOMARG	Aspleniaceae	33	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	12
ECHILOBA	Cucurbitaceae	1	H	A	N	OF	capsule	-	-	-	SP	-	EM	-	MM	-	1; 14
ELYMREPE	Poaceae	2	G	P	A	OF	caryopsis	-	-	-	SP	-	-	-	-	VE	60; 25
ELYMVIRG	Poaceae	8	G	P	N	FO	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
EPIFVIRG	Orobanchaceae	5	H	P	N	F	capsule	-	-	-	-	-	-	U	-	-	25
EPILCILI	Onagraceae	5	H	P	N	OF	capsule	-	-	-	SP	W	-	-	MM	-	60; 25
EPILCOLO	Onagraceae	29	H	P	N	OF	capsule	-	-	-	-	W	-	-	-	-	25
EPILLEPT	Onagraceae	4	H	P	N	OF	capsule	-	-	-	-	W	-	-	-	VE	25
EPILPARV	Onagraceae	7	H	P	A	OF	capsule	-	-	-	-	W	-	-	-	VE	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
EPIPHELL	Orchidaceae	130	H	P	A	FO	capsular	-	-	-	-	W	-	-	-	-	2, 41
EQUIARVE	Equisetaceae	34	FA	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12
EQUIHYEM	Equisetaceae	7	FA	P	N	O	spore	-	-	-	-	W	-	-	-	VE	12
EQUILAEV	Equisetaceae	2	FA	P	N	O	spore	-	-	-	-	W	-	-	-	VE	12
EQUISCIR	Equisetaceae	4	FA	P	N	OF	spore	-	-	-	-	W	-	-	-	VE	12
ERIGANNU	Asteraceae	10	H	B	N	O	achene	-	-	-	SP	W	-	-	MM	-	60; 25
ERIGPHIL	Asteraceae	34	H	P	N	O	achene	-	-	-	-	W	-	-	-	-	25
ERIGSTRI	Asteraceae	8	H	B	N	OF	achene	-	-	-	-	W	-	-	-	-	25
ERIG_SP	Asteraceae	2	H	B	N	-	achene	-	-	-	-	W	-	-	-	-	25
ERYTAMER	Liliaceae	114	H	P	N	FO	capsule	-	-	EL	-	-	-	-	-	VE	30, 40, 63; 25
EUPAMACU	Asteraceae	15	H	P	N	OF	achene	-	-	-	-	W	-	-	-	-	20, 25; 25
EUPAPERF	Asteraceae	7	H	P	N	OF	achene	-	-	-	-	W	-	-	-	-	20, 25; 25
EUPARUGO	Asteraceae	21	H	P	N	FO	achene	-	-	-	SP	W	-	-	MM	-	34, 43; 20, 25
EUTHGRAM	Asteraceae	6	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	47; 25
FAGUGRAN	Fagaceae	67	T	P	N	-	nut		-	NF	-	-	-	-	-	-	16, 18
FESTARUN	Poaceae	1	G	P	A	O	caryopsis	-	-	-	-	-	-	U	-	-	25
FESTPRAT	Poaceae	2	G	P	A	O	caryopsis	-	-	-	-	-	-	U	-	-	25
FESTRUBR	Poaceae	2	G	P	N	O	caryopsis	-	-	-	SP	-	-	-	-	VE	60; 25
FESTSUBV	Poaceae	30	G	P	N	F	caryopsis	-	-	-	-	-	-	U	-	-	25
FRAGVESC	Rosaceae	27	H	P	N	FO	achene	FF	-	-	SP	-	-	-	MM	VE	64; 60; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
FRAGVIRG	Rosaceae	27	H	P	N	OF	achene	FF	-	-	-	-	-	-	-	VE	64; 25
FRAXAMER	Oleaceae	95	T	P	N	-	samara	-	-	-	-	W	-	-	-	-	19
FRAXNIGR	Oleaceae	52	T	P	N	-	samara	-	-	-	-	W	-	-	-	-	19
FRAXPENN	Oleaceae	51	T	P	N	-	samara	-	-	-	-	W	-	-	-	-	19
GALESPEC	Orchidaceae	2	H	P	N	F	capsular	-	-	-	-	W	-	-	-	VE	2, 41; 25
GALETETR	Lamiaceae	3	H	A	A	OF	nutlet	-	-	-	SP	-	-	-	-	-	60
GALIAPAR	Rubiaceae	12	H	A	N	FO	schizocarp	-	AD	EL	-	-	-	-	MM	-	24, 25; 48
GALIASPR	Rubiaceae	3	H	P	N	OF	schizocarp	-	AD	-	-	-	-	-	-	-	24, 25
GALICIRC	Rubiaceae	4	H	P	N	F	schizocarp	-	AD	EL	-	-	-	-	MM	-	24, 25; 21
GALILANC	Rubiaceae	14	H	P	N	F	schizocarp	-	AD	-	-	-	-	-	-	-	24, 25
GALIOBTU	Rubiaceae	15	H	P	N	FO	schizocarp	-	AD	-	-	-	-	-	-	-	24, 25
GALIPALU	Rubiaceae	3	H	P	N	O	schizocarp	-	AD	-	SP	-	-	-	MM	-	24, 25; 60
GALITRIF	Rubiaceae	105	H	P	N	FO	schizocarp	-	AD	-	-	-	-	-	-	-	24, 25
GALI_SP	Rubiaceae	1	H	P	N	-	schizocarp	-	AD	-	-	-	-	-	-	-	24, 25
GENTANDR	Gentianaceae	7	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	-	25
GERAMACU	Geraniaceae	12	H	P	N	OF	schizocarp	-	-	-	-	-	EM	-	-	VE	54; 25
GERAROBE	Geraniaceae	53	H	B	A	OF	schizocarp	-	-	-	SP	-	EM	-	MM	-	60; 41
GEUMALEP	Rosaceae	1	H	P	N	OF	achene	-	AD	-	-	-	-	-	-	-	24, 25, 38
GEUMCANA	Rosaceae	13	H	P	N	FO	achene	-	AD	-	-	-	-	-	-	-	24, 25, 38
GEUMLACI	Rosaceae	21	H	P	N	FO	achene	-	AD	-	-	-	-	-	-	-	24, 25, 38

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
GEUMRIVA	Rosaceae	2	H	P	N	FO	achene	-	AD	-	-	-	-	-	-	-	24, 25, 38
GEUMURBA	Rosaceae	2	H	P	A	OF	achene	-	AD	-	-	-	-	-	-	-	24, 25, 38, 53
GEUM_SP	Rosaceae	23	H	P	U	-	achene	-	AD	-	-	-	-	-	-	-	24, 25
GLYCSTRI	Poaceae	62	G	P	N	FO	caryopsis	-	-	-	-	-	-	U	-	-	25
GYMNDRYO	Aspleniaceae	24	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12; 25
HACKVIRG	Boraginaceae	4	H	B	N	FO	nutlet	-	AD	-	-	-	-	-	-	-	25, 38
HEPAACUT	Ranunculaceae	25	H	P	N	F	achene	-	-	EL	-	-	-	-	-	-	3, 5, 30, 50
HIERAURA	Asteraceae	1	H	P	A	OF	achene	-	-	-	-	W	-	-	-	VE	20, 25
HIERCAES	Asteraceae	60	H	P	A	OF	achene	-	-	-	-	W	-	-	-	VE	20, 25
HYDRVIRG	Hydrophyllaceae	14	H	P	N	FO	capsule	-	-	-	-	-	-	U	-	VE	25
HYPEPERF	Clusiaceae	14	H	P	A	O	capsule	-	-	-	SP	-	-	-	-	-	60
HYSTPATU	Poaceae	3	G	P	N	FO	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
IMPACAPE	Balsaminaceae	60	H	A	N	OF	capsule	-	-	-	-	-	EM	-	-	-	54
INULHELI	Asteraceae	2	H	P	A	O	achene	-	-	-	-	W	-	-	-	-	20, 25
IRISVERS	Iridaceae	1	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	VE	25
IRIS_SP	Iridaceae	5	H	P	U	-	capsule	-	-	-	-	-	-	U	-	VE	25
JUNCTENU	Juncaceae	3	H	P	N	OF	capsule	-	-	-	SP	-	-	-	-	-	60
LACTCANA	Asteraceae	5	H	B	N	OF	achene	-	-	-	-	W	-	-	-	-	20, 25
LACTSERR	Asteraceae	5	H	B	A	O	achene	-	-	-	SP	W	-	-	MM	-	60; 20, 25
LACT_SP	Asteraceae	2	H	B	U	-	achene	-	-	-	-	W	-	-	-	-	20, 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
LAPOCANA	Urticaceae	18	H	P	N	FO	achene	-	-	-	-	-	-	U	-	VE	25
LEERORYZ	Poaceae	6	G	P	N	O	caryopsis	-	AD	-	SP	-	-	-	MM	VE	33, 39; 60; 25
LEERVIRG	Poaceae	1	G	P	N	FO	caryopsis	-	AD	-	-	-	-	-	-	VE	33, 39; 25
LEONCARD	Lamiaceae	4	H	P	A	OF	nutlet	-	-	-	-	-	-	U	-	-	25
LIPALOES	Orchidaceae	4	H	P	N	OF	capsular	-	-	-	-	W	-	-	-	-	2, 41
LOBEINFL	Campanulaceae	1	H	A	N	O	capsule	-	-	-	-	-	WM	-	-	-	25, ST
LOBE__SP	Campanulaceae	1	H	U	N	-	capsule	-	-	-	-	-	-	U	-	-	25
LONICANA	Caprifoliaceae	32	S	P	N	F	berry	FF	-	-	-	-	-	-	-	-	55, 64
LONIDIOI	Caprifoliaceae	14	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	55, 64
LONIHIRS	Caprifoliaceae	10	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	55, 64
LYCOAMER	Lamiaceae	6	H	P	N	OF	nutlet	-	-	-	-	-	-	U	-	VE	25
LYCOANNO	Lycopodiaceae	6	FA	P	N	FO	spore	-	-	-	-	W	-	-	-	-	12
LYCODEND	Lycopodiaceae	2	FA	P	N	FO	spore	-	-	-	-	W	-	-	-	-	12
LYCOOBOB	Lycopodiaceae	4	FA	P	N	F	spore	-	-	-	-	W	-	-	-	-	12
LYCOTRIS	Lycopodiaceae	1	FA	P	N	FO	spore	-	-	-	-	W	-	-	-	-	12
LYCOUNIF	Lamiaceae	18	H	P	N	OF	nutlet	-	-	-	-	-	-	U	-	VE	25
LYSICILI	Primulaceae	14	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	VE	25
LYSINUMM	Primulaceae	9	H	P	A	OF	capsule	-	-	-	SP	-	-	-	-	-	60
LYSITERR	Primulaceae	1	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	VE	25
MAIACANA	Liliaceae	130	H	P	N	FO	berry	FF	-	-	-	-	-	-	-	VE	64; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
MAIARACE	Liliaceae	91	H	P	N	F	berry	FF	-	-	-	-	-	-	-	VE	64; 25
MAIASTEL	Liliaceae	10	H	P	N	OF	berry	FF	-	-	-	-	-	-	-	VE	64; 25
MATTSTRU	Onocleaceae	18	F	P	N	F	spore	-	-	-	-	W	-	-	-	VE	25
MEDILUPU	Fabaceae	11	H	B	A	OF	legume	-	-	EL	SP	-	-	-	MM	-	48; 60
MELIALBA	Fabaceae	4	H	B	A	O	legume	-	-	-	-	-	-	U	-	-	25
MELIOFFI	Fabaceae	2	H	B	A	O	legume	-	-	EL	SP	-	-	-	MM	-	48; 60
MENICANA	Menispermaceae	2	V	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	55, 59
MENTARVE	Lamiaceae	12	H	P	N	OF	nutlet	-	-	-	SP	-	-	-	-	-	60
MILIEFFU	Poaceae	7	G	P	N	F	caryopsis	-	-	-	-	-	-	U	-	-	25
MITCREPE	Rubiaceae	18	V	P	N	F	berry	FF	-	-	-	-	-	-	-	VE	64; 25
MITEDIPH	Saxifragaceae	23	H	P	N	F	capsule	-	-	-	-	-	SM	-	-	VE	9, 45; 25
MONAFIST	Lamiaceae	1	H	P	N	OF	nutlet	-	-	-	-	-	-	U	-	VE	25
MONOHYPO	Monotropaceae	2	H	P	N	F	capsule	-	-	-	-	-	-	U	-	-	25
MONOUNIF	Monotropaceae	45	H	P	N	F	capsule	-	-	-	-	-	-	U	-	-	25
MUHLFRON	Poaceae	1	G	P	N	O	caryopsis	-	AD	-	-	-	-	-	-	VE	33, 39; 25
MUHLMEXI	Poaceae	7	G	P	N	OF	caryopsis	-	AD	-	-	-	-	-	-	VE	33, 39; 25
NEPECATA	Lamiaceae	1	H	P	A	O	nutlet	-	-	-	-	-	-	U	-	-	25
ONOCSENS	Onocleaceae	40	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12
ONOPACAN	Asteraceae	3	H	B	A	O	achene	-	-	-	SP	W	-	-	MM	-	60; 25
ORYZASPE	Poaceae	51	G	P	N	F	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
OSMOCLAY	Apiaceae	36	H	P	N	F	schizocarp	-	AD	-	-	-	-	-	-	-	25, 53, 66
OSMUCLAY	Osmundaceae	5	F	P	N	FO	spore	-	-	-	-	W	-	-	-	-	12
OSMUREGA	Osmundaceae	1	F	P	N	FO	spore	-	-	-	-	W	-	-	-	-	12
OSTRVIRG	Betulaceae	81	T	P	N	-	nutlet	-	-	-	-	W	-	-	-	-	19
OXALSTRI	Oxalidaceae	3	H	P	N	OF	capsule	-	-	-	SP	-	EM	-	MM	VE	60; 42; 25
OXAL__SP	Oxalidaceae	1	H	P	N	-	capsule	-	-	-	-	-	EM	-	-	-	42
PANAQUIN	Araliaceae	1	H	P	N	F	berry-like-drupe	FF	-	-	-	-	-	-	-	-	67
PANIACUM	Poaceae	3	G	P	N	OF	caryopsis	-	-	-	-	-	-	U	-	-	25
PANICAPI	Poaceae	1	G	A	N	O	caryopsis	-	-	-	SP	W	-	-	MM	-	31, 43; 25
PANI__SP	Poaceae	2	G	U	N	-	caryopsis	-	-	-	-	-	-	U	-	-	25
PARTINSE	Vitaceae	60	V	P	N	OF	berry	FF	-	-	-	-	-	-	-	-	64
PHALARUN	Poaceae	3	G	P	N	O	caryopsis	-	AD	-	SP	-	-	-	MM	VE	33, 39; 60; 25
PHEGCONN	Thelypteridaceae	1	F	P	N	O	spore	-	-	-	-	W	-	-	-	VE	12
PHLEPRAT	Poaceae	5	G	P	A	OF	caryopsis	-	AD	-	SP	-	-	-	MM	-	33, 39; 60
PHLO__SP	Polemoniaceae	2	H	P	N	-	capsule	-	-	-	-	-	-	U	-	-	25
PHRYLEPT	Verbenaceae	19	H	P	N	F	achene	-	AD	-	-	-	-	-	-	-	38
PICEGLAU	Pinaceae	5	T	P	N	-	winged seed	-	-	-	-	W	-	-	-	-	19
PILEPUMI	Urticaceae	25	H	A	N	FO	achene	-	-	-	-	-	-	U	-	-	25
PINUSTRO	Pinaceae	13	T	P	N	-	winged seed	-	-	-	-	W	-	-	-	-	19

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
PLANLANC	Plantaginaceae	2	H	P	A	O	capsule	-	-	-	SP	-	-	-	-	-	60
PLANMAJO	Plantaginaceae	10	H	P	A	OF	capsule	-	-	-	SP	-	-	-	-	-	60
PLANRUGE	Plantaginaceae	9	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	-	25
POA_ALSO	Poaceae	16	G	P	N	FO	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
POA_COMP	Poaceae	24	G	P	N	OF	caryopsis	-	AD	-	-	-	-	-	-	VE	17, 33, 39; 25
POA_PALU	Poaceae	23	G	P	N	O	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
POA_PRAT	Poaceae	26	G	P	N	OF	caryopsis	-	AD	-	SP	-	-	-	MM	VE	33,39; 60; 25
POA_SALT	Poaceae	3	G	P	N	FO	caryopsis	-	-	-	-	-	-	U	-	-	25
POA__SP	Poaceae	2	G	P	N	-	caryopsis	-	-	-	-	-	-	U	-	-	25
PODOPELT	Berberidaceae	5	H	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	67
POLYACRO	Aspleniaceae	10	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12
POLYPAUC	Polygalaceae	6	H	P	N	FO	capsule	-	-	EL	-	-	-	-	-	VE	38, ST, 25
POLYPERS	Polygonaceae	4	H	A	A	O	achene	-	-	-	SP	-	-	-	-	-	36
POLYPUBE	Liliaceae	92	H	P	N	F	berry	FF	-	-	-	-	-	-	-	VE	67; 25
POPUBALS	Salicaceae	13	T	P	N	-	capsule	-	-	-	-	W	-	-	-	-	19
POPUGRAN	Salicaceae	20	T	P	N	-	capsule	-	-	-	-	W	-	-	-	-	19
POPUTREM	Salicaceae	30	T	P	N	-	capsule	-	-	-	-	W	-	-	-	-	19
POTENORV	Rosaceae	1	H	P	A	OF	achene	-	-	-	SP	-	-	-	-	-	60
POTERECT	Rosaceae	7	H	P	A	OF	achene	-	-	-	-	-	-	U	-	-	25
PREN__SP	Asteraceae	20	H	P	N	F	achene	-	-	-	-	W	-	-	-	-	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
PRUNSERO	Rosaceae	80	T	P	N	-	drupe	FF	-	-	-	-	-	-	-	-	64
PRUNVIRG	Rosaceae	123	S	P	N	OF	drupe	FF	-	-	-	-	-	-	-	VE	64; 25
PRUNVULG	Lamiaceae	14	H	P	N	OF	nutlet	-	-	-	SP	-	-	-	-	-	60
PTERAQUI	Dennstaedtiaceae	42	F	P	N	OF	spore	-	-	-	-	W	-	-	-	VE	12
PYROELLI	Pyrolaceae	17	S	P	N	FO	capsule	-	-	-	-	-	-	U	-	VE	25
QUERALBA	Fagaceae	9	T	P	N	-	nut	-	-	NF	-	-	-	-	-	-	35, 49
QUERMACR	Fagaceae	12	T	P	N	-	nut	-	-	NF	-	-	-	-	-	-	35, 49
QUERRUBR	Fagaceae	72	T	P	N	-	nut	-	-	NF	-	-	-	-	-	-	32, 49
QUER__SP	Fagaceae	1	T	P	N	-	nut	-	-	NF	-	-	-	-	-	-	35, 49
RANUABOR	Ranunculaceae	59	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
RANUACRI	Ranunculaceae	31	H	P	A	O	achene	-	-	-	SP	-	-	-	-	-	60
RANUHICA	Ranunculaceae	1	H	P	N	FO	achene	-	-	-	-	-	-	U	-	VE	25
RANURECU	Ranunculaceae	61	H	P	N	F	achene	-	-	-	-	-	-	U	-	-	25
RHAMALNI	Rhamnaceae	1	S	P	N	OF	drupe	FF	-	-	-	-	-	-	-	-	53, 67
RHAMCATH	Rhamnaceae	76	S	P	A	OF	drupe	FF	-	-	-	-	-	-	-	-	51, 67
RHUSRADI	Anacardiaceae	45	S	P	N	OF	drupaceous	FF	-	-	-	-	-	-	-	VE	64; 25
RHUSTYPH	Anacardiaceae	1	S	P	N	OF	drupaceous	FF	-	-	-	-	-	-	-	VE	55, 64; 25
RIBEAMER	Grossulariaceae	14	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	55
RIBECYNO	Grossulariaceae	94	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	55
RIBEGLAN	Grossulariaceae	4	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
RIBELACU	Grossulariaceae	1	S	P	N	FO	berry	FF	-	-	-	-	-	-	-	-	25
RIBERUBR	Grossulariaceae	5	S	P	A	OF	berry	FF	-	-	-	-	-	-	-	-	25
RIBETRIS	Grossulariaceae	30	S	P	N	F	berry	FF	-	-	-	-	-	-	-	-	25
RIBE_827	Grossulariaceae	1	S	P	N	-	berry	FF	-	-	-	-	-	-	-	-	25
ROBIPSEU	Fabaceae	20	T	P	A	-	legume	-	-	-	SP	-	EM	-	MM	-	60
ROSABLAN	Rosaceae	3	S	P	N	OF	achene	FF	-	-	-	-	-	-	-	-	25
ROSAPALU	Rosaceae	3	S	P	N	OF	achene	FF	-	-	-	-	-	-	-	-	25
RUBUALLE	Rosaceae	18	S	P	N	OF	drupelet	FF	-	-	-	-	-	-	-	-	64
RUBUIDAE	Rosaceae	53	S	P	A	OF	drupelet	FF	-	-	SP	-	-	-	MM	VE	64; 60, 65; 25
RUBUOCCI	Rosaceae	16	S	P	N	OF	drupelet	FF	-	-	-	-	-	-	-	VE	64; 25
RUBUODOR	Rosaceae	11	S	P	N	O	drupelet	FF	-	-	-	-	-	-	-	VE	25
RUBUPUBE	Rosaceae	46	S	P	N	O	drupelet	FF	-	-	-	-	-	-	-	VE	64, 25
RUBU_840	Rosaceae	2	S	P	N	-	drupelet	FF	-	-	-	-	-	-	-	VE	25
RUDBHIRT	Asteraceae	1	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
RUMEORBI	Polygonaceae	1	H	P	N	O	achene	-	-	-	-	W	-	-	-	-	25
SALIBEBB	Salicaceae	4	S	P	N	OF	capsule	-	-	-	-	W	-	-	-	VE	19; 25
SALIDISC	Salicaceae	6	S	P	N	OF	capsule	-	-	-	-	W	-	-	-	VE	19; 25
SALIERIO	Salicaceae	10	S	P	N	O	capsule	-	-	-	-	W	-	-	-	VE	19; 25
SALIPETI	Salicaceae	1	S	P	N	O	capsule	-	-	-	-	W	-	-	-	VE	19; 25
SAMBCANA	Caprifoliaceae	8	S	P	N	OF	berry-like	FF	-	-	-	-	-	-	-	VE	64; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
SAMBRAPU	Caprifoliaceae	40	S	P	N	FO	berry-like	FF	-	-	SP	-	-	-	MM	-	55; 26, 60
SANGCANA	Papaveraceae	11	H	P	N	F	capsule	-	-	EL	-	-	-	-	-	VE	3,7,23,30,31,40,57;25
SANIMARI	Apiaceae	6	H	P	N	FO	schizocarp	-	AD	-	-	-	-	-	-	-	25, 38, 53
SANITRIF	Apiaceae	1	H	B	N	F	schizocarp	-	AD	-	-	-	-	-	-	-	25, 38. 53
SANI_SP	Apiaceae	1	H	U	N	-	schizocarp	-	AD	-	-	-	-	-	-	-	25, 38, 53
SCHIPURP	Poaceae	29	G	P	N	F	caryopsis	-	AD	-	-	-	-	-	-	-	33, 39
SCIRATRO	Cyperaceae	5	H	P	N	O	achene	-	AD	-	-	-	-	-	-	-	25
SCUTLATE	Lamiaceae	10	H	P	N	FO	nutlet	-	-	-	-	-	-	U	-	VE	25
SICYANGU	Cucurbitaceae	1	H	A	N	FO	capsule	-	-	-	-	-	-	U	-	-	25
SILEVULG	Caryophyllaceae	1	H	P	A	O	capsule	-	-	-	SP	-	WM	-	MM	-	60; 25, 42
SISYMONT	Iridaceae	3	H	P	N	O	capsule	-	-	-	-	-	-	U	-	-	25
SIUMSUAV	Apiaceae	2	H	P	N	OF	schizocarp	-	-	-	-	-	-	U	-	-	25
SMILHERB	Smilacaceae	50	V	P	N	OF	berry	FF	-	-	-	-	-	-	-	-	64
SMILHISP	Smilacaceae	2	V	P	N	OF	berry	FF	-	-	-	-	-	-	-	-	59
SOLADULC	Solonaceae	50	V	P	A	FO	berry	FF	-	-	SP	-	-	-	MM	VE	55, 64; 43, 60; 25
SOLIALTI	Asteraceae	28	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	47; 25
SOLICAES	Asteraceae	9	H	P	N	F	achene	-	-	-	-	W	-	-	-	VE	47; 25
SOLICANA	Asteraceae	66	H	P	N	OF	achene	-	-	-	SP	W	-	-	MM	VE	60; 47; 25
SOLIFLEX	Asteraceae	42	H	P	N	F	achene	-	-	-	-	W	-	-	-	VE	47; 25
SOLIGIGA	Asteraceae	16	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	47; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
SOLIJUNC	Asteraceae	2	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	47; 25
SOLINEMO	Asteraceae	11	H	P	N	OF	achene	-	-	-	-	W	-	-	-	-	47; 25
SOLIRUGO	Asteraceae	4	H	P	N	OF	achene	-	-	-	-	W	-	-	-	VE	47; 25
SONCARVE	Asteraceae	5	H	P	A	O	achene	-	-	-	SP	W	-	-	MM	VE	60; 25
SONCOLER	Asteraceae	2	H	A	A	O	achene	-	-	-	SP	W	-	-	MM	-	60; 25
SPHEINTE	Poaceae	15	G	P	N	OF	caryopsis	-	AD	-	-	W	-	-	MM	-	33, 39; 17
STELLONG	Caryophyllaceae	1	H	P	N	OF	capsule	-	-	-	-	-	-	U	-	-	25
STREROSE	Liliaceae	8	H	P	N	F	berry	-	-	EL	-	-	-	-	-	VE	ST
SYMPALBU	Caprifoliaceae	6	S	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	25
TARAOFFI	Asteraceae	99	H	P	A	OF	achene	-	-	-	SP	W	-	-	MM	-	60; 25
TAXUCANA	Taxaceae	5	S	P	N	F	arillate seed	FF	-	-	-	-	-	-	-	-	19
THALDIOI	Ranunculaceae	16	H	P	N	FO	achene	-	-	-	-	-	-	U	-	-	25
THALPUBE	Ranunculaceae	2	H	P	N	OF	achene	-	-	-	-	-	-	U	-	-	25
THELNOVE	Aspleniaceae	2	F	P	N	FO	spore	-	-	-	-	W	-	-	-	VE	12; 25
THELPALU	Aspleniaceae	4	F	P	N	OF	spore	-	-	-	-	W	-	-	-	VE	12; 25
THUJOCCI	Cupressaceae	47	T	P	N	-	winged seed	-	-	-	-	W	-	-	-	-	19
TIARCORD	Saxifragaceae	65	H	P	N	F	capsule	-	-	-	-	-	SM	-	-	VE	45; 25
TILIAMER	Tiliaceae	115	T	P	N	-	nut-like	-	-	-	-	W	-	-	-	-	19
TRAGDUBI	Asteraceae	2	H	B	A	O	achene	-	-	-	-	W	-	-	-	-	25
TRIEBORE	Primulaceae	41	H	P	N	FO	capsule	-	-	-	-	-	-	U	-	VE	25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
TRIFREPE	Fabaceae	7	H	P	A	O	legume	-	-	-	SP	-	-	-	-	-	60
TRILEREC	Liliaceae	50	H	P	N	F	berry	-	-	EL	-	-	-	-	-	VE	3, 27; 25
TRILGRAN	Liliaceae	138	H	P	N	FO	berry	-	-	EL	-	-	-	-	-	VE	3, 22, 27, 30; 25
TRIOAURA	Caprifoliaceae	1	H	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	67
TSUGCANA	Pinaceae	50	T	P	N	-	winged seed	-	-	-	-	W	-	-	-	VE	19
TUSSFARF	Asteraceae	2	H	P	A	O	achene	-	-	-	-	W	-	-	-	-	25
TYPHLATI	Typhaceae	1	H	P	N	O	achene	-	-	-	SP	W	-	-	MM	VE	60; 25
ULMUAMER	Ulmaceae	66	T	P	N	-	samara	-	-	-	-	W	-	-	-	-	19
UNKN_751	Poaceae	1	G	U	U	-	caryopsis	-	-	-	-	-	-	-	-	-	
UNKN_791	Poaceae	1	G	U	U	-	caryopsis	-	-	-	-	-	-	-	-	-	
UNKN_822	-	1	H	U	U	-	-	-	-	-	-	-	-	-	-	-	
URTIDIGR	Urticaceae	9	H	P	N	FO	achene	-	-	-	-	-	-	U	-	VE	25
URTIDIOI	Urticaceae	1	H	P	A	FO	achene	-	-	-	SP	-	-	-	-	VE	36, 60; 25
UVULGRAN	Liliaceae	11	H	P	N	FO	capsule	-	-	EL	-	-	-	-	-	VE	7, 15, 57, 58, 62
VACCANGU	Ericaceae	5	S	P	N	OF	berry	FF	-	-	-	-	-	-	-	VE	64
VERBHAST	Verbenaceae	1	H	B	N	O	nutlet	-	-	-	-	-	-	U	-	-	25
VERBTHAP	Scrophulariaceae	3	H	P	A	O	capsular	-	-	-	SP	-	WM	-	MM	-	60; 42
VERBURTI	Verbenaceae	1	H	P	N	FO	nutlet	-	-	-	-	-	-	U	-	-	25
VEROOFFI	Scrophulariaceae	2	H	P	A	FO	capsular	-	-	-	SP	-	-	-	-	-	36, 60
VEROSERP	Scrophulariaceae	3	H	P	A	OF	capsular	-	-	-	SP	-	-	-	-	VE	36, 60; 25

Appendix 2. Summary of plant attributes by species.

SPECIES	FAMILY	# Q	LF	LH	P	HA	Fruit Type	AI	AA	AC	PD	W	ME	U	MM	VE	REFERENCE
VIBUACER	Caprifoliaceae	39	S	P	N	F	drupe	FF	-	-	-	-	-	-	-	-	51, 55, 64
VIBULENT	Caprifoliaceae	28	S	P	N	OF	drupe	FF	-	-	-	-	-	-	-	-	51, 55, 64
VIBUOPUL	Caprifoliaceae	2	S	P	A	FO	drupe	FF	-	-	-	-	-	-	-	-	51
VIBUTRIL	Caprifoliaceae	3	S	P	N	FO	drupe	FF	-	-	-	-	-	-	-	-	51
VICICRAC	Fabaceae	2	H	P	A	O	legume	-	-	-	SP	-	EM	-	MM	-	60; 42
VIOLAFFI	Violaceae	14	H	P	N	FO	capsule	-	-	EL	-	-	-	-	-	VE	7; 25
VIOLBLAN	Violaceae	19	H	P	N	FO	capsule	-	-	EL	-	-	EM	-	MM	VE	3, 5, 10, 30; 4; 25
VIOLCANA	Violaceae	2	H	P	N	F	capsule	-	-	EL	-	-	-	-	-	VE	30; 25
VIOLCUCU	Violaceae	12	H	P	N	FO	capsule	-	-	EL	-	-	EM	-	MM	VE	15; 4; 25
VIOLLABR	Violaceae	15	H	P	N	OF	capsule	-	-	EL	-	-	-	-	-	VE	ST; 25
VIOLPUBE	Violaceae	68	H	P	N	F	capsule	-	-	EL	-	-	-	-	-	VE	48; 25
VIOLROST	Violaceae	2	H	P	N	F	capsule	-	-	EL	-	-	EM	-	MM	VE	3, 5, 15, 31; 4; 25
VIOLSORO	Violaceae	2	H	P	N	FO	capsule	-	-	EL	-	-	-	-	-	VE	15; 25
VIOL_788	Violaceae	1	H	P	N	-	capsule	-	-	EL	-	-	-	-	-	VE	ST; 25
VIOL__SP	Violaceae	9	H	P	N	-	capsule	-	-	EL	-	-	-	-	-	VE	ST; 25
VITIRIPA	Vitaceae	63	V	P	N	OF	berry	FF	-	-	-	-	-	-	-	-	64
WALDFRAG	Rosaceae	23	H	P	N	FO	achene	FF	-	-	-	-	-	-	-	VE	25

APPENDIX 3

SPECIES CODES

Appendix 3. Species codes.

Species Code	Scientific Name
ABIEBALS	*Abies balsamea* (L.) Miller
ACERNEGU	*Acer negundo* L.
ACERRUBR	*Acer rubrum* L.
ACERSACC	*Acer saccharum* Marshall ssp. *saccharum*
ACERSACN	*Acer saccharinum* L.
ACERSANI	*Acer saccharum* Marshall ssp. *nigrum* (Michaux f.) Desmarais
ACERSPIC	*Acer spicatum* Lam.
ACHIMILL	*Achillia millefolium* L. ssp. *millefolium*
ADIAPEDA	*Adiantum pedatum* L. ssp. *pedatum*
AGRIGRYP	*Agrimonia gryposepala* Wallr.
AGROGIGA	*Agrostis gigantea* Roth
AGROSTOL	*Agrostis stolonifera* L.
ALLITRIC	*Allium tricoccum* Aiton
ALNUINCA	*Alnus incana* (L.) Moench ssp. *rugosa* (Duroi) Clausen
AMBRARTE	*Ambrosia artemisiifolia* L.
AMELARBO	*Amelanchier arborea* (Michaux f.) Fern.
AMELINTE	*Amelanchier interior* Nielsen
AMEL_SP	*Amelanchier* species
AMPHBRAC	*Amphicarpaea bracteata* (L.) Fern.
ANEMCANA	*Anemone canadensis* L.
ANEMQUIN	*Anemone quinqefolia* L.
ANEMVIRG	*Anemone virginiana* L.
ANTENEGL	*Antennaria neglecta* E. Greene
APOCANDR	*Apocynum androsaemifolium* L. ssp. *androsaemifolium*
AQUICANA	*Aquilegia canadensis* L.
ARALNUDI	*Aralia nudicaulis* L.
ARCTMINU	*Arctium minus* (Hill) Bernh. ssp. *minus*
ARISTRIP	*Arisaema triphyllum* (L.) Schott ssp. *triphyllum*
ASARCANA	*Asarum canadense* L.
ASCLINCA	*Asclepias incarnata* L. ssp. *incarnata*
ASCLSYRI	*Asclepias syriaca* L.
ASTECILI	*Aster ciliolatus* Lindley
ASTECORD	*Aster cordifolius* L.
ASTEERIC	*Aster ericoides* L.
ASTELANC	*Aster lanceolatus* L.
ASTELATE	*Aster lateriflorus* (L.) Britton
ASTEMACR	*Aster macrophyllus* L.
ASTENOVA	*Aster novae-angliae* L.
ASTEPUNI	*Aster puniceus* L.

Appendix 3. Species codes.

Species Code	Scientific Name
ASTEUMBE	*Aster umbellatus* Miller
ATHYFILI	*Athyrium filix-femina* (L.) ssp. *angustum* (Willd.) Clausen
ATHYTHEL	*Athyrium thelypterioides* (Michaux) Desv.
BETUALLE	*Betula alleghaniensis* Britton
BETUPAPY	*Betula papyrifera* Marshall
BIDEFRON	*Bidens frondosa* L.
BOEHCYLI	*Boehmeria cylindrica* (L.) Sw.
BOTRMATR	*Botrychium matricariaefolium* A. Braun ex Koch
BOTRMULT	*Botrychium multifidum* (S. Gmelin) Rupr.
BOTRVIRG	*Botrychium virginianum* (L.) Sw.
BRACEREC	*Brachyelytrum erectum* (Schreber in Roth ex Sprengel) P. Beauv.
BROMINER	*Bromus inermis* Leysser
CALTPALU	*Calthus palustris* L. ssp. *palustris*
CALYSEPI	*Calystegia sepium* L.
CARDACAN	*Carduus acanthoides* L.
CARDNUTA	*Carduus nutans* L.
CARDDIPH	*Cardamine diphylla* (Michx.) A. Wood
CARDPENS	*Cardamine pensylvanica* Muhlenb. ex Willd.
CAREALBU	*Carex albursina* E. Sheldon
CAREALOP	*Carex alopecoidea* Tuckerman
CAREARCT	*Carex arctata* Boott
CAREBACK	*Carex backii* F. Boott
CAREBEBB	*Carex bebbii* (L. Bailey) Olney ex Fern.
CAREBLAN	*Carex blanda* Dewey
CAREBREV	*Carex brevior* (Dewey) Mackenzie ex Lunell
CARECEPH	*Carex cephaloidea* Dewey
CARECOMM	*Carex communis* L. Bailey
CARECRIN	*Carex crinita* Lam.
CARECRIS	*Carex cristatella* Britton
CAREDEWE	*Carex deweyana* Schwein.
CAREDIGI	*Carex digitalis* Willd.
CAREGRAC	*Carex gracillima* Schwein.
CAREGRAN	*Carex granularis* Muhlenb. ex Willd.
CAREHIRT	*Carex hirtifolia* Mackenzie
CAREHITC	*Carex hitchcockiana* Dewey
CAREINTU	*Carex intumescens* Rudge
CARELANU	*Carex lanuginosa* Michaux
CARELAXI	*Carex laxiflora* Lam.
CAREPECK	*Carex peckii* Howe

Appendix 3. Species codes.

Species Code	Scientific Name
CAREPEDU	*Carex pedunculata* Muhlenb. ex Willd.
CAREPENS	*Carex pensylvanica* Lam.
CAREPLAT	*Carex plantaginea* Lam.
CAREPLAT	*Carex platyphylla* J.Carey
CAREPRAI	*Carex prairea* Dewey
CAREPROJ	*Carex projecta* Mackenzie
CAREPSEU	*Carex pseudo-cyperus* L.
CARERADI	*Carex radiata* (Wahlenb.) Small
CARERETR	*Carex retrorsa* Schwein.
CAREROSE	*Carex rosea* Schk. ex Willd.
CARESPAR	*Carex sparganioides* Muhlenb. ex Willd.
CARESTIP	*Carex stipata* Muhlenb. ex Willd.
CARETENE	*Carex tenera* Dewey
CARETRIB	*Carex tribuloides* Wahlenb.
CAREVULP	*Carex vulpinoidea* Michaux
CAREWOOD	*Carex woodii* Dewey
CARE_719	*Carex* specimen D719
CARE_858	*Carex* specimen D858
CARE_868	*Carex* specimen D868
CARE_870	*Carex* specimen D870
CARE_879	*Carex* specimen D879
CARE__OV	*Carex* sect. Ovales
CARE__SP	*Carex* species
CARYCORD	*Carya cordiformis* (Wangenh.) K. Koch
CAULTHAL	*Caulophyllum thalictroides* (L.) Michaux
CEANAMER	*Ceanothus americanus* L.
CELASCAN	*Celastrus scandens* L.
CERAFONT	*Cerastium fontanum* Baumg. ssp. *triviale* (Link) Jalas
CHIMUMBE	*Chimaphila umbellata* (L.) Barton
CHRYLEU	*Chrysanthemum leucanthemum* L.
CICUBULB	*Cicuta bulbifera* L.
CICUMACU	*Cicuta maculatum* L.
CINNLATI	*Cinna latifolia* (Trevir. ex Goeppinger) Griseb. in Ledeb.
CIRCALPI	*Circea alpina* L.
CIRCLUTE	*Circea lutetiana* L. ssp. *canadensis* (L.) Aschers.& Magnus
CIRSARVE	*Cirsium arvense* (L.) Scop.
CIRSVULG	*Cirsium vulgare* (Savi) Ten.
CLAYCARO	*Claytonia caroliniana* Michaux
CLEMVIRG	*Clematis virginiana* L.

Appendix 3. Species codes.

Species Code	Scientific Name
CLINBORE	*Clintonia borealis* (Aiton) Raf.
CONYCANA	*Conyza canadensis* (L.) Cronq.
CORNALTE	*Cornus alternifolia* L.f.
CORNFOEM	*Cornus foemina* Miller ssp. *racemosa* (Lam.) J.S. Wilson
CORNRUGO	*Cornus rugosa* Lam.
CORNSTOL	*Cornus stolonifera* Michaux
CORYCORN	*Corylus cornuta* Marshall
CRAT_SP1	*Crataegus* species #1
CRAT_SP2	*Crataegus* species #2
CRAT_SP3	*Crataegus* species #3
CRAT__SP	*Crataegus* species
CRYPCANA	*Cryptotaenia canadensis* (L.) DC.
CYPRCALC	*Cypripedium calceolus* L.
CYSTBULB	*Cystopteris bulbifera* (L.) Bernh.
CYSTFRAG	*Cystopteris fragilis* (L.) Bernh.
CYSTTENU	*Cystopteris tenuis* (Michaux) Desv.
DACTGLOM	*Dactylis glomerata* L.
DANTSPIC	*Danthonia spicata* (L.) P. Beauv. ex Roemer & Schultes
DAUCCARO	*Daucus carota* L.
DESMGLUT	*Desmodium glutinosum* (Muhlenb. ex Willd.) DC ex Loudon
DIANARME	*Dianthus armeria* L.
DICECANA	*Dicentra canadensis* (Goldie) Walp.
DICECUCU	*Dicentra cucullaria* (L.) Bernh.
DIERLONI	*Diervilla lonicera* Miller
DIRCPALU	*Dirca palustris* L.
DRYOCART	*Dryopteris carthusiana* (Villars) H.P. Fuchs
DRYOCRIS	*Dryopteris cristata* (L.) Gray
DRYOINTE	*Dryopteris intermedia* (Muhlenb. ex Willd.) A.Gray
DRYOMARG	*Dryopteris marginalis* (L.) A. Gray
ECHILOBA	*Echinocystis lobata* (Michaux) Torrey & A.Gray
ELYMREPE	*Elymus repens* (L.) Gould
ELYMVIRG	*Elymus virginicus* L.
EPIFVIRG	*Epifagus virginiana* (L.) Barton
EPILCILI	*Epilobium ciliatum* Raf.
EPILCOLO	*Epilobium coloratum* Biehler
EPILLEPT	*Epilobium leptophyllum* Raf.
EPILPARV	*Epilobium parviflorum* Schreber
EPIPHELL	*Epipactis helleborine* (L.) Crantz
EQUIARVE	*Equisetum arvense* L.

Appendix 3. Species codes.

Species Code	Scientific Name
EQUIHYEM	*Equisetum hyemale* L. ssp. *affine* (Engelm.) Stone
EQUILAEV	*Equisetum laevigatum* A. Braun
EQUISCIR	*Equisetum scirpoides* Michaux
ERIGANNU	*Erigeron annuus* (L.) Pers.
ERIGPHIL	*Erigeron philadelphicus* L. ssp. *philadelphicus*
ERIGSTRI	*Erigeron strigosus* Muhlenb. ex. Willd.
ERIG__SP	*Erigeron* species
ERYTAMER	*Erythronium americanum* Ker Gawler ssp. americanum
EUPAMACU	*Eupatorium maculatum* L.
EUPAPERF	*Eupatorium perfoliatum* L.
EUPARUGO	*Eupatorium rugosum* Houtt.
EUTHGRAM	*Euthamia graminifolia* (L.) Nutt.
FAGUGRAN	*Fagus grandifolia* Ehrh.
FESTARUN	*Festuca arundinacea* Schreber
FESTPRAT	*Festuca pratensis* Hudson
FESTRUBR	*Festuca rubra* L.
FESTSUBV	*Festuca subverticillata* (Pers.) E. Alexeev.
FRAGVESC	*Fragaria vesca* L. ssp. *americana* (Porter) Staudt
FRAGVIRG	*Fragaria virginiana* Miller
FRAXAMER	*Fraxinus americana* L.
FRAXNIGR	*Fraxinus nigra* Marshall
FRAXPENN	*Fraxinus pennsylvanica* Marshall
GALETETR	*Galeopsis tetrahit* L.
GALIAPAR	*Galium aparine* L.
GALIASPR	*Galium asprellum* Michaux
GALICIRC	*Galium circaezans* Michaux
GALILANC	*Galium lanceolatum* Torrey
GALIOBTU	*Galium obtusum* Bigelow
GALIPALU	*Galium palustre* L.
GALITRIF	*Galium triflorum* Michaux
GALI__SP	*Galium* species
GENTANDR	*Gentiana andrewsii* Griseb.
GERAMACU	*Geranium maculatum* L.
GERAROBE	*Geranium robertianum* L.
GEUMALEP	*Geum allepicum* Jacq.
GEUMLACI	*Geum laciniatum* Murray
GEUMRIVA	*Geum rivale* L.
GEUMURBA	*Geum urbanum* L.
GEUM__SP	*Geum* species

Appendix 3. Species codes.

Species Code	Scientific Name
GLYCSTRI	*Glyceria striata* (Lam.) A. Hitch.
GYMNDRYO	*Gymnocarpium dryopteris* (L.) Newman ssp. *dryopteris*
HACKVIRG	*Hackelia virginiana* (L.) I.M. Johnston
HEPAACUT	*Hepatica acutiloba* DC.
HIERAURA	*Hieracium aurantiacum* L.
HIERCAES	*Hieracium caespitosum* Dumort. ssp. *caespitosum*
HYDRVIRG	*Hydrophyllum virginianum* L.
HYPEPERF	*Hypericum perforatum* L.
HYSTPATU	*Hystrix patula* Moench
IMPACAPE	*Impatiens capensis* Meerb.
IRISVERS	*Iris versicolor* L.
IRIS_SP	*Iris* species
JUNCTENU	*Juncus tenuis* Willd.
LACTCANA	*Lactuca canadensis* L.
LACTSERR	*Lactuca serriola* L.
LACT_SP	*Lactuca* species
LAPOCANA	*Laportea canadensis* (L.) Wedd.
LEERORYZ	*Leersia oryzoides* (L.) Sw.
LEERVIRG	*Leersia virginica* Willd.
LEONCARD	*Leonurus cardiaca* L. ssp. cardiaca
LIPALOES	*Liparis loeselii* (L.) Rich. ex Lindley
LOBEINFL	*Lobelia inflata* L.
LOBE_SP	*Lobelia* species
LONICANA	*Lonicera canadensis* Bartram
LONIDIOI	*Lonicera dioica* L.
LONIHIRS	*Lonicera hirsuta* Eaton
LONIOBLO	*Lonicera oblongifolia* (Goldie) Hook.
LSYINUMM	*Lysimachia nummularia* L.
LYCOAMER	*Lycopus americanus* Muhlenb. ex Bartram
LYCOANNO	*Lycopodium annotinum* L.
LYCODEND	*Lycopodium dendroideum* Michaux
LYCOOBOB	*Lycopodium obscurum* L.var. obscurum
LYCOTRIS	*Lycopodium tristachyum* Pursh
LYCOUNIF	*Lycopus uniflorus* Michaux
LYSICILI	*Lysimachia* ciliata L.
LYSITERR	*Lysimachia terrestris* (L.) Britton. Sterns& Pogg.
MAIACANA	*Maianthemum canadense* Desf.
MAIARACE	*Maianthemum racemosum* (L.) Link ssp. *racemosum*
MAIASTEL	*Maianthemum stellatum* (L.) Link

Appendix 3. Species codes.

Species Code	Scientific Name
MATTSTRU	*Matteuccia struthiopteris* (L.) Tod.
MEDILUPU	*Medicago lupulina* L.
MELIALBA	*Melilotus alba* Medikus
MELIOFFI	*Melilotus officinalis* (L.) Pallas
MENICANA	*Menispermum canadense* L.
MENTARVE	*Mentha arvensis* L.
MILIEFFU	*Milium effusum* L.
MITCREPE	*Mitchella repens* L.
MITEDIPH	*Mitella diphylla* L.
MONOHYPT	*Monotropa hypopithys* L.
MONOUNIF	*Monotropa uniflora* L.
MUHLFRON	*Muhlenbergia frondosa* (Poiret in Lam.) Fern.
MUHLMEXI	*Muhlenbergia mexicana* (L.) Trin.
ONOCSENS	*Onoclea sensibilis* L.
ONOPACAN	*Onopordon acanthium* L.
ORYZASPE	*Oryzopsis asperifolia* Michaux
OSMOCLAY	*Osmorhiza claytonii* (Michaux) C.B. Clarke
OSMUCLAY	*Osmunda claytoniana* L.
OSMUREGA	*Osmunda regalis* L.
OSTRYVIRG	*Ostrya virginiana* (Miller) K. Koch
OXALSTRI	*Oxalis stricta* L.
OXAL__SP	*Oxalis* species
PANAQUIN	*Panax quinquefolium* L.
PANIACUM	*Panicum acuminatum* Sw.
PANICAPI	*Panicum capillare* L.
PARTINSE	*Parthenocissus inserta* (A. Kerner) Fritsch
PHALARUN	*Phalaris arundinacea* L.
PHEGCONN	*Phegopteris connectilis* (Michaux) Watt
PHLEPRAT	*Phleum pratense* L.
PHLO__SP	*Phlox* species
PHRYLEPT	*Phryma leptostachya* L.
PICEGLAU	*Picea glauca* (Moench) Voss
PILEPUMI	*Pilea pumila* (L.) A. Gray
PINUSTRO	*Pinus strobus* L.
PLANLANC	*Plantago lanceolata* L.
PLANMAJO	*Plantago major* L.
PLANRUGE	*Plantago rugelii* Decne.
POA_ALSO	*Poa alsodes* A. Gray
POA_COMP	*Poa compressa* L.

Appendix 3. Species codes.

Species Code	Scientific Name
POA_PALU	*Poa palustris* L.
POA_PRAT	*Poa pratensis* L. ssp. *pratensis*
POA_SALU	*Poa saltuensis* Fern. & Wieg.
POA__SP	*Poa* species
PODOPELT	*Podophyllum peltatum* L.
POLYACRO	*Polystichum acrostichoides* (Michaux.) Schott
POLYPAUC	*Polygala paucifolia* Willd.
POLYPERS	*Polygonum persicaria* L.
POLYPUBE	*Polygonatum pubescens* (Willd.) Pursh
POPUBALS	*Populus balsamifera* L.
POPUGRAN	*Populus grandidentata* Michaux
POPUTREM	*Populus tremuloides* Michaux
POTENORV	*Potentilla norvegica* L.
POTERECT	*Potentilla recta* L.
PREN__SP	*Prenanthes* species
PRUNSERO	*Prunus serotina* Ehrh.
PRUNVIRG	*Prunus virginiana* L. spp. *virginiana*
PRUNVULG	*Prunella vulgaris* L.
PTERAQUI	*Pteridium aquilinum* (L.) Kuhn
PYROELLI	*Pyrola elliptica* Nutt.
QUERALBA	*Quercus alba* L.
QUERMACR	*Quercus macrocarpa* Michaux
QUERRUBR	*Quercus rubra* L.
QUER__SP	*Quercus* species
RANUABOR	*Ranunculus abortivus* L.
RANUACRI	*Ranunculus acris* L.
RANUHISP	*Ranunculus hispidus* Michaux
RANURECU	*Ranunculus recurvatus* Poiret ex Lam.
RHAMALNI	*Rhamnus alnifolia* L'Her.
RHAMCATH	*Rhamnus cathartica* L.
RHUSRADI	*Rhus radicans* L. ssp. *negundo* (E. Greene) McNeill
RHUSTYPH	*Rhus typhina* L.
RIBEAMER	*Ribes americanum* Miller
RIBECYNO	*Ribes cynosbati* L.
RIBEGLAN	*Ribes glandulosum* Grauer
RIBELACU	*Ribes lacustre* (Pers.) Poiret
RIBERUBR	*Ribes rubrum* L.
RIBETRIS	*Ribes triste* Pall.
RIBE_827	*Ribes* specimen D827

Appendix 3. Species codes.

Species Code	Scientific Name
ROBIPSEU	*Robinia pseudoacacia* L.
ROSABLAN	*Rosa blanda* Aiton
ROSAPALU	*Rosa palustris* Marshall
RUBUALLE	*Rubus allegheniensis* Porter
RUBUIDAE	*Rubus idaeus* L.
RUBUOCCI	*Rubus occidentalis* L.
RUBUODOR	*Rubus odoratus* L.
RUBUPUBE	*Rubus pubescens* Raf.
RUBU_840	*Rubus* specimen D840
RUDBHIRT	*Rudbeckia hirta* L.
RUMEORBI	*Rumex orbiculatus* A.Gray
SALIBEBB	*Salix bebbiana* Sarg.
SALIDISC	*Salix discolor* Muhlenb.
SALIERIO	*Salix eriocephala* Michaux
SALIPETI	*Salix petiolaris* Smith
SAMBCANA	*Sambucus canadensis* L.
SAMBRACE	*Sambucus racemosa* L. ssp. *pubens* (Michaux) House
SANGCANA	*Sanquinaria canadensis* L.
SANIMARI	*Sanicula marilandica* L.
SANITRIF	*Sanicula trifoliata* Bickn.
SANI__SP	*Sanicula* species
SCHIZPURP	*Schizachne purpurascens* (Torrey) Swallen ssp. *purpurascens*
SCIRATRO	*Scirpus atrovirens* Willd
SCUTLATE	*Scutellaria lateriflora* L.
SICYANGU	*Sicyos angulatus* L.
SILEVULG	*Silene vulgaris* (Moench) Garcke
SMILHERB	*Smilax herbacea* L.
SMILHISP	*Smilax hispida* Muhlenb.
SOLADULC	*Solanum dulcamera* L.
SOLIALT	*Solidago altissima* L.
SOLICAES	*Solidago caesia* L.
SOLICANA	*Solidago canadensis* L.
SOLIFLEX	*Solidago flexicaulis* L.
SOLIGIGA	*Solidago gigantea* Aiton
SOLIJUNC	*Solidago juncea* Aiton
SOLINEMO	*Solidago nemoralis* Aiton
SOLIRUGO	*Solidago rugosa* Aiton ssp. *rugosa*
SONCARVE	*Sonchus arvensis* L.
SONCOLER	*Sonchus oleraceus* L.

Appendix 3. Species codes.

Species Code	Scientific Name
SPHENINTE	*Spenopholis intermedia* (Rydb.) Rydb.
STELLONG	*Stellaria longifolia* Muhlenb. ex Willd.
STREROSE	*Streptopus roseus* Michaux
TARAOFFI	*Taraxacum officinale* G. Weber
TAXUCANA	*Taxus canadensis* Marshall
THALDIOI	*Thalictrum dioicum* L.
THALPUBE	*Thalictrum pubescens* Pursh
THELNOVE	*Thelypteris noveboracensis* (L.) Nieuwl.
THELPALU	*Thelypteris palustris* (Salisb.) Schott
THUJOCCI	*Thuja occidentalis* L
TIARCORD	*Tiarella cordifolia* L.
TILIAMER	*Tilia americana* L.
TRAGDUBI	*Tragopagon dubius* Scop.
TRIEBORE	*Trientalis borealis* Raf. ssp. borealis
TRIFREPE	*Trifolium repens* L.
TRILEREC	*Trillium erectum* L.
TRILGRAN	*Trillium grandiflorum* (Michaux) Salisb.
TRIOAURA	*Triosteum aurantiacum* E. Bickn.
TSUGCANA	*Tsuga canadensis* (L.) Carriere
TUSSFARF	*Tussilago farfara* L.
TYPHLATI	*Typha latifolia* L
ULMUAMER	*Ulmus americana* L.
URTIDIGR	*Urtica dioica* L. ssp. *gracilis*
URTIDIOI	*Urtica dioica* L. ssp. *dioica*
UVULGRAN	*Uvularia grandiflora* Smith
VACCANGU	*Vaccinium angustifolium* Aiton
VERBHAST	*Verbena hastata* L.
VERBTHAP	*Verbascum thapsus* L.
VERBURTI	*Verbena urticifolia* L.
VEROOFFI	*Veronica officinalis* L.
VEROSERP	*Veronica serpyllifolia* L.
VIBUACER	*Viburnum acerfolium* L.
VIBULENT	*Viburnum lentago* L.
VIBUOPUL	*Viburnum opulus* L.
VIBUTRI	*Viburnum trilobum* Marshall
VICICRAC	*Vicia cracca* L.
VIOLAFFI	*Viola affinis* Le Conte
VIOLBLAN	*Viola blanda* Willd.
VIOLCANA	*Viola canadensis* L.

Appendix 3. Species codes.

Species Code	Scientific Name
VIOLCUCU	*Viola cucullata* Aiton
VIOLLABR	*Viola labradorica* Schrank
VIOLPUBE	*Viola pubescens* Aiton
VIOLROST	*Viola rostrata* Pursh
VIOLSORO	*Viola sororia* Willd.
VITARIPA	*Vita riparia* Michaux
WALDFRAG	*Waldsteinia fragarioides* (Michaux) Tratt.

APPENDIX 4

DISTRIBUTION OF SPECIES BY SOIL PARENT MATERIAL, SOIL ORDER, SOIL MOISTURE AND CANOPY CLOSURE

Legend

Column Heading	Description	Unit
# Q	# quadrats	# quadrats
GF	Glacio-fluvial parent material	# quadrats
CT	Calcareous till parent material	# quadrats
LAC	Lacustrine parent material	# quadrats
CO	Calcareous outwash parent material	# quadrats
B	Brunisol soil order	# quadrats
GB	Gleyed Brunisol soil order	# quadrats
L	Luvisol soil order	# quadrats
GL	Gleyed Luvisol soil order	# quadrats
G	Gleysolic soil order	# quadrats
SD	Seasonally dry depressions	# quadrats[1]
SM	Seasonally moist depressions	# quadrats[1]
SW	Seasonally wet depressions	# quadrats[1]
OC	Open canopy	# quadrats[2]
CC	Closed canopy	# quadrats[2]

Notes:

1. Frequency based on presence in dry, moist and wet microhabitats, respectively; frequency may not sum to number of quadrats recorded in column 2 (#Q) since occurrences on logs, stumps, raised root mats, lanes, ditches and regenerating fields were not included.

2. Frequency based on presence in open and closed microhabitats, respectively; frequency may not sum to number of quadrats recorded in column 2 (#Q) since species sometimes present in both open and closed microhabtats in the same quadrat.

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material			Soil Order						Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
ABIEBALS	61	0	38	5	18	10	13	21	15	2	47	6	1	7	57
ACERNEGU	4	0	4	0	0	1	2	0	0	1	3	1	0	0	4
ACERRUBR	86	28	30	8	20	46	5	21	14	0	65	7	2	20	75
ACERSACC	175	40	96	6	33	68	22	56	28	1	152	15	3	29	157
ACERSACN	22	0	12	0	10	4	5	1	6	6	4	5	6	9	17
ACERSANI	7	0	6	0	1	1	5	0	1	0	6	1	0	0	7
ACERSPIC	34	0	26	8	0	2	3	4	20	5	15	9	3	8	29
ACHIMILL	10	0	2	0	8	4	6	0	0	0	0	2	1	7	7
ACTAPACH	29	3	15	0	11	6	0	21	2	0	29	0	0	7	23
ACTARUBR	22	0	18	1	3	5	6	6	3	2	17	3	0	2	21
ACTA__SP	40	6	21	1	12	14	5	13	6	2	30	1	2	4	35
ADIAPEDA	20	0	10	0	10	0	8	8	4	0	17	3	3	3	17
AGRIGRYP	9	0	5	0	4	2	3	3	1	0	5	2	0	2	7
AGROGIGA	13	0	5	0	8	4	9	0	0	0	0	4	2	10	7
AGROSTOL	3	0	2	0	1	1	2	0	0	0	0	0	1	2	1
ALLITRIC	27	0	14	0	13	0	3	19	5	0	26	0	4	4	24
ALNUINCA	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1
AMBRARTE	2	0	2	0	0	0	2	0	0	0	0	0	0	2	0
AMELARBO	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1
AMELINTE	5	2	1	0	2	3	0	2	0	0	4	0	0	2	4
AMEL__SP	47	28	15	0	4	42	0	5	0	0	47	0	0	2	45
AMPHBRAC	11	0	3	0	8	3	3	3	2	0	7	1	3	2	9
ANEMCANA	4	0	0	0	4	3	1	0	0	0	0	1	0	3	2
ANEMQUIN	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1
ANEMVIRG	11	0	1	1	9	5	2	3	1	0	2	1	0	8	6
ANTENEGL	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
APOCANDR	16	4	6	0	6	9	1	6	0	0	13	1	0	1	16
AQUICANA	13	6	5	0	2	9	0	4	0	0	11	0	0	2	12
ARALNUDI	40	16	19	5	0	19	4	4	13	0	28	8	0	6	37

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
ARCTMINU	9	0	8	1	0	1	4	3	1	0	6	1	0	4	5
ARISTRIP	97	0	69	8	20	2	21	37	31	6	72	29	12	22	83
ASARCANA	38	0	23	0	15	0	9	20	9	0	35	3	2	7	34
ASCLINCA	2	0	0	0	2	0	1	1	0	0	0	0	0	1	1
ASCLSYRI	16	0	8	0	8	7	4	5	0	0	8	3	0	11	10
ASTECILI	24	5	9	0	10	18	2	4	0	0	16	0	1	10	17
ASTECORD	13	2	5	0	6	4	1	6	2	0	11	0	1	2	11
ASTEERIC	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
ASTELANC	5	0	2	0	3	1	2	1	1	0	0	0	0	5	0
ASTELATE	66	0	44	6	16	16	25	8	13	4	35	21	6	19	58
ASTEMACR	7	5	2	0	0	7	0	0	0	0	7	0	0	1	6
ASTENOVE	18	0	9	1	8	9	5	1	3	0	6	2	2	8	13
ASTEPUNI	15	0	6	1	8	4	9	0	1	1	0	6	3	10	10
ASTEUMBE	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1
ATHYFILI	64	0	42	6	16	3	17	21	20	3	44	15	8	14	57
ATHYTHEL	6	0	0	0	6	0	0	3	3	0	5	0	2	0	6
BETUALLE	32	0	20	5	7	0	6	5	17	4	6	4	3	4	28
BETUPAPY	29	5	12	2	10	13	4	8	2	2	15	1	0	9	24
BIDEFRON	14	0	14	0	0	0	6	1	3	4	3	2	3	8	8
BOEHCYLI	28	0	16	0	12	0	11	6	6	5	7	5	10	10	20
BOTRMATR	2	1	0	0	1	1	0	1	0	0	1	0	0	1	1
BOTRMULT	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
BOTRVIRG	44	9	12	0	23	18	0	22	4	0	40	1	0	6	41
BRACEREC	5	1	1	0	3	1	0	4	0	0	5	0	0	2	3
BROMINER	3	0	2	0	1	1	2	0	0	0	0	0	1	3	1
CALTPALU	1	0	1	0	0	0	0	0	1	0	0	1	1	0	1
CALYSEPI	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0
CARDACAN	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0
CARDDIPH	47	1	28	1	17	1	12	16	18	0	37	12	3	11	41

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
CARDNUTA	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
CARDPENS	3	0	2	0	1	0	2	0	0	1	0	1	1	2	1
CAREALBU	5	0	1	0	4	0	0	5	0	0	5	0	0	2	3
CAREALOP	3	0	0	0	3	2	1	0	0	0	0	1	1	2	1
CAREARCT	35	4	14	3	14	7	3	18	7	0	29	2	0	10	27
CAREBACK	9	2	7	0	0	6	0	3	0	0	8	0	0	3	6
CAREBEBB	9	0	6	0	3	1	6	0	2	0	0	3	2	6	4
CAREBLAN	61	0	31	1	29	10	17	17	17	0	41	10	2	14	52
CAREBREV	4	0	0	0	4	1	3	0	0	0	0	1	1	2	2
CARECEPH	2	0	1	0	1	0	2	0	0	0	0	1	1	0	2
CARECOMM	2	0	2	0	0	0	1	1	0	0	2	0	0	0	2
CARECRIN	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0
CARECRIS	16	0	9	0	7	2	9	1	1	3	2	5	4	7	10
CAREDEWE	82	8	52	8	14	26	12	21	22	1	57	13	0	20	66
CAREDIGI	5	0	5	0	0	1	0	4	0	0	5	0	0	1	4
CAREGRAC	63	0	37	4	22	5	22	16	16	4	36	16	5	16	54
CAREGRAN	7	0	3	0	4	2	5	0	0	0	1	1	1	5	5
CAREHIRT	6	0	0	0	6	0	0	3	3	0	6	0	2	0	6
CAREHITC	3	0	1	0	2	1	0	2	0	0	3	0	0	0	3
CAREINTU	28	0	16	0	12	0	5	9	9	5	10	4	6	9	20
CARELANU	7	0	0	0	7	4	3	0	0	0	0	1	1	5	6
CARELAXI	14	1	8	0	5	4	5	5	0	0	12	0	0	4	10
CAREPECK	2	0	0	0	2	0	0	0	2	0	2	0	0	0	2
CAREPEDU	80	10	48	6	16	15	18	19	24	4	61	17	1	13	72
CAREPENS	120	33	58	3	26	57	17	36	9	1	104	7	1	19	112
CAREPLAN	9	0	4	0	5	0	0	6	3	0	8	1	1	1	9
CAREPLAT	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1
CAREPRAI	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
CAREPROJ	5	0	2	0	3	1	2	1	1	0	0	2	2	4	2

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
CAREPSEU	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1
CARERADI	49	0	29	4	16	9	18	11	8	3	25	14	4	11	41
CARERETR	12	0	9	0	3	0	5	0	3	4	0	2	7	6	6
CAREROSE	69	3	48	4	14	21	25	12	11	0	52	12	2	10	63
CARESPAR	5	0	4	1	0	4	0	0	1	0	4	1	0	1	4
CARESTIP	17	0	9	1	7	2	8	1	3	3	0	5	6	9	9
CARETENE	14	0	2	0	12	4	4	3	3	0	2	3	2	7	10
CARETRIB	6	0	2	0	4	0	5	1	0	0	0	3	1	2	4
CAREVULP	9	0	5	0	4	1	8	0	0	0	0	3	3	6	4
CAREWOOD	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1
CARE_719	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1
CARE_868	2	0	2	0	0	0	2	0	0	0	0	0	0	2	0
CARE_870	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
CARE_879	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
CARE_OV	5	0	3	0	2	0	1	2	2	0	2	1	1	1	4
CARE_SP	6	0	5	0	1	1	0	3	1	1	3	1	0	2	4
CARPCARO	26	1	9	1	16	8	1	13	5	0	20	2	2	3	24
CARYCORD	70	25	30	5	9	43	1	19	6	0	61	2	0	9	67
CAULTHAL	57	1	40	0	16	4	10	33	10	0	54	2	2	7	52
CEANAMER	2	0	2	0	0	2	0	0	0	0	2	0	0	1	1
CELASCAN	33	11	9	1	12	19	1	11	2	0	29	0	0	7	28
CERAFONT	10	0	4	0	6	4	6	0	0	0	2	1	1	7	4
CHIMUMBE	2	2	0	0	0	2	0	0	0	0	2	0	0	0	2
CHRYLEUC	7	0	2	0	5	4	3	0	0	0	0	0	0	7	3
CICUBULB	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1
CICUMACU	4	0	2	0	2	1	2	0	1	0	0	0	3	2	2
CINNLATI	11	0	8	1	2	0	0	0	8	3	1	3	4	2	9
CIRCALPI	36	0	17	7	12	0	2	8	23	3	15	14	3	8	29
CIRCLUTE	95	1	69	8	17	13	21	31	25	5	71	28	5	27	78

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
CIRSARVE	10	0	6	1	3	3	2	4	1	0	3	2	0	9	3
CIRSVULG	6	0	4	0	2	2	0	3	0	1	3	0	0	6	0
CLAYCARO	13	2	5	0	6	2	0	10	1	0	12	0	0	3	10
CLEMVIRG	12	0	8	2	2	0	6	1	4	1	1	6	3	5	8
CLINBORE	2	1	0	1	0	1	0	0	1	0	1	1	0	0	2
CONYCANA	5	0	5	0	0	0	0	4	0	1	3	0	0	5	0
CORNALTE	90	4	65	8	13	19	17	26	25	3	70	25	2	10	83
CORNFOEM	16	0	15	0	1	13	3	0	0	0	14	3	0	2	14
CORNRUGO	29	9	16	0	4	19	7	1	1	1	18	2	4	10	22
CORNSTOL	22	0	13	1	8	5	12	0	4	1	3	7	4	12	15
CORYCORN	45	19	19	0	7	31	0	11	3	0	43	1	0	7	43
CRAT_SP1	3	3	0	0	0	3	0	0	0	0	3	0	0	0	3
CRAT_SP2	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1
CRAT_SP3	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1
CRAT_SP	26	9	7	0	10	15	4	4	3	0	18	1	1	9	19
CRYPCANA	2	0	2	0	0	0	0	1	1	0	2	0	0	2	1
CYPRCALC	2	0	1	0	1	0	2	0	0	0	0	2	0	0	2
CYSTBULB	35	0	25	0	10	1	16	5	11	2	21	13	7	7	31
CYSTFRAG	4	0	1	0	3	0	0	2	2	0	3	0	0	0	4
CYSTTENU	2	0	2	0	0	1	1	0	0	0	2	0	0	1	1
DACTGLOM	6	0	5	0	1	2	2	2	0	0	3	1	0	4	3
DANTSPIC	4	0	3	0	1	2	1	1	0	0	3	0	0	2	3
DAUCCARO	6	0	3	0	3	2	3	1	0	0	0	0	0	5	1
DESMGLUT	7	0	1	0	6	1	0	6	0	0	6	0	0	2	7
DIANARME	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
DICECANA	18	0	10	0	8	0	0	18	0	0	18	0	0	6	13
DICECUCU	4	0	3	0	1	0	0	4	0	0	4	0	0	0	4
DIERLONI	12	6	6	0	0	9	2	1	0	0	12	0	0	1	11
DIRCPALU	9	0	1	0	8	1	0	8	0	0	9	0	0	4	6

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
DRYOCART	107	7	69	6	25	17	23	37	22	8	74	17	4	25	92
DRYOCRIS	23	0	16	4	3	0	6	2	12	3	6	9	2	5	19
DRYOINTE	72	11	37	8	16	12	1	27	29	3	51	12	1	14	61
DRYOMARG	33	1	22	8	2	3	3	2	22	3	17	12	1	8	26
ECHILOBA	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1
ELYMREPE	2	0	1	0	1	0	1	1	0	0	0	1	0	2	1
ELYMVIRG	10	0	6	0	3	0	6	0	1	2	0	5	2	4	7
EPIFVIRG	4	0	4	0	1	1	0	4	0	0	4	0	0	1	3
EPILCILI	5	0	0	0	5	2	3	0	0	0	0	2	1	1	5
EPILCOLO	30	0	20	4	6	2	9	3	12	4	5	11	5	16	14
EPILLEPT	4	0	0	0	4	2	2	0	0	0	0	1	0	1	4
EPILPARV	7	0	5	2	0	0	1	0	5	1	0	1	1	5	2
EPIPHELL	130	29	72	8	21	53	24	29	20	4	100	22	4	21	117
EQUIARVE	34	0	24	0	10	8	17	4	4	1	17	11	6	15	31
EQUIHYEM	7	2	4	0	1	6	0	1	0	0	6	0	0	1	6
EQUILAEV	2	0	2	0	0	0	2	0	0	0	1	1	0	1	2
EQUISCIR	4	0	4	0	0	1	1	2	0	0	3	0	0	0	4
ERIGANNU	10	0	9	0	1	0	7	3	0	0	5	2	2	6	4
ERIGPHIL	34	0	25	0	9	4	20	8	2	0	23	9	2	12	26
ERIGSTRI	8	0	2	0	6	3	3	2	0	0	0	2	0	6	4
ERIG__SP	2	0	2	0	0	0	2	0	0	0	0	1	0	1	1
ERYTAMER	107	14	69	0	24	24	20	41	22	0	98	19	3	19	94
EUPAMACU	15	0	8	1	6	3	8	1	3	0	1	3	3	11	7
EUPAPERF	7	0	4	0	3	2	4	1	0	0	1	2	0	5	3
EUPARUGO	21	0	11	0	10	0	12	5	4	0	11	8	6	6	15
EUTHGRAM	6	0	1	0	5	4	1	1	0	0	1	0	0	6	1
FAGUGRAN	67	15	37	2	13	21	7	32	7	0	57	4	0	9	59
FESTARUN	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0
FESTPRAT	2	0	2	0	0	0	2	0	0	0	0	0	0	2	0

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
FESTRUBR	2	0	0	0	2	2	0	0	0	0	0	0	0	2	0
FESTSUBV	30	2	19	0	9	14	7	6	3	0	28	1	1	5	26
FRAGVESC	28	2	25	0	1	4	12	5	6	1	22	3	0	9	20
FRAGVIRG	28	2	10	6	10	7	10	2	8	1	4	11	1	14	22
FRAXAMER	95	23	49	3	20	47	9	33	6	0	86	5	1	18	84
FRAXNIGR	52	0	34	7	11	3	21	4	21	3	19	20	7	18	40
FRAXPENN	51	0	30	5	16	5	24	5	17	0	27	23	5	16	41
GALESPEC	2	0	1	0	1	0	0	2	0	0	2	0	0	0	2
GALETETR	3	0	2	0	1	0	1	2	0	0	2	1	0	2	1
GALIAPAR	11	0	3	0	8	3	0	8	0	0	11	0	0	4	8
GALIASPR	3	0	2	0	1	0	1	0	0	2	0	1	0	0	3
GALICIRC	4	0	0	0	4	0	0	4	0	0	3	0	0	1	3
GALILANC	15	11	4	0	0	15	0	0	0	0	15	0	0	1	14
GALIOBTU	15	0	7	0	8	4	10	0	1	0	1	3	4	10	11
GALIPALU	3	0	3	0	0	0	0	0	0	3	0	0	0	2	1
GALITRIF	105	11	59	5	30	36	19	24	25	1	76	13	5	29	90
GALI_SP	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
GENTANDR	7	0	0	0	7	3	4	0	0	0	0	2	1	4	5
GERAMACU	12	0	12	0	0	11	1	0	0	0	11	0	0	2	10
GERAROBE	53	0	35	8	10	0	13	11	24	5	28	15	5	15	41
GEUMALEP	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1
GEUMCANA	13	0	10	2	1	1	5	0	7	0	4	5	1	5	9
GEUMLACI	21	0	13	2	6	0	5	4	7	5	6	8	1	7	16
GEUMRIVA	2	0	2	0	0	0	0	0	2	0	0	1	2	0	2
GEUMURBA	2	0	2	0	0	0	0	0	2	0	2	0	0	1	1
GEUM_SP	23	0	14	6	3	4	8	1	6	4	6	9	3	7	17
GLYCSTRI	62	0	40	7	15	3	23	5	23	8	27	26	11	20	50
GYMNDRYO	24	0	9	5	10	1	3	9	11	0	15	4	1	2	23
HACKVIRG	4	0	4	0	0	0	0	4	0	0	4	0	0	4	0

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
HEPAACUT	25	3	12	0	10	9	3	13	0	0	22	1	0	4	23
HIERAURA	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1
HIERCAES	60	0	42	7	11	16	23	9	12	0	33	10	2	21	44
HYDRVIRG	14	5	6	0	3	5	1	5	3	0	11	0	1	1	13
HYPEPERF	11	0	4	0	8	6	4	2	0	0	1	1	0	8	6
HYSTPATU	3	0	2	0	1	0	2	1	0	0	1	2	1	2	2
IMPACAPE	60	0	28	7	25	2	11	15	26	6	27	14	15	21	50
INULHELI	2	0	1	0	1	0	2	0	0	0	0	1	1	2	0
IRISVERS	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0
IRIS__SP	5	0	1	0	4	1	4	0	0	0	0	0	2	2	3
JUNCTENU	3	0	3	0	0	0	2	1	0	0	1	0	0	3	0
LACTCANA	4	0	2	0	2	0	0	4	0	0	1	0	0	4	1
LACTSERR	5	0	5	0	0	0	2	2	0	1	2	0	0	5	0
LACT__SP	2	0	2	0	0	0	1	0	1	0	0	0	0	1	1
LAPOCANA	19	0	12	0	7	1	5	0	13	0	9	5	8	7	12
LEERORYZ	7	0	5	0	2	2	4	1	0	0	0	2	2	6	1
LEERVIRG	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0
LEONCARD	4	0	4	0	0	0	0	4	0	0	4	0	0	3	1
LIPALOES	4	0	0	0	4	1	3	0	0	0	0	1	1	1	3
LOBEINFL	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0
LOBE__SP	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
LONICANA	33	19	11	2	0	26	0	4	2	0	31	0	0	3	30
LONIDIOI	14	6	8	0	0	13	0	1	0	0	14	0	0	1	13
LONIHIRS	10	10	0	0	0	10	0	0	0	0	10	0	0	0	10
LYCOAMER	6	0	2	0	4	1	3	0	2	0	0	1	3	2	4
LYCOANNO	5	2	2	0	1	3	0	2	0	0	5	0	0	0	5
LYCODEND	2	1	1	0	0	2	0	0	0	0	1	0	0	0	2
LYCOOBOB	4	4	0	0	0	4	0	0	0	0	4	0	0	0	4
LYCOTRIS	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

SPECIES	#Q	Soil Parent Material				Soil Order					Soil Moisture			Canopy	
		GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
LYCOUNIF	18	0	12	0	6	2	8	0	3	5	0	3	5	9	11
LYSICILI	14	0	6	0	8	4	8	0	2	0	0	5	3	7	11
LYSINUMM	9	0	6	0	3	0	5	0	4	0	1	3	5	1	8
LYSITERR	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1
MAIACANA	130	36	66	5	23	60	18	33	18	1	107	10	0	21	124
MAIARACE	91	31	45	2	13	52	11	22	5	1	82	7	1	10	86
MAIASTEL	10	2	4	0	4	5	2	3	0	0	8	1	0	1	9
MATTSTRU	18	0	8	1	9	2	8	3	5	0	11	5	4	5	16
MEDILUPU	11	0	6	0	5	7	3	0	1	0	3	0	0	8	6
MELIALBA	4	0	1	0	3	3	0	1	0	0	1	0	0	4	2
MELIOFFI	2	0	0	0	2	2	0	0	0	0	0	0	0	2	1
MENICANA	2	0	0	0	2	0	0	2	0	0	2	0	0	1	2
MENTARVE	12	2	5	0	5	3	8	0	0	1	1	3	2	5	8
MILIEFFU	7	0	3	0	4	0	0	5	2	0	7	0	0	1	7
MITCREPE	17	17	0	0	0	17	0	0	0	0	17	0	0	1	16
MITEDIPH	23	10	6	0	7	10	0	2	11	0	18	3	0	4	19
MONAFIST	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1
MONOHYPO	2	2	0	0	0	2	0	0	0	0	2	0	0	0	2
MONOUNIF	15	9	6	0	0	14	0	1	0	0	15	0	0	0	15
MUHLFRON	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1
MUHLMEXI	7	0	2	0	5	2	4	1	0	0	0	1	1	5	3
NEPECATA	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0
ONOCSENS	40	0	24	3	13	4	13	5	12	6	12	11	12	15	30
ONOPACAN	3	0	3	0	0	0	0	3	0	0	3	0	0	3	0
ORYZASPE	51	32	15	0	4	46	0	5	0	0	51	0	0	9	48
OSMOCLAY	36	4	12	0	20	9	0	22	5	0	34	0	1	10	28
OSMUCLAY	5	3	2	0	0	3	0	1	1	0	4	1	0	0	5
OSMUREGA	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1
OSTRVIRG	82	21	42	1	18	37	9	32	4	0	77	2	0	9	76

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material			Soil Order						Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
OXALSTRI	3	0	0	0	3	0	0	3	0	0	1	0	0	2	2
OXAL__SP	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1
PANAQUIN	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
PANIACUM	3	0	0	0	3	1	0	2	0	0	0	0	0	3	2
PANICAPI	1	0	1	0	0	0	0	1	0	0	1	0	0	1	0
PANI__SP	2	0	2	0	0	1	0	1	0	0	1	0	0	1	1
PARTINSE	60	0	30	3	27	8	22	13	14	3	32	15	10	19	52
PHALARUN	3	0	0	0	3	3	0	0	0	0	0	0	0	2	2
PHEGCONN	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1
PHLEPRAT	5	0	2	0	3	2	3	0	0	0	0	0	0	5	2
PHLO__SP	2	0	0	0	2	0	0	2	0	0	2	0	0	1	1
PHRYLEPT	19	0	5	0	13	3	2	11	2	0	15	1	0	8	12
PICEGLAU	5	0	5	0	0	2	3	0	0	0	3	0	0	1	4
PILEPUMI	25	0	19	0	6	3	6	3	9	4	6	5	6	16	14
PINUSTRO	13	1	10	0	2	5	3	5	0	0	12	1	0	1	12
PLANLANC	2	0	0	0	2	2	0	0	0	0	0	0	0	1	1
PLANMAJO	11	0	6	0	5	2	8	1	0	0	1	4	1	5	6
PLANRUGE	10	0	3	0	7	2	6	2	0	0	1	2	1	7	5
POA_ALSO	16	2	2	0	12	2	3	6	5	0	10	2	4	2	14
POA_COMP	24	0	14	1	9	13	5	4	2	0	12	2	3	12	19
POA_PALU	23	0	14	0	9	3	16	1	2	1	3	11	3	11	17
POA_PRAT	27	0	14	0	13	12	9	6	0	0	10	4	3	18	15
POA_SALT	3	2	1	0	0	3	0	0	0	0	3	0	0	1	2
POA___SP	2	0	2	0	0	0	2	0	0	0	2	0	0	0	2
PODOPELT	5	0	4	0	1	3	0	1	1	0	4	0	0	0	5
POLYACRO	10	0	7	0	3	1	6	2	1	0	9	1	0	0	10
POLYPAUC	6	0	6	0	0	3	0	3	0	0	5	0	0	2	4
POLYPERS	4	0	4	0	0	0	4	0	0	0	0	0	2	4	0
POLYPUBE	93	40	43	0	10	60	5	21	7	0	83	2	1	9	88

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
POPUBALS	13	0	8	0	5	4	2	1	4	2	4	6	0	3	11
POPUGRAN	20	4	16	0	0	13	0	7	0	0	20	0	0	0	20
POPUTREM	30	6	11	0	13	16	5	9	0	0	21	2	1	7	26
POTENORV	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
POTERECT	7	0	1	0	6	4	1	2	0	0	0	0	0	6	3
PREN_SP	20	3	16	0	1	16	3	0	1	0	19	0	0	4	17
PRUNSERO	80	24	38	3	15	44	7	24	5	0	66	5	0	10	73
PRUNVIRG	123	34	64	3	22	57	16	32	13	5	101	10	4	22	110
PRUNVULG	14	0	6	0	8	4	10	0	0	0	2	5	3	8	9
PTERAQUI	42	19	15	0	8	31	0	11	0	0	39	0	0	9	41
PYROELLI	18	6	6	1	5	10	1	5	2	0	16	0	1	1	18
QUERALBA	9	0	9	0	0	5	0	4	0	0	8	0	0	1	9
QUERMACR	12	0	7	0	5	0	7	5	0	0	9	2	0	1	11
QUERRUBR	72	34	28	0	10	53	0	19	0	0	67	0	0	7	68
QUER_SP	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1
RANUABOR	60	8	33	1	18	16	14	19	11	0	40	10	4	13	48
RANUACRI	31	0	20	1	10	10	16	3	1	1	13	9	3	14	25
RANUHICA	1	0	1	0	0	0	0	0	1	0	0	1	1	0	1
RANURECU	61	0	42	6	13	12	20	11	17	1	39	18	7	10	54
RHAMALNI	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1
RHAMCATH	76	2	58	1	15	22	11	23	13	7	50	9	2	23	61
RHUSRADI	45	15	25	1	4	31	10	2	2	0	38	6	3	7	42
RHUSTYPH	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
RIBEAMER	14	0	9	0	5	3	6	0	2	3	1	5	5	4	10
RIBECYNO	93	17	60	4	12	32	20	22	14	5	70	18	2	10	87
RIBEGLAN	4	0	4	0	0	0	0	0	4	0	1	3	2	1	3
RIBELACU	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1
RIBERUBR	5	0	3	0	2	0	3	1	1	0	2	1	1	2	3
RIBETRIS	30	4	19	5	2	6	11	0	11	2	10	11	4	12	21

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
RIBE_827	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1
ROBIPSEU	19	0	2	0	18	3	3	11	3	0	14	0	2	4	16
ROSABLAN	3	2	0	0	1	2	1	0	0	0	2	1	0	0	3
ROSAPALU	3	0	0	0	3	1	2	0	0	0	0	1	1	1	2
RUBUALLE	18	5	6	1	6	8	0	8	2	0	14	1	1	5	16
RUBUIDAE	53	0	33	7	13	6	5	16	20	6	28	6	1	25	37
RUBUOCCI	16	0	11	0	5	2	3	10	1	0	13	1	2	9	9
RUBUODOR	11	0	7	4	0	1	6	0	4	0	6	2	0	2	10
RUBUPUBE	47	0	29	7	10	5	13	3	20	5	16	16	5	16	38
RUBU_840	2	0	2	0	0	0	0	0	2	0	0	0	0	1	1
RUDBHIRT	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1
RUMEORBI	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0
SALIBEBB	4	0	0	0	4	2	2	0	0	0	0	1	1	2	4
SALIDISC	6	0	0	0	6	4	2	0	0	0	0	1	0	5	3
SALIERIO	10	0	1	0	9	4	5	1	0	0	0	3	1	6	7
SALIPETI	2	0	0	0	2	2	0	0	0	0	0	0	0	2	0
SAMBCANA	7	0	7	0	0	0	0	0	6	1	2	1	2	4	5
SAMBRAPU	40	0	20	2	18	2	1	29	8	0	34	1	0	9	33
SANGCANA	11	6	0	0	5	6	0	3	2	0	11	0	0	2	10
SANIMARI	6	0	2	0	4	2	0	4	0	0	6	0	0	2	4
SANITRIF	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
SANI__SP	1	0	1	0	0	1	0	0	0	0	1	0	0	0	1
SCHIPURP	29	5	20	0	4	13	12	4	0	0	26	4	0	5	26
SCIRATRO	5	0	2	0	3	1	4	0	0	0	0	1	2	3	2
SCUTLATE	11	0	6	2	3	2	6	0	2	1	0	3	2	7	4
SICYANGU	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0
SILEVULG	2	0	1	0	1	2	0	0	0	0	1	0	0	1	1
SISYMONT	3	0	0	0	3	2	0	1	0	0	0	0	0	2	2
SIUMSUAV	2	0	2	0	0	0	0	0	0	2	0	0	1	0	2

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
SMILHERB	50	32	10	0	8	40	0	10	0	0	46	0	0	6	46
SMILHISP	2	2	0	0	0	2	0	0	0	0	2	0	0	1	1
SOLADULC	49	0	33	7	9	0	13	11	17	8	18	11	14	16	35
SOLIALTI	28	0	14	3	11	7	9	5	7	0	11	4	2	16	17
SOLICAES	9	0	8	0	1	8	0	1	0	0	9	0	0	1	9
SOLICANA	67	2	40	7	18	16	14	17	17	3	41	9	3	25	50
SOLIFLEX	42	5	29	0	8	11	18	8	5	0	38	4	3	7	39
SOLIGIGA	16	0	7	1	8	5	9	0	2	0	1	4	2	12	7
SOLIJUNC	2	0	2	0	0	2	0	0	0	0	2	0	0	1	1
SOLINEMO	10	0	5	0	5	7	0	3	0	0	6	0	0	5	7
SOLIRUGO	4	0	1	2	1	0	0	2	2	0	2	1	0	2	2
SONCARVE	5	0	4	0	1	2	1	2	0	0	4	0	0	4	1
SONCOLER	2	0	2	0	0	0	0	2	0	0	1	0	0	2	0
SPHEINTE	15	0	10	4	1	4	5	1	4	1	4	4	2	9	7
STELLONG	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1
STREROSE	8	3	3	0	2	3	0	5	0	0	8	0	0	0	8
SYMPALBU	6	6	0	0	0	6	0	0	0	0	6	0	0	1	5
TARAOFFI	100	1	66	6	27	21	26	27	20	6	64	13	5	28	82
TAXUCANA	5	0	2	3	0	0	0	1	4	0	1	2	0	1	4
THALDIOI	16	3	12	0	1	14	1	1	0	0	15	1	0	5	13
THALPUBE	2	0	1	1	0	0	0	0	2	0	0	2	0	0	2
THELNOVE	2	0	2	0	0	0	0	1	1	0	1	1	0	0	2
THELPALU	4	0	4	0	0	0	2	0	2	0	1	2	1	0	4
THUJOCCI	47	0	30	6	11	10	18	11	8	0	29	14	2	9	40
TIARCORD	65	0	39	7	19	0	13	17	30	5	37	14	4	19	53
TILIAMER	115	19	68	8	20	43	21	29	18	4	88	19	2	22	101
TRAGDUBI	2	0	1	0	1	1	0	1	0	0	1	0	0	1	2
TRIEBORE	41	24	8	3	6	24	2	7	8	0	32	3	2	7	37
TRIFREPE	7	0	4	0	3	2	2	3	0	0	3	0	0	5	2

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

SPECIES	#Q	Soil Parent Material				Soil Order					Soil Moisture			Canopy	
		GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
TRILEREC	50	2	32	1	15	2	6	25	17	0	44	6	3	9	44
TRILGRAN	138	40	69	2	27	64	15	48	10	1	128	5	1	22	128
TRIOAURA	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0
TSUGCANA	50	1	36	6	7	6	20	11	13	0	37	9	0	8	44
TUSSFARF	2	0	0	0	2	2	0	0	0	0	0	0	0	2	1
TYPHLATI	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1
ULMUAMER	66	0	45	1	20	6	23	12	19	6	27	18	11	17	52
UNKN_751	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1
UNKN_791	1	0	0	0	1	0	0	0	1	0	0	0	1	0	1
UNKN_822	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0
URTIDIGR	8	0	5	0	4	0	0	6	2	1	3	0	1	4	4
URTIDIOI	2	0	0	0	1	0	1	0	0	0	0	1	0	1	1
UVULGRAN	11	0	9	0	2	8	0	2	1	0	11	0	0	1	11
VACCANGU	5	1	4	0	0	5	0	0	0	0	5	0	0	1	4
VERBHAST	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0
VERBTHAP	3	0	2	0	1	0	0	2	1	0	2	0	0	2	1
VERBURTI	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0
VEROOFFI	2	0	2	0	0	0	2	0	0	0	2	0	0	0	2
VEROSERP	3	0	3	0	0	0	3	0	0	0	2	0	0	1	2
VIBUACER	39	20	13	0	6	26	0	13	0	0	38	0	0	7	38
VIBULENT	29	0	16	0	13	15	7	7	0	0	21	4	2	5	28
VIBUOPUL	2	0	0	0	2	0	2	0	0	0	0	0	1	1	1
VIBUTRIL	3	0	1	0	2	2	1	0	0	0	1	1	0	1	2
VICICRAC	2	0	0	0	2	2	0	0	0	0	0	0	0	2	1
VIOLAFFI	15	0	7	0	8	4	10	1	0	0	3	4	3	9	11
VIOLBLAN	19	0	9	0	10	0	2	9	6	2	11	2	1	5	16
VIOLCANA	2	0	2	0	0	0	1	0	0	1	0	1	0	1	1
VIOLCUCU	12	0	12	0	0	0	9	0	3	0	7	0	2	6	8
VIOLLABR	15	1	11	0	3	1	3	4	6	1	11	4	0	2	14

Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

		Soil Parent Material				Soil Order					Soil Moisture			Canopy	
SPECIES	#Q	GF	CT	LAC	CO	B	GB	L	GL	G	SD	SM	SW	OC	CC
VIOLPUBE	68	18	28	0	22	27	0	29	12	0	64	3	3	12	61
VIOLROST	2	2	0	0	0	2	0	0	0	0	2	0	0	0	2
VIOLSORO	2	0	0	0	2	0	0	2	0	0	1	0	0	1	2
VIOL_788	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1
VIOL__SP	8	0	6	0	2	2	3	1	2	0	4	0	1	1	8
VITIRIPA	64	1	42	1	20	24	23	14	3	0	45	11	3	17	55
WALDFRAG	23	20	1	0	2	21	0	0	2	0	21	1	0	5	21

APPENDIX 5

LISTING OF SPECIES BY MICROHABITAT

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

1. Dry Floors

(n=265 species)

ABIEBALS
ACERNEGU
ACERRUBR
ACERSACC
ACERSACN
ACERSANI
ACERSPIC
ACTAPACH
ACTARUBR
ACTA_SP
ADIAPEDA
AGRIGRYP
ALLITRIC
AMELINTE
AMEL_SP
AMPHBRAC
ANEMVIRG
APOCANDR
AQUICANA
ARALNUDI
ARCTMINU
ARISTRIP
ASARCANA
ASCLSYRI
ASTECILI
ASTECORD
ASTELATE
ASTEMACR
ASTENOVE
ATHYFILI
ATHYTHEL
BETUALLE
BETUPAPY
BIDEFRON
BOEHCYLI
BOTRMATR
BOTRMULT
BOTRVIRG
BRACEREC
CARDDIPH
CAREALBU
CAREARCT
CAREBACK
CAREBLAN
CARECOMM
CARECRIS
CAREDEWE
CAREDIGI
CAREGRAC
CAREGRAN
CAREHIRT
CAREHITC
CAREINTU
CARELAXI
CAREPECK
CAREPEDU
CAREPENS
CAREPLAN
CAREPLAT
CARERADI
CAREROSE
CARESPAR
CARETENE
CAREWOOD
CARE_OV
CARE_SP
CARPCARO
CARYCORD
CAULTHAL
CELASCAN
CERAFONT
CHIMUMBE
CINNLATI
CIRCALPI
CIRCLUTE
CLAYCARO
CLINBORE
CORNALTE
CORNFOEM
CORNRUGO
CORNSTOL
CORYCORN
CRAT_SP1
CRAT_SP2
CRAT_SP3
CRAT_SP
CRYPCANA
CYSTBULB
CYSTFRAG
CYSTTENU
DACTGLOM
DANTSPIC
DESMGLUT
DICECANA
DICECUCU
DIERLONI
DIRCPALU
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPIFVIRG
EPIPHELL
EQUIARVE
EQUIHYEM
EQUILAEV
EQUISCIR
ERIGANNU
ERIGPHIL
ERYTAMER
EUPARUGO
FAGUGRAN
FESTSUBV
FRAGVESC
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALESPEC
GALIAPAR
GALICIRC
GALILANC
GALIOBTU
GALITRIF
GALI_SP
GERAMACU
GERAROBE
GEUMALEP
GEUMCANA
GEUMLACI
GEUMURBA
GEUM_SP
GLYCSTRI
GYMNDRYO
HEPAACUT
HIERAURA
HIERCAES
HYDRVIRG
HYPEPERF
IMPACAPE
LAPOCANA
LONICANA
LONIDIOI
LONIHIRS
LYCOANNO
LYCODEND
LYCOOBOB
LYSINUMM
MAIACANA
MAIARACE
MAIASTEL
MATTSTRU
MEDILUPU
MENICANA
MENTARVE
MILIEFFU
MITCREPE
MITEDIPH
MONOHYPO
MONOUNIF
ONOCSENS
ORYZASPE
OSMOCLAY
OSMUCLAY
OSTRVIRG
OXALSTRI
PANAQUIN
PARTINSE
PHEGCONN
PHLO_SP
PHRYLEPT
PICEGLAU
PILEPUMI
PINUSTRO
POA_ALSO
POA_COMP
POA_PALU
POA_PRAT
PODOPELT
POLYACRO
POLYPAUC
POLYPUBE
POPUBALS
POPUGRAN
POPUTREM
PREN_SP
PRUNSERO
PRUNVIRG
PRUNVULG
PTERAQUI
PYROELLI
QUERALBA
QUERMACR
QUERRUBR
RANUABOR
RANUACRI
RANURECU
RHAMALNI
RHAMCATH
RHUSRADI
RIBEAMER
RIBECYNO
RIBEGLAN
RIBERUBR
RIBETRIS
ROBIPSEU
ROSABLAN
RUBUALLE
RUBUIDAE
RUBUOCCI
RUBUODOR
RUBUPUBE
SAMBCANA
SAMBRAPU
SANGCANA
SANIMARI
SANITRIF
SANI_SP
SCHIPURP
SMILHERB
SMILHISP
SOLADULC
SOLIALTI
SOLICAES
SOLICANA
SOLIFLEX
SOLINEMO
SOLIRUGO
SPHEINTE
STREROSE
SYMPALBU
TARAOFFI
TAXUCANA
THALDIOI
THELNOVE
THELPALU
THUJOCCI
TIARCORD
TILIAMER
TRAGDUBI

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

1. (cont'd)

TRIEBORE
TRIFREPE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
URTIDIGR
UVULGRAN
VACCANGU
VERBTHAP
VEROOFFI
VEROSERP
VIBUACER
VIBULENT
VIBUTRIL
VIOLAFFI
VIOLBLAN
VIOLCUCU
VIOLLABR
VIOLPUBE
VIOLROST
VIOL_788
VIOL__SP
VITIRIPA
WALDFRAG

2. Moist Floors (n=197 species)

ABIEBALS
ACERNEGU
ACERRUBR
ACERSACC
ACERSACN
ACERSANI
ACERSPIC
ACHIMILL
ACTARUBR
ACTA__SP
ADIAPEDA
AGRIGRYP
AGROGIGA
AMELARBO
AMPHBRAC
ANEMCANA
ANEMVIRG
APOCANDR
ARALNUDI
ARCTMINU
ARISTRIP
ASARCANA
ASCLSYRI
ASTELATE
ASTENOVE
ASTEPUNI
ATHYFILI
BETUALLE
BETUPAPY
BIDEFRON
BOEHCYLI
BOTRVIRG
CARDDIPH
CARDPENS
CAREALOP
CAREARCT
CAREBEBB
CAREBLAN
CAREBREV
CARECEPH
CARECRIS
CAREDEWE
CAREGRAC
CAREINTU
CARELANU
CAREPEDU
CAREPENS
CARERADI
CAREROSE
CARESPAR
CARESTIP
CARETENE
CARETRIB
CAREVULP
CARPCARO
CARYCORD
CAULTHAL
CERAFONT
CIRCALPI
CIRCLUTE
CIRSARVE
CLEMVIRG
CLINBORE
CORNALTE
CORNFOEM
CORNRUGO
CORNSTOL
CORYCORN
CRAT__SP
CYPRCALC
CYSTBULB
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
ELYMVIRG
EPILCILI
EPILCOLO
EPILLEPT
EPILPARV
EPIPHELL
EQUIARVE
ERIGPHIL
ERIGSTRI
ERYTAMER
EUPAMACU
EUPAPERF
EUPARUGO
FAGUGRAN
FESTSUBV
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALETETR
GALIASPR
GALIOBTU
GALITRIF
GENTANDR
GERAROBE
GEUMCANA
GEUMLACI
GEUM__SP
GLYCSTRI
GYMNDRYO
HIERCAES
HYPEPERF
IMPACAPE
LAPOCANA
LIPALOES
LYCOAMER
LYCOUNIF
LYSICILI
LYSINUMM
MAIACANA
MAIARACE
MAIASTEL
MATTSTRU
MENTARVE
MITEDIPH
MUHLMEXI
ONOCSENS
OSTRVIRG
PARTINSE
PHRYLEPT
PILEPUMI
PINUSTRO
PLANMAJO
PLANRUGE
POA_ALSO
POA_PALU
POA_PRAT
POLYACRO
POPUBALS
POPUTREM
PRUNSERO
PRUNVIRG
PRUNVULG
QUERMACR
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBEAMER
RIBECYNO
RIBEGLAN
RIBERUBR
RIBETRIS
ROSABLAN
ROSAPALU
RUBUALLE
RUBUIDAE
RUBUODOR
RUBUPUBE
SALIBEBB
SALIDISC
SALIERIO
SAMBRAPU
SCHIPURP
SCIRATRO
SCUTLATE
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
SOLIGIGA
SOLIRUGO
SPHEINTE
STELLONG
TARAOFFI
TAXUCANA
THALDIOI
THALPUBE
THELPALU
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
TYPHLATI
ULMUAMER
UNKN_751
URTIDIOI
VIBULENT
VIBUTRIL
VIOLAFFI
VIOLBLAN
VIOLCANA
VIOLCUCU
VIOLLABR
VIOLPUBE
VIOL__SP
VITIRIPA
WALDFRAG

3. Wet Floors (n=152 species)

ACERRUBR
ACERSACN
ACHIMILL
AGROGIGA
AMPHBRAC
ASCLINCA
ASTECILI
ASTELATE
ASTEUMBE
BIDEFRON
BOEHCYLI
CAREALOP

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

3. (cont'd)

CAREBEBB
CAREBLAN
CAREBREV
CARECRIS
CAREGRAC
CAREGRAN
CARELANU
CARERADI
CAREROSE
CARESTIP
CARETENE
CARETRIB
CAREVULP
CERAFONT
CICUMACU
CORNSTOL
CRAT__SP
ELYMVIRG
EQUIARVE
ERIGPHIL
FRAGVIRG
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GENTANDR
GEUM__SP
GLYCSTRI
HIERCAES
IMPACAPE
IRIS__SP
LIPALOES
LYCOAMER
LYCOUNIF
LYSICILI
LYSINUMM
MATTSTRU
MENTARVE
MUHLMEXI
ONOCSENS
PARTINSE
PILEPUMI
PLANMAJO
PLANRUGE
POA_ALSO
POA_COMP
POA_PALU
POA_PRAT
POPUTREM
PRUNVIRG
PRUNVULG
RANUABOR
RANUACRI
RHAMCATH
RHUSRADI
RIBETRIS
ROBIPSEU
ROSAPALU
RUBUPUBE
SALIBEBB
SALIERIO
SCUTLATE
SOLADULC
SOLICANA
SOLIGIGA
TARAOFFI
ULMUAMER
VIBULENT
VIBUOPUL
VIOLAFFI
VITIRIPA

4. Moist Depressions (n=136 species)

ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACERSPIC
ACTARUBR
ADIAPEDA
ARALNUDI
ARISTRIP
ASARCANA
ASCLSYRI
ASTELATE
ASTEPUNI
ATHYFILI
BOEHCYLI
CALTPALU
CARDDIPH
CAREBEBB
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREGRAN
CAREINTU
CAREPEDU
CAREPENS
CAREPLAN
CAREPROJ
CARERADI
CARERETR
CARESTIP
CARETENE
CARE__OV
CARE__SP
CAULTHAL
CINNLATI
CIRCALPI
CIRCLUTE
CIRSARVE
CLEMVIRG
CORNALTE
CORNFOEM
CORNSTOL
CYSTBULB
DACTGLOM
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
ELYMREPE
ELYMVIRG
EPILCOLO
EPIPHELL
EQUIARVE
EQUILAEV
ERIGANNU
ERIGPHIL
ERIG__SP
ERYTAMER
EUPARUGO
FAGUGRAN
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GERAROBE
GEUMCANA
GEUMLACI
GEUMRIVA
GEUM__SP
GLYCSTRI
GYMNDRYO
HEPAACUT
HIERCAES
HYSTPATU
IMPACAPE
LAPOCANA
LYSICILI
LYSINUMM
MAIACANA
MAIARACE
MAIASTEL
MATTSTRU
MITEDIPH
ONOCSENS
OSMUCLAY
OSTRVIRG
PARTINSE
PILEPUMI
PLANMAJO
POA_COMP
POA_PALU
POLYPUBE
POPUBALS
PRUNVIRG
PRUNVULG
RANUABOR
RANUACRI
RANUHICA
RANURECU
RHAMCATH
RHUSRADI
RIBEAMER
RIBECYNO
RIBEGLAN
RIBELACU
RIBETRIS
RUBUIDAE
RUBUPUBE
SAMBCANA
SCHIPURP
SCUTLATE
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
TARAOFFI
THELNOVE
THELPALU
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
VIBULENT
VIOLAFFI
VIOLBLAN
VIOLLABR
VIOLPUBE
VITIRIPA

5. Wet Depressions (n=115 species)

ABIEBALS
ACERSACC
ACERSACN
ACERSPIC
ACTA__SP
ADIAPEDA
AGROGIGA
ALLITRIC
ALNUINCA
AMPHBRAC
ARISTRIP
ASARCANA
ASCLINCA
ASTECORD
ASTELATE
ASTENOVE
ASTEPUNI
ATHYFILI
ATHYTHEL
BETUALLE
BIDEFRON
BOEHCYLI
CARDDIPH
CAREBLAN

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

5. (cont'd)

CARECEPH
CARECRIS
CAREGRAC
CAREHIRT
CAREINTU
CAREPEDU
CAREPLAN
CAREPSEU
CARERADI
CARERETR
CARETENE
CARETRIB
CARPCARO
CAULTHAL
CICUBULB
CINNLATI
CIRCALPI
CIRCLUTE
CORNALTE
CORNRUGO
CORNSTOL
CYSTBULB
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPILCILI
EPILCOLO
EPILPARV
EPIPHELL
EQUIARVE
EUPAMACU
EUPARUGO
FESTSUBV
FRAXAMER
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GERAROBE
GLYCSTRI
HIERCAES
HYDRVIRG
IMPACAPE
IRIS__SP
LAPOCANA
LIPALOES
LYCOUNIF
LYSICILI
LYSINUMM
MAIARACE
MATTSTRU
MENTARVE
ONOCSENS
OSMUREGA
PARTINSE
PILEPUMI
POA_ALSO
POA_PALU
POLYPUBE
PRUNVIRG
RANUABOR
RANURECU
RHAMCATH
RHUSRADI
RIBEAMER
RIBECYNO
RIBETRIS
RIBE_827
RUBUIDAE
RUBUOCCI
RUBUPUBE
SALIERIO
SCIRATRO
SIUMSUAV
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
TARAOFFI
THELPALU
THUJOCCI
TIARCORD
TILIAMER
TRILEREC
TRILGRAN
ULMUAMER
VIOLBLAN
VIOLCUCU
VIOLPUBE
VITIRIPA

6. Seep

(n=33 species)

ASTENOVE
BOEHCYLI
CALTPALU
CAREINTU
CARESTIP
CARE__OV
CICUMACU
CINNLATI
EPILCOLO
EQUIARVE
FRAXNIGR
GEUMRIVA
GLYCSTRI
GYMNDRYO
IMPACAPE
LAPOCANA
LYCOAMER
LYCOUNIF
LYSICILI
LYSINUMM
MATTSTRU
ONOCSENS
PILEPUMI
POA_PALU
RANUHICA
RIBEAMER
RIBEGLAN
SAMBCANA
SOLADULC
TIARCORD
ULMUAMER
UNKN_791
VIOL__SP

7. Dry Gap

(n=115 species)

ABIEBALS
ACERRUBR
ACERSACC
ACERSPIC
ACTAPACH
ACTARUBR
ACTA__SP
ADIAPEDA
ALLITRIC
AMEL__SP
APOCANDR
ARISTRIP
ASCLSYRI
ASTECILI
ASTECORD
ASTELATE
ATHYFILI
BETUPAPY
BOTRVIRG
CARDDIPH
CAREBLAN
CAREDEWE
CAREDIGI
CAREGRAC
CAREPEDU
CAREPENS
CAREPLAN
CARERADI
CAREROSE
CARESPAR
CARPCARO
CARYCORD
CEANAMER
CELASCAN
CIRCLUTE
CORNALTE
CORNFOEM
CORNRUGO
CORYCORN
CRAT__SP
CYSTFRAG
DESMGLUT
DICECANA
DIRCPALU
DRYOCART
DRYOINTE
DRYOMARG
EPIPHELL
ERYTAMER
FESTSUBV
FRAGVESC
FRAGVIRG
FRAXAMER
GALESPEC
GALITRIF
GERAMACU
GERAROBE
GEUMLACI
GEUM__SP
GLYCSTRI
HIERCAES
IMPACAPE
LONICANA
LONIDIOI
MAIACANA
MAIARACE
MAIASTEL
MENICANA
MONOUNIF
ONOCSENS
ORYZASPE
OSMOCLAY
OSTRVIRG
PANI__SP
PARTINSE
PLANMAJO
POA_COMP
POA_PRAT
PODOPELT
POLYPUBE
PRUNSERO
PRUNVIRG
PTERAQUI
PYROELLI
QUERRUBR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBECYNO
RIBETRIS
ROBIPSEU
RUBUALLE
RUBUIDAE
SAMBRAPU
SMILHERB
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
SOLIJUNC
TARAOFFI
THALDIOI
THUJOCCI
TIARCORD
TILIAMER
TRILGRAN
VIBUACER
VIBULENT

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

7. (cont'd)
VIOLBLAN
VIOLLABR
VIOLPUBE
VIOL__SP
VITIRIPA
WALDFRAG

8. Moist Gap
(n=68 species)
ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACERSPIC
ARALNUDI
ARISTRIP
ATHYFILI
BOEHCYLI
CAREBEBB
CAREBLAN
CAREDEWE
CAREGRAC
CAREPEDU
CARERADI
CAREROSE
CAULTHAL
CINNLATI
CIRCALPI
CIRCLUTE
CORNALTE
CORNSTOL
CYSTBULB
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPILCOLO
EPILPARV
EPIPHELL
ERYTAMER
EUPAMACU
FRAGVESC
FRAXNIGR
FRAXPENN
GALITRIF
GERAROBE
GEUMCANA
GEUMLACI
GLYCSTRI
IMPACAPE
LACT__SP
LAPOCANA
MAIACANA
ONOCSENS
PARTINSE
POPUBALS
PRUNVIRG
RANUABOR
RANURECU
RHAMCATH
RIBECYNO
RIBERUBR
RIBETRIS
RUBUIDAE
RUBUPUBE
SAMBCANA
SOLADULC
SOLIALTI
SOLICANA
SOLIGIGA
TARAOFFI
THALPUBE
TIARCORD
TRILEREC
ULMUAMER
VIOLCUCU
VIOLPUBE

9. MOUND
(n=165 species)
ABIEBALS
ACERRUBR
ACERSACC
ACERSANI
ACERSPIC
ACTAPACH
ACTARUBR
ACTA__SP
ADIAPEDA
ALLITRIC
AMEL__SP
APOCANDR
AQUICANA
ARALNUDI
ARISTRIP
ASARCANA
ASCLSYRI
ASTECILI
ASTECORD
ASTELATE
ASTEMACR
ASTENOVE
ATHYFILI
ATHYTHEL
BETUPAPY
BOTRVIRG
CARDDIPH
CAREARCT
CAREBACK
CAREBLAN
CAREDEWE
CAREDIGI
CAREGRAC
CAREHITC
CAREINTU
CARELAXI
CAREPEDU
CAREPENS
CAREPLAN
CARERADI
CAREROSE
CARYCORD
CAULTHAL
CELASCAN
CIRCALPI
CIRCLUTE
CLAYCARO
CORNALTE
CORNRUGO
CORYCORN
CRAT_SP3
CRAT__SP
DANTSPIC
DESMGLUT
DICECANA
DICECUCU
DIERLONI
DRYOCART
DRYOINTE
DRYOMARG
EPIFVIRG
EPILCOLO
EPIPHELL
EQUIARVE
ERIGANNU
ERIGPHIL
ERYTAMER
FAGUGRAN
FESTSUBV
FRAGVESC
FRAXAMER
FRAXNIGR
FRAXPENN
GALIAPAR
GALITRIF
GERAROBE
GEUMLACI
GLYCSTRI
GYMNDRYO
HEPAACUT
HIERCAES
HYDRVIRG
IMPACAPE
LEONCARD
LONICANA
LYCOOBOB
MAIACANA
MAIARACE
MAIASTEL
MATTSTRU
MITCREPE
MITEDIPH
MONAFIST
ONOCSENS
ORYZASPE
OSMOCLAY
OSTRVIRG
OXAL__SP
PARTINSE
PHRYLEPT
PILEPUMI
PINUSTRO
POA_ALSO
POA_COMP
POA_SALT
POA___SP
PODOPELT
POLYPUBE
POPUGRAN
POPUTREM
PREN__SP
PRUNSERO
PRUNVIRG
PTERAQUI
PYROELLI
QUERRUBR
QUER__SP
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBECYNO
RIBETRIS
ROBIPSEU
ROSABLAN
RUBUALLE
RUBUIDAE
RUBUOCCI
RUBUODOR
RUBUPUBE
SAMBRAPU
SANGCANA
SANIMARI
SCHIPURP
SILEVULG
SMILHERB
SOLIALTI
SOLICAES
SOLICANA
SOLIFLEX
SOLINEMO
SONCARVE
STREROSE
SYMPALBU
TARAOFFI
THALDIOI
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
UVULGRAN
VIBUACER
VIBULENT
VIOLAFFI
VIOLBLAN

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

9. (cont'd)
VIOLCUCU
VIOLPUBE
VIOL_SP
VITIRIPA
WALDFRAG

10. Dry Pit
(n=81 species)
ABIEBALS
ACERRUBR
ACERSACC
ACTA_SP
AMEL_SP
ARALNUDI
ARISTRIP
ASARCANA
ASTEMACR
ATHYFILI
BOEHCYLI
BOTRVIRG
CAREDEWE
CAREPEDU
CAREPENS
CARPCARO
CARYCORD
CAULTHAL
CELASCAN
CIRCLUTE
CLAYCARO
CORNALTE
CORNRUGO
CORYCORN
DESMGLUT
DICECANA
DRYOCART
DRYOINTE
DRYOMARG
EPIFVIRG
EPIPHELL
ERYTAMER
FAGUGRAN
FESTSUBV
FRAXAMER
GALITRIF
GERAROBE
GYMNDRYO
HEPAACUT
HYDRVIRG
IMPACAPE
LONICANA
MAIACANA
MAIARACE
MAIASTEL
MITCREPE
MITEDIPH
ORYZASPE
OSMOCLAY
OSTRVIRG
PINUSTRO
POA_ALSO
POLYACRO
POLYPUBE
POPUGRAN
PRUNSERO
PRUNVIRG
PTERAQUI
PYROELLI
QUERRUBR
RANUABOR
RHUSRADI
RIBECYNO
ROBIPSEU
ROSABLAN
RUBUALLE
SAMBRAPU
SANGCANA
SMILHERB
SOLIFLEX
SYMPALBU
TARAOFFI
THUJOCCI
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
VIBUACER
VIBULENT
VIOLPUBE
WALDFRAG

11. Moist Pit
(n=5 species)
CAREINTU
CIRCALPI
CIRCLUTE
ERYTAMER
IMPACAPE

12. Log
(n=102 species)
ABIEBALS
ACERRUBR
ACERSACN
ACERSPIC
ACTA_SP
ANEMQUIN
ARALNUDI
ARISTRIP
ASTELATE
ATHYFILI
BETUALLE
BETUPAPY
BIDEFRON
BOEHCYLI
CARDDIPH
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREINTU
CAREPEDU
CAREPENS
CARERADI
CAREROSE
CARESTIP
CARETENE
CARPCARO
CARYCORD
CAULTHAL
CINNLATI
CIRCALPI
CIRCLUTE
CLEMVIRG
CORNALTE
CORNFOEM
CYSTBULB
DRYOCART
DRYOCRIS
DRYOINTE
ECHILOBA
EPILCOLO
EPILLEPT
EPIPHELL
EQUIARVE
ERYTAMER
EUPARUGO
FRAGVESC
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIASPR
GALIPALU
GALITRIF
GERAROBE
GEUMLACI
GLYCSTRI
GYMNDRYO
HEPAACUT
HIERCAES
IMPACAPE
LAPOCANA
LYCOUNIF
LYSINUMM
MAIACANA
MAIARACE
MENTARVE
MILIEFFU
MITEDIPH
ONOCSENS
PARTINSE
PILEPUMI
POA_PALU
POLYPUBE
RANUABOR
RANURECU
RHAMCATH
RIBECYNO
RIBEGLAN
RUBUALLE
RUBUIDAE
RUBUODOR
RUBUPUBE
RUBU_840
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
TARAOFFI
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TSUGCANA
ULMUAMER
VIOLBLAN
VIOLLABR
VIOLPUBE
VIOL_SP
VITIRIPA
WALDFRAG

13. Stump
(n=51 species)
ABIEBALS
ACERRUBR
ACERSACC
ACERSPIC
ARALNUDI
ARISTRIP
ASTELATE
BETUALLE
BOEHCYLI
CARECRIS
CAREDEWE
CAREGRAC
CAREPEDU
CAREPENS
CARE_OV
CIRCALPI
CIRCLUTE
DRYOCART
DRYOINTE
EPIPHELL
FAGUGRAN
FRAGVIRG
GERAROBE
GYMNDRYO
IMPACAPE
MAIACANA
MAIARACE
PARTINSE
PICEGLAU
PILEPUMI
POLYPAUC
POLYPUBE
QUERALBA

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

13. (cont'd)
QUERRUBR
RANUABOR
RIBEAMER
RUBUIDAE
RUBUODOR
RUBUPUBE
SAMBRAPU
SOLADULC
SOLICANA
SOLIFLEX
SPHEINTE
TARAOFFI
THUJOCCI
TIARCORD
TRIEBORE
TSUGCANA
ULMUAMER
VIOLCUCU

14. Raised Root Mat
(n=138 species)
ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACERSPIC
ACTARUBR
ACTA_SP
ALLITRIC
ARALNUDI
ARCTMINU
ARISTRIP
ASARCANA
ASTECORD
ASTELATE
ASTENOVE
ATHYFILI
BETUALLE
BETUPAPY
BIDEFRON
BOEHCYLI
CARDDIPH
CAREARCT
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREINTU
CAREPECK
CAREPEDU
CAREPENS
CAREPLAN
CARERADI
CAREROSE
CARESTIP
CARETENE
CARE_OV
CARYCORD
CAULTHAL
CELASCAN
CINNLATI
CIRCALPI
CIRCLUTE
CLEMVIRG
CLINBORE
CORNALTE
CORNRUGO
CORNSTOL
CYSTBULB
CYSTFRAG
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPILCOLO
EPIPHELL
EQUIARVE
EQUISCIR
ERIGPHIL
FAGUGRAN
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIASPR
GALIOBTU
GALIPALU
GALITRIF
GERAROBE
GEUMCANA
GEUMLACI
GEUM_SP
GLYCSTRI
GYMNDRYO
HIERCAES
HYDRVIRG
IMPACAPE
LACT_SP
LONICANA
LYCOANNO
LYCOUNIF
MAIACANA
MAIARACE
MEDILUPU
MILIEFFU
MITEDIPH
OSMOCLAY
OSTRVIRG
PARTINSE
PINUSTRO
POA_ALSO
POA_COMP
POLYACRO
POLYPUBE
POPUBALS
PREN_SP
PRUNSERO
PRUNVIRG
PYROELLI
QUERMACR
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBECYNO
RIBEGLAN
RIBELACU
RUBUALLE
RUBUIDAE
RUBUODOR
RUBUPUBE
SAMBCANA
SAMBRAPU
SCHIPURP
SCUTLATE
SIUMSUAV
SOLADULC
SOLICANA
SOLIFLEX
SOLIRUGO
SPHEINTE
TARAOFFI
TAXUCANA
THALPUBE
THELPALU
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
URTIDIGR
VIBULENT
VIOLBLAN
VIOL_SP
VITIRIPA

15. Stone
(n=20 species)
ANEMQUIN
ASTELATE
CAREBLAN
CAREPEDU
CAREPENS
DRYOCRIS
EPIPHELL
EQUIHYEM
ERIGPHIL
FRAXAMER
GALITRIF
LONIDIOI
MAIACANA
PARTINSE
PRUNVIRG
RHUSRADI
RIBECYNO
SCHIPURP
SOLIFLEX
TRILGRAN

16. Lane
(n=89 species)
ABIEBALS
ACERRUBR
ACERSACC
ACTA_SP
ARALNUDI
ARISTRIP
ASTELATE
ATHYFILI
BOEHCYLI
BOTRVIRG
CARDDIPH
CAREARCT
CAREBLAN
CAREDEWE
CAREGRAC
CAREINTU
CAREPEDU
CAREPENS
CAREPROJ
CARERADI
CAREROSE
CARETENE
CARETRIB
CARE_SP
CARYCORD
CAULTHAL
CIRCALPI
CIRCLUTE
CORNALTE
DRYOCART
DRYOCRIS
DRYOINTE
EPIPHELL
EQUISCIR
ERYTAMER
FAGUGRAN
FRAGVESC
FRAXAMER
GALILANC
GALITRIF
GLYCSTRI
HIERCAES
HYDRVIRG
IMPACAPE
LYCODEND
MAIACANA
MAIARACE
MENTARVE
MITCREPE
ONOCSENS
ORYZASPE
OSMOCLAY
OSMUCLAY
OSTRVIRG

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

CLOSED CANOPY

16. (cont'd)
POA_PRAT
PODOPELT
POLYPUBE
POPUGRAN
POPUTREM
PRUNSERO
PRUNVIRG
PTERAQUI
QUERRUBR
RANUABOR
RHAMCATH
RHUSRADI
RIBECYNO
ROBIPSEU
RUBUIDAE
RUBUOCCI
SALIERIO
SAMBRAPU
SANGCANA
SMILHERB
SOLIALTI
SOLICANA
TARAOFFI
THALDIOI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
ULMUAMER
URTIDIGR
VIOLLABR
VIOLPUBE
VIOLSORO
VITIRIPA

17. Ditch
(n=68 species)
ACERSACC
ACERSACN
ACHIMILL
AGROGIGA
ANEMCANA
ASTELATE
ASTEPUNI
CARECRIS
CAREGRAN
CARELANU
CARERADI
CARESTIP
CARETENE
CAREVULP
CARYCORD
CLAYCARO
CORNRUGO
CORNSTOL
EPILCILI
EPILLEPT
EPIPHELL
EQUIARVE
ERIGPHIL
ERYTAMER
EUPAMACU
EUPAPERF
FRAGVIRG
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GLYCSTRI
HYDRVIRG
IMPACAPE
LEERORYZ
LYCOUNIF
LYSICILI
LYSITERR
MAIACANA
MEDILUPU
MENTARVE
MUHLMEXI
ONOCSENS
PARTINSE
PHALARUN
PILEPUMI
PLANRUGE
POA_PALU
POA_PRAT
POLYPUBE
PRUNVIRG
RANUACRI
RANURECU
ROBIPSEU
SALIDISC
SALIERIO
SANGCANA
SCUTLATE
SOLIALTI
SOLIGIGA
TARAOFFI
TILIAMER
TUSSFARF
ULMUAMER
VIOLPUBE
VIOL__SP
VITIRIPA

18. Regenerating Field
(n=125 species)
ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACHIMILL
ACTARUBR
AGRIGRYP
AGROGIGA
AGROSTOL
AMELINTE
ANEMVIRG
APOCANDR
AQUICANA
ASCLSYRI
ASTECILI
ASTELATE
ASTENOVE
ASTEPUNI
BETUPAPY
BOTRVIRG
BROMINER
CAREBLAN
CARECRIS
CAREGRAC
CAREGRAN
CARELANU
CAREPENS
CARERADI
CARESTIP
CARETENE
CARE_719
CARPCARO
CARYCORD
CELASCAN
CERAFONT
CHRYLEUC
CIRSARVE
CORNSTOL
CORYCORN
CRAT__SP
DAUCCARO
DESMGLUT
ELYMVIRG
EPILCILI
EPILLEPT
EPIPHELL
EQUIARVE
ERIGPHIL
ERIGSTRI
EUPAMACU
EUPAPERF
EUTHGRAM
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALICIRC
GALIOBTU
GALITRIF
GENTANDR
HIERCAES
HYPEPERF
IMPACAPE
IRIS__SP
LACTCANA
LIPALOES
LYCOAMER
LYCOUNIF
LYSICILI
MAIACANA
MATTSTRU
MEDILUPU
MELIALBA
MELIOFFI
MUHLFRON
ONOCSENS
OXALSTRI
PANIACUM
PARTINSE
PHALARUN
PHLEPRAT
PILEPUMI
PLANLANC
PLANRUGE
POA_COMP
POA_PALU
POA_PRAT
POPUBALS
POPUTREM
POTERECT
PRUNSERO
PRUNVIRG
PRUNVULG
PTERAQUI
QUERRUBR
RANUACRI
RHAMCATH
RIBEAMER
RIBECYNO
RUBUALLE
RUBUIDAE
RUBUPUBE
RUDBHIRT
SALIBEBB
SALIDISC
SALIERIO
SISYMONT
SMILHERB
SOLIALTI
SOLICANA
SOLIGIGA
SOLINEMO
TARAOFFI
THUJOCCI
TILIAMER
TRAGDUBI
TRIFREPE
TRILGRAN
ULMUAMER
VIBUACER
VIBULENT
VICICRAC
VIOLAFFI
VIOL__SP
VITIRIPA

OPEN CANOPY

19. Dry Floors

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

19. Dry Floors (n=205 species)

ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACERSPIC
ACTAPACH
ACTA__SP
ADIAPEDA
AGRIGRYP
ALLITRIC
AMELINTE
AMEL__SP
AQUICANA
ARALNUDI
ARCTMINU
ARISTRIP
ASARCANA
ASCLSYRI
ASTECILI
ASTELATE
ASTEMACR
ASTENOVE
ATHYFILI
BETUPAPY
BOEHCYLI
BOTRVIRG
BRACEREC
CALYSEPI
CARDACAN
CARDDIPH
CAREALBU
CAREARCT
CAREBACK
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREHITC
CAREINTU
CARELAXI
CAREPEDU
CAREPENS
CAREPLAN
CARERADI
CAREROSE
CARESPAR
CARE__OV
CARE__SP
CARPCARO
CARYCORD
CAULTHAL
CEANAMER
CELASCAN
CERAFONT
CIRCALPI
CIRCLUTE
CIRSARVE
CIRSVULG
CLAYCARO
CLEMVIRG
CONYCANA
CORNALTE
CORNFOEM
CORNRUGO
CORYCORN
CRAT__SP
CRYPCANA
CYSTBULB
DACTGLOM
DANTSPIC
DICECANA
DICECUCU
DIERLONI
DIRCPALU
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPIFVIRG
EPILCOLO
EPIPHELL
ERIGANNU
ERIGPHIL
ERYTAMER
EUPAPERF
EUPARUGO
FAGUGRAN
FESTSUBV
FRAGVESC
FRAXAMER
FRAXNIGR
FRAXPENN
GALETETR
GALIAPAR
GALILANC
GALITRIF
GERAMACU
GERAROBE
GEUMCANA
GEUMLACI
GEUMURBA
GLYCSTRI
GYMNDRYO
HACKVIRG
HEPAACUT
HIERCAES
HYDRVIRG
HYSTPATU
IMPACAPE
JUNCTENU
LACTCANA
LACTSERR
LAPOCANA
LEONCARD
LOBEINFL
LONICANA
LONIDIOI
MAIACANA
MAIARACE
MAIASTEL
MEDILUPU
MELIALBA
MENICANA
MILIEFFU
MITCREPE
MITEDIPH
NEPECATA
ONOCSENS
ONOPACAN
ORYZASPE
OSMOCLAY
OSTRVIRG
PANICAPI
PARTINSE
PHLO__SP
PHRYLEPT
PILEPUMI
PINUSTRO
PLANRUGE
POA_COMP
POA_PALU
POA_PRAT
POA_SALT
POLYPAUC
POLYPUBE
PREN__SP
PRUNSERO
PRUNVIRG
PTERAQUI
QUERALBA
QUERMACR
QUERRUBR
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBECYNO
RIBETRIS
ROBIPSEU
RUBUALLE
RUBUIDAE
RUBUOCCI
RUBUPUBE
SAMBRAPU
SANGCANA
SANI__SP
SCHIPURP
SMILHERB
SMILHISP
SOLADULC
SOLIALTI
SOLICAES
SOLICANA
SOLIFLEX
SOLIGIGA
SOLINEMO
SOLIRUGO
SONCARVE
SONCOLER
SPHEINTE
SYMPALBU
TARAOFFI
THALDIOI
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRIFREPE
TRILEREC
TRILGRAN
TRIOAURA
TSUGCANA
ULMUAMER
URTIDIGR
UVULGRAN
VACCANGU
VERBTHAP
VIBUACER
VIBULENT
VIOLBLAN
VIOLPUBE
VIOLSORO
VITIRIPA
WALDFRAG

20. Moist Floors (n=153 species)

ABIEBALS
ACERRUBR
ACERSACC
ACERSACN
ACERSPIC
ACHIMILL
ACTARUBR
ACTA__SP
AGROGIGA
AMPHBRAC
ANEMVIRG
ARALNUDI
ARISTRIP
ASARCANA
ASCLSYRI
ASTECILI
ASTELANC
ASTELATE
ASTENOVE
ASTEPUNI
ATHYFILI
BETUALLE
BIDEFRON
BOEHCYLI
CARDDIPH
CAREARCT
CAREBEBB
CAREBLAN
CAREBREV
CARECRIS

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

20. (cont'd)

CAREDEWE
CAREGRAC
CAREGRAN
CAREINTU
CARELANU
CAREPEDU
CAREPENS
CARERADI
CAREROSE
CARESTIP
CARETENE
CAREVULP
CAULTHAL
CELASCAN
CERAFONT
CHRYLEUC
CINNLATI
CIRCALPI
CIRCLUTE
CORNALTE
CORNSTOL
CRAT__SP
CRYPCANA
CYSTBULB
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
ELYMVIRG
EPILCOLO
EPILPARV
EPIPHELL
EQUIARVE
ERIGANNU
ERYTAMER
EUPAMACU
EUTHGRAM
FAGUGRAN
FRAGVESC
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GENTANDR
GERAROBE
GEUMCANA
GEUMLACI
GEUM__SP
GLYCSTRI
HIERCAES
IMPACAPE
INULHELI
IRISVERS
IRIS__SP
LACT__SP
LAPOCANA
LEERVIRG
LIPALOES
LYCOUNIF
LYSICILI
MAIACANA
MATTSTRU
MEDILUPU
MENTARVE
MITEDIPH
ONOCSENS
OSMOCLAY
PARTINSE
PHLEPRAT
PILEPUMI
PLANMAJO
PLANRUGE
POA_ALSO
POA_PALU
POA_PRAT
POLYPUBE
POPUBALS
POPUTREM
PRUNVIRG
PRUNVULG
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBEAMER
RIBEGLAN
RIBERUBR
RIBETRIS
ROBIPSEU
RUBUIDAE
RUBUODOR
RUBUPUBE
SALIDISC
SALIERIO
SAMBCANA
SAMBRAPU
SCUTLATE
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
SOLIGIGA
SOLIRUGO
SONCARVE
SPHEINTE
TARAOFFI
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
VIBUOPUL
VIOLAFFI
VIOLBLAN
VIOLCUCU
VIOLPUBE
VITIRIPA

21. Wet Floors

(n=82 species)

ACERSACN
ACERSPIC
ADIAPEDA
AGROGIGA
ARISTRIP
ASTELANC
ASTELATE
ASTEPUNI
ATHYFILI
BIDEFRON
BOEHCYLI
CAREBEBB
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREINTU
CAREPROJ
CARERADI
CARERETR
CARESTIP
CARETRIB
CAREVULP
CIRCLUTE
CLEMVIRG
CORNRUGO
CORNSTOL
CYSTBULB
DRYOCART
ELYMVIRG
EPILCOLO
EPILPARV
EPIPHELL
EQUIARVE
ERIGANNU
EUPAMACU
EUPAPERF
EUPARUGO
FRAXNIGR
GALIOBTU
GALIPALU
GERAROBE
GEUMLACI
GEUM__SP
GLYCSTRI
HYSTPATU
IMPACAPE
INULHELI
LAPOCANA
LEERORYZ
LYCOUNIF
LYSICILI
MENTARVE
ONOCSENS
PARTINSE
PILEPUMI
POA_COMP
POA_PALU
POA_PRAT
PRUNVULG
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBEAMER
RIBECYNO
RIBETRIS
RUBUOCCI
SALIERIO
SAMBCANA
SCUTLATE
SOLADULC
SOLICANA
SOLIGIGA
SPHEINTE
TARAOFFI
THUJOCCI
TILIAMER
ULMUAMER
VIOLCUCU
VITIRIPA

22. Moist Depressions

(n=42 species)

ABIEBALS
ACERSACN
ACERSPIC
ARISTRIP
ASTELATE
BOEHCYLI
CARECRIS
CAREGRAC
CAREINTU
CARERADI
CIRCALPI
CIRCLUTE
CORNALTE
CORNSTOL
CYSTBULB
DRYOCART
DRYOINTE
EQUIARVE
ERIGPHIL
ERYTAMER
FRAXNIGR
GALIPALU
GALITRIF
GERAROBE
GEUMLACI
GLYCSTRI
IMPACAPE

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

22. (cont'd)
ONOCSENS
PARTINSE
POA_PALU
PRUNVIRG
RANUACRI
RANURECU
RHAMCATH
RIBETRIS
RUBUIDAE
RUBUPUBE
SAMBCANA
SOLADULC
TARAOFFI
TIARCORD
ULMUAMER

23. Wet Depressions
(n=38 species)
ACERSACN
ACERSPIC
ARISTRIP
ASTELANC
ATHYFILI
BIDEFRON
BOEHCYLI
CAREBEBB
CAREBLAN
CARECRIS
CAREDEWE
CAREGRAC
CAREINTU
CARERETR
CARESTIP
CORNRUGO
ELYMVIRG
EPILPARV
EQUIARVE
FRAXNIGR
GALIPALU
GERAROBE
GEUMLACI
GLYCSTRI
IMPACAPE
LAPOCANA
LYCOUNIF
ONOCSENS
PILEPUMI
RANURECU
RHAMCATH
SAMBCANA
SOLADULC
SOLICANA
TARAOFFI
TILIAMER
ULMUAMER
VIOLCUCU

24. Seep
(n=25 species)
ARISTRIP
ATHYFILI
BOEHCYLI
CARECRIN
CARECRIS
CAREGRAC
CAREINTU
CAREPROJ
CARERETR
CARETENE
CARPCARO
CIRCALPI
EPILCOLO
EUPAMACU
FRAXPENN
GALITRIF
GLYCSTRI
IMPACAPE
LYCOAMER
ONOCSENS
RANUABOR
RANURECU
SOLADULC
TIARCORD
URTIDIGR

25. Mound
(n=76 species)
ABIEBALS
ACERRUBR
ACERSACC
ACTAPACH
ACTARUBR
ADIAPEDA
ARALNUDI
ARISTRIP
ASARCANA
ASTELATE
CARDDIPH
CAREARCT
CAREBLAN
CAREDIGI
CAREPEDU
CAREPENS
CARERADI
CAREROSE
CARYCORD
CAULTHAL
CIRCLUTE
CIRSARVE
CIRSVULG
CONYCANA
CORNFOEM
CORNRUGO
CYSTTENU
DICECANA
DIERLONI
DRYOCART
DRYOINTE
EPIFVIRG
EPILCOLO
EPIPHELL
ERYTAMER
EUTHGRAM
FRAGVESC
FRAXAMER
GALITRIF
GERAMACU
GERAROBE
GYMNDRYO
HACKVIRG
MAIACANA
MAIARACE
MITCREPE
ONOPACAN
ORYZASPE
OSMOCLAY
OSTRVIRG
PHRYLEPT
POA_PRAT
POLYPAUC
POLYPUBE
PRUNVIRG
QUERRUBR
RANUABOR
RHAMCATH
RUBUIDAE
RUBUOCCI
SAMBRAPU
SANGCANA
SMILHERB
SOLADULC
SOLICANA
SOLIJUNC
SONCARVE
SONCOLER
SYMPALBU
TARAOFFI
THALDIOI
TILIAMER
TRIFREPE
TRILGRAN
VIOLPUBE
WALDFRAG

26. Dry Pit
(n=26 species)
ACERSACC
ARISTRIP
ASARCANA
CIRCLUTE
CIRSVULG
DICECANA
DRYOCART
DRYOINTE
EPILCOLO
ERYTAMER
EUPAMACU
FAGUGRAN
FESTSUBV
FRAXAMER
GALITRIF
GERAROBE
HACKVIRG
MAIARACE
POLYPUBE
PRUNVIRG
RANUABOR
RUBUIDAE
RUBUOCCI
SAMBRAPU
SOLADULC
TARAOFFI

27. Wet Pit
(n= 1 species)
IMPACAPE

28. Log
(n= 64 species)
ACERSACC
ACERSPIC
AGROSTOL
ARALNUDI
ARISTRIP
ASTELATE
ASTEPUNI
ATHYFILI
BETUALLE
BETUPAPY
BOEHCYLI
CAREARCT
CAREDEWE
CAREINTU
CAREPEDU
CARERADI
CICUMACU
CINNLATI
CIRCALPI
CIRCLUTE
CLEMVIRG
CYSTBULB
DRYOCART
DRYOINTE
ELYMVIRG
EPILCOLO
EPILPARV
FRAGVESC
FRAGVIRG
FRAXNIGR
FRAXPENN
GALIAPAR
GALIOBTU
GALIPALU
GALITRIF
GERAROBE
GLYCSTRI
HIERCAES

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

28. (cont'd)
IMPACAPE
LACT_SP
LYCOUNIF
MAIACANA
OSTRVIRG
PARTINSE
PILEPUMI
PRUNVIRG
RANURECU
RIBETRIS
RUBUIDAE
RUBUPUBE
RUBU_840
SOLIALTI
SOLICANA
SOLIGIGA
SPHEINTE
TARAOFFI
TAXUCANA
TIARCORD
TRIEBORE
TSUGCANA
ULMUAMER
VIOLAFFI
VIOLCUCU
VIOL_SP

29. Stump
(n= 34 species)
ACERSACC
ARISTRIP
ASARCANA
ASTELATE
ASTEPUNI
BETUPAPY
CAREDEWE
CAREGRAC
CAREPEDU
CAREROSE
CAREVULP
CIRCALPI
DRYOCART
DRYOINTE
EPIPHELL
EQUIARVE
ERIGPHIL
FESTSUBV
FRAGVIRG
GALITRIF
GLYCSTRI
HIERCAES
IMPACAPE
MAIACANA
PARTINSE
RANURECU
RUBUIDAE
RUBUPUBE
SOLICANA
SOLIFLEX
SOLIRUGO
SPHEINTE
TARAOFFI
TIARCORD

30. Raised Root Mat
(n=96 species)
ACERRUBR
ACERSACC
ACERSPIC
ACTA_SP
ADIAPEDA
ARALNUDI
ARISTRIP
ASTELATE
ASTEPUNI
BETUALLE
BIDEFRON
BOEHCYLI
CARDPENS
CAREARCT
CAREBLAN
CAREDEWE
CAREGRAC
CAREPEDU
CAREPENS
CARE_SP
CIRCALPI
CIRCLUTE
CIRSVULG
CLEMVIRG
CONYCANA
CORNALTE
CORNSTOL
CYSTBULB
DAUCCARO
DRYOCART
DRYOCRIS
DRYOINTE
DRYOMARG
EPILCOLO
EPILPARV
EPIPHELL
EQUIARVE
ERIGANNU
ERIGPHIL
ERIG_SP
EUPAMACU
FRAGVESC
FRAGVIRG
FRAXNIGR
FRAXPENN
GALITRIF
GERAMACU
GERAROBE
GEUMCANA
GEUM_SP
GLYCSTRI
HIERCAES
IMPACAPE
LACTSERR
LYCOUNIF
MAIACANA
MATTSTRU
MENTARVE
ONOCSENS
PARTINSE
PICEGLAU
PILEPUMI
POA_PRAT
PREN_SP
PRUNVIRG
RANUABOR
RANUACRI
RHAMCATH
RHUSRADI
RIBECYNO
RUBUIDAE
RUBUOCCI
RUBUODOR
RUBUPUBE
SAMBCANA
SAMBRAPU
SCUTLATE
SICYANGU
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
SPHEINTE
TARAOFFI
THUJOCCI
TIARCORD
TILIAMER
TRIEBORE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
VIOLBLAN
VIOLLABR
VIOLSORO
VITIRIPA

31. Lane
(n= 181 species)
ACERSACC
ACERSACN
ACHIMILL
ACTA_SP
AGROGIGA
AGROSTOL
AMBRARTE
ANEMCANA
ANEMVIRG
ARCTMINU
ARISTRIP
ASCLSYRI
ASTECILI
ASTECORD
ASTELANC
ASTELATE
ASTENOVE
ASTEPUNI
ATHYFILI
BETUPAPY
BIDEFRON
BOEHCYLI
BOTRVIRG
BROMINER
CARDDIPH
CARDNUTA
CAREARCT
CAREBACK
CAREBEBB
CAREBLAN
CAREGRAC
CAREGRAN
CAREINTU
CARELANU
CARELAXI
CAREPENS
CAREPROJ
CARERETR
CAREROSE
CARESTIP
CARETENE
CARETRIB
CAREVULP
CARE_868
CARE_870
CARE_SP
CARYCORD
CAULTHAL
CERAFONT
CHRYLEUC
CIRCALPI
CIRCLUTE
CIRSARVE
CIRSVULG
CLEMVIRG
CONYCANA
CORNRUGO
CORNSTOL
CYSTBULB
DACTGLOM
DAUCCARO
DIANARME
DICECANA
DRYOCART
ELYMREPE
EPILCOLO
EPIPHELL
EQUIARVE
EQUILAEV
ERIGANNU
ERIGPHIL
ERIGSTRI
ERYTAMER

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

31. (cont'd)

EUPAMACU
EUPAPERF
EUPARUGO
FESTPRAT
FRAGVESC
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GERAROBE
GEUMLACI
GEUM__SP
GLYCSTRI
GYMNDRYO
HACKVIRG
HEPAACUT
HIERCAES
HYPEPERF
HYSTPATU
IMPACAPE
IRIS__SP
JUNCTENU
LACTCANA
LACTSERR
LEERORYZ
LEONCARD
LOBE__SP
LYCOAMER
LYCOUNIF
LYSICILI
MAIACANA
MATTSTRU
MEDILUPU
MELIALBA
MENICANA
MENTARVE
MUHLMEXI
ONOCSENS
ONOPACAN
OSMOCLAY
OSTRVIRG
OXALSTRI
PANI__SP
PARTINSE
PHALARUN
PHLEPRAT
PHRYLEPT
PILEPUMI
PLANLANC
PLANMAJO
PLANRUGE
POA_ALSO
POA_COMP
POA_PALU
POA_PRAT
POLYPERS
POLYPUBE
POPUTREM
POTENORV
POTERECT
PRUNSERO
PRUNVIRG
PRUNVULG
RANUABOR
RANUACRI
RANURECU
RHAMCATH
RHUSRADI
RIBECYNO
RUBUALLE
RUBUIDAE
RUBUOCCI
RUBUPUBE
SALIERIO
SAMBRAPU
SCIRATRO
SCUTLATE
SOLADULC
SOLIALTI
SOLICANA
SOLIFLEX
SOLIGIGA
SONCOLER
SPHEINTE
TARAOFFI
TIARCORD
TRIFREPE
TRILEREC
TRILGRAN
TSUGCANA
ULMUAMER
UNKN_822
URTIDIGR
URTIDIOI
VERBHAST
VERBURTI
VEROSERP
VIBUACER
VICICRAC
VIOLAFFI
VIOLBLAN
VIOLCANA
VIOLCUCU
VIOLPUBE
VIOLSORO
VITIRIPA

32. Ditch

(n=33 species)

ACERSACC
AGROGIGA
ASTECILI
ASTELANC
ASTELATE
ASTEPUNI
CARETENE
CICUMACU
CORNALTE
CORNSTOL
EPILCILI
EPILCOLO
EQUIARVE
ERYTAMER
FRAXAMER
GALIOBTU
GLYCSTRI
IMPACAPE
LEERORYZ
LYCOUNIF
LYSITERR
MENTARVE
PARTINSE
PILEPUMI
POA_PALU
POLYPUBE
RANUACRI
RIBEAMER
RUBUPUBE
SALIERIO
SCUTLATE
SOLIGIGA
TUSSFARF

33. Regenerating Field

(n=147 species)

ACERRUBR
ACERSACC
ACERSACN
ACHIMILL
AGRIGRYP
AGROGIGA
AMPHBRAC
ANEMCANA
ANEMVIRG
ANTENEGL
APOCANDR
AQUICANA
ASCLINCA
ASCLSYRI
ASTECILI
ASTEERIC
ASTELANC
ASTELATE
ASTENOVE
ASTEPUNI
BETUPAPY
BOTRMATR
BOTRVIRG
BROMINER
CAREALOP
CAREBEBB
CAREBLAN
CAREBREV
CARECRIS
CAREDEWE
CAREGRAC
CAREGRAN
CARELANU
CAREPENS
CAREPRAI
CAREPROJ
CARERADI
CARESTIP
CARETENE
CAREVULP
CARE_879
CARYCORD
CERAFONT
CHRYLEUC
CIRSARVE
CIRSVULG
CORNRUGO
CORNSTOL
CRAT__SP
DANTSPIC
DAUCCARO
DIANARME
ELYMREPE
ELYMVIRG
EPILCILI
EPILLEPT
EPIPHELL
EQUIARVE
EQUIHYEM
ERIGPHIL
ERIGSTRI
EUPAMACU
EUPAPERF
EUTHGRAM
FAGUGRAN
FESTARUN
FESTRUBR
FESTSUBV
FRAGVIRG
FRAXAMER
FRAXNIGR
FRAXPENN
GALIOBTU
GALITRIF
GENTANDR
GEUM__SP
GLYCSTRI
HIERCAES
HYPEPERF
LACTCANA
LYCOTRIS
LYCOUNIF
LYSICILI
MAIACANA
MATTSTRU
MEDILUPU
MELIALBA
MELIOFFI
MENTARVE
MUHLFRON
MUHLMEXI

Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

OPEN CANOPY

33. (Cont'd)
ONOCSENS
OXALSTRI
PANIACUM
PARTINSE
PHALARUN
PHLEPRAT
PHRYLEPT
PILEPUMI
PLANLANC
PLANMAJO
PLANRUGE
POA_COMP
POA_PALU
POA_PRAT
POPUBALS
POPUTREM
POTERECT
PRUNSERO
PRUNVIRG
PRUNVULG
PTERAQUI
QUERRUBR
RANUACRI
RHAMCATH
RHUSTYPH
RIBECYNO
ROBIPSEU
ROSAPALU
RUBUIDAE
RUBUPUBE
SALIBEBB
SALIDISC
SALIERIO
SALIPETI
SCIRATRO
SILEVULG
SISYMONT
SMILHERB
SOLIALTI
SOLICANA
SOLIGIGA
SOLINEMO
TARAOFFI
THUJOCCI
TILIAMER
TRAGDUBI
TRIFREPE
TUSSFARF
ULMUAMER
VERBTHAP
VIBULENT
VIBUTRIL
VICICRAC
VIOLAFFI
VIOLBLAN
VITIRIPA

34. Riparian Marsh
(n=46 species)
AGROSTOL
ASTELATE
ATHYFILI
BIDEFRON
BROMINER
CARDPENS
CICUMACU
CIRCLUTE
CLEMVIRG
CORNRUGO
ERIGANNU
EUPAPERF
GEUMLACI
IRIS__SP
LYCOUNIF
MATTSTRU
MENTARVE
PILEPUMI
POA_COMP
RIBERUBR
RUMEORBI
SCIRATRO
SOLADULC
SOLIALTI
SPHEINTE
VIOLCUCU
VITIRIPA
ASTEPUNI
CARESTIP
CYSTBULB
EPILCOLO
LAPOCANA
ONOCSENS
POLYPERS
SOLIGIGA
AGROGIGA
BOEHCYLI
CORNSTOL
EQUIARVE
EUPAMACU
GALIOBTU
GLYCSTRI
IMPACAPE
LEERORYZ
PARTINSE
POA_PALU

35. Riparian Meadow
(n=75 species)
ADIAPEDA
AGROGIGA
ARISTRIP
ASTELANC
ASTELATE
ASTEPUNI
ATHYFILI
BIDEFRON
BOEHCYLI
CAREBEBB
CAREGRAC
CAREPROJ
CARERADI
CARERETR
CARESTIP
CARETRIB
CAREVULP
CIRCLUTE
CLEMVIRG
CORNRUGO
CORNSTOL
CYSTBULB
DRYOCART
DRYOCRIS
EPILCOLO
EPIPHELL
EQUIARVE
ERIGANNU
EUPAMACU
EUPAPERF
EUPARUGO
FRAXNIGR
GALIOBTU
GEUM__SP
GLYCSTRI
HYPEPERF
HYSTPATU
IMPACAPE
INULHELI
LAPOCANA
LEERORYZ
LYCOUNIF
LYSICILI
LYSINUMM
MATTSTRU
MENTARVE
ONOCSENS
PARTINSE
PILEPUMI
POA_COMP
POA_PALU
POA_PRAT
PRUNVULG
RANUACRI
RHUSRADI
RIBEAMER
RIBECYNO
RIBETRIS
RUBUOCCI
RUBUPUBE
SALIERIO
SCUTLATE
SOLADULC
SOLICANA
SOLIGIGA
SPHEINTE
THUJOCCI
TIARCORD
TILIAMER
ULMUAMER
VIOLAFFI
VIOLCUCU
VIOL__SP
VITIRIPA

36. Riparian Thicket
(n=37 species)
ACERRUBR
ASTELATE
ASTEPUNI
ATHYFILI
BETUALLE
BIDEFRON
BOEHCYLI
CAREBEBB
CAREGRAC
CARESTIP
CIRCLUTE
CLEMVIRG
CORNSTOL
EPILCOLO
EPIPHELL
EQUIARVE
ERIGPHIL
EUPAMACU
FRAXPENN
GALIOBTU
GALITRIF
GEUMCANA
GEUM__SP
GLYCSTRI
IMPACAPE
PARTINSE
PILEPUMI
POA_PALU
POA_PRAT
RANUABOR
RANUACRI
RANURECU
RIBETRIS
RUBUPUBE
SOLADULC
TARAOFFI
VIOLAFFI

APPENDIX 6

DISTRIBUTION OF SPECIES BY MICROHABITAT: CLOSED CANOPY

Legend

Column Heading	Description	Unit
dFLR	seasonally dry forest floor	# quadrats
mFLR	seasonally moist forest floor	# quadrats
wFLR	seasonally wet forest floor	# quadrats
mDEP	seasonally moist depression	# quadrats
wDEP	seasonally wet depression	# quadrats
SEEP	seep	# quadrats
dGAP	seasonally dry gap	# quadrats
mGAP	seasonally moist gap	# quadrats
MOUN	tip-up mound	# quadrats
dPIT	seasonally dry tree pit	# quadrats
mPIT	seasonally moist tree pit	# quadrats
LOG	log on dry, moist or wet substrate	# quadrats
STMP	stump on dry, moist or wet substrate	# quadrats
RMAT	raised root mat on dry, moist or wet substrate	# quadrats
STON	stone	# quadrats
LANE	lane or access road	# quadrats
DITCH	ditch associated with lane/access road	# quadrats
F	regenerating farm field	# quadrats

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
ABIEBALS	3	8	-	5	1	-	2	1	7	1	-	6	1	7	-	1	-	3
ACERNEGU	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACERRUBR	5	7	1	1	-	-	2	1	6	1	-	1	5	6	-	1	-	2
ACERSACC	1	8	-	5	3	-	5	2	5	3	-	-	2	1	-	1	1	3
ACERSACN	3	3	3	2	6	-	-	2	-	-	-	1	-	2	-	-	1	2
ACERSANI	5	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
ACERSPIC	1	8	-	9	3	-	1	2	3	-	-	8	3	1	-	-	-	-
ACHIMILL	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
ACTAPACH	1	-	-	-	-	-	2	-	4	-	-	-	-	-	-	-	-	-
ACTARUBR	1	2	-	3	-	-	1	-	1	-	-	-	-	1	-	-	-	1
ACTA__SP	2	1	-	-	1	-	2	-	3	1	-	1	-	4	-	1	-	-
ADIAPEDA	1	1	-	1	1	-	1	-	2	-	-	-	-	-	-	-	-	-
AGRIGRYP	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
AGROGIGA	-	2	1	-	1	-	-	-	-	-	-	-	-	-	-	-	1	3
AGROSTOL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
ALLITRIC	2	-	-	-	4	-	1	-	2	-	-	-	-	1	-	-	-	-
ALNUINCA	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
AMBRARTE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMELARBO	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMELINTE	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
AMEL__SP	4	-	-	-	-	-	2	-	4	2	-	-	-	-	-	-	-	-
AMPHBRAC	7	1	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
ANEMCANA	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
ANEMQUIN	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-
ANEMVIRG	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
ANTENEGL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
APOCANDR	8	1	-	-	-	-	1	-	5	-	-	-	-	-	-	-	-	2
AQUICANA	8	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	2
ARALNUDI	2	5	-	1	-	-	-	1	3	3	-	5	4	1	-	1	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
ARCTMINU	3	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
ARISTRIP	6	1	-	2	9	-	2	3	1	7	-	6	2	1	-	5	-	-
ASARCANA	2	2	-	1	2	-	-	-	6	1	-	-	-	2	-	-	-	-
ASCLINCA	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
ASCLSYRI	2	2	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	3
ASTECILI	9	-	1	-	-	-	2	-	3	-	-	-	-	-	-	-	-	4
ASTECORD	8	-	-	-	1	-	1	-	1	-	-	-	-	1	-	-	-	-
ASTEERIC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ASTELANC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ASTELATE	2	1	2	1	3	-	1	-	7	-	-	7	2	7	1	1	2	4
ASTEMACR	6	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-
ASTENOVE	3	2	-	-	1	1	-	-	3	-	-	-	-	1	-	-	-	2
ASTEPUNI	-	4	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	3
ASTEUMBE	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ATHYFILI	3	1	-	4	3	-	4	1	6	2	-	1	-	7	-	2	-	-
ATHYTHEL	5	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-
BETUALLE	6	2	-	-	2	-	-	-	-	-	-	1	3	6	-	-	-	-
BETUPAPY	9	1	-	-	-	-	2	-	4	-	-	4	-	1	-	-	-	5
BIDEFRON	3	1	1	-	1	-	-	-	-	-	-	5	-	2	-	-	-	-
BOEHCYLI	6	4	3	2	7	1	-	1	-	1	-	3	1	3	-	2	-	-
BOTRMATR	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BOTRMULT	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BOTRVIRG	3	1	-	-	-	-	2	-	4	2	-	-	-	-	-	1	-	1
BRACEREC	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BROMINER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
CALTPALU	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CALYSEPI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARDACAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARDDIPH	3	4	-	8	3	-	1	-	5	-	-	1	-	2	-	1	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
CARDNUTA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARDPENS	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREALBU	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREALOP	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREARCT	2	2	-	-	-	-	-	-	3	-	-	-	-	2	-	2	-	-
CAREBACK	5	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
CAREBEBB	-	1	1	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-
CAREBLAN	3	6	1	4	1	-	2	1	5	-	-	2	-	3	1	2	-	1
CAREBREV	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECEPH	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECOMM	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECRIN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECRIS	1	3	2	2	1	-	-	-	-	-	-	2	1	1	-	-	1	1
CAREDEWE	4	9	-	4	-	-	1	1	1	1	-	3	1	1	-	2	-	-
CAREDIGI	2	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-
CAREGRAC	3	1	1	6	1	-	2	1	1	-	-	4	1	4	-	2	-	1
CAREGRAN	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1
CAREHIRT	6	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREHITC	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CAREINTU	8	1	-	2	4	1	-	-	2	-	1	3	-	1	-	1	-	-
CARELANU	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3
CARELAXI	9	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CAREPECK	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CAREPEDU	4	1	-	5	1	-	2	2	1	2	-	9	5	1	1	3	-	-
CAREPENS	8	5	-	2	-	-	4	-	3	1	-	2	3	7	1	7	-	2
CAREPLAN	7	-	-	1	1	-	1	-	1	-	-	-	-	1	-	-	-	-
CAREPLAT	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREPRAI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREPROJ	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
CAREPSEU	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
CARERADI	1	7	2	8	1	-	3	1	1	-	-	2	-	1	-	1	1	1
CARERETR	-	-	-	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREROSE	4	7	1	2	-	-	3	1	1	-	-	2	-	5	-	2	1	-
CARESPAR	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CARESTIP	-	2	2	1	-	2	-	-	-	-	-	1	-	1	-	-	2	1
CARETENE	2	2	1	1	2	-	-	-	-	-	-	2	-	2	-	1	1	2
CARETRIB	-	2	1	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
CAREVULP	-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
CAREWOOD	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_719	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
CARE_868	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_870	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_879	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE__OV	1	-	-	1	-	1	-	-	-	-	-	-	1	1	-	-	-	-
CARE__SP	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
CARPCARO	1	2	-	-	1	-	2	-	-	2	-	1	-	-	-	-	-	2
CARYCORD	5	2	-	-	-	-	2	-	1	5	-	3	-	4	-	2	1	2
CAULTHAL	4	1	-	3	2	-	-	1	1	5	-	1	-	2	-	1	-	-
CEANAMER	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CELASCAN	2	-	-	-	-	-	2	-	3	1	-	-	-	1	-	-	-	2
CERAFONT	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
CHIMUMBE	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CHRYLEUC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
CICUBULB	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
CICUMACU	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CINNLATI	1	-	-	2	3	1	-	1	-	-	-	3	-	3	-	-	-	-
CIRCALPI	1	6	-	5	2	-	-	2	2	-	1	6	2	3	-	1	-	-
CIRCLUTE	5	1	-	1	2	-	3	3	1	4	1	6	1	9	-	5	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
CIRSARVE	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
CIRSVULG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLAYCARO	9	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	1	-
CLEMVIRG	-	5	-	3	-	-	-	-	-	-	-	1	-	2	-	-	-	-
CLINBORE	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
CONYCANA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CORNALTE	6	1	-	1	2	-	3	2	1	1	-	3	-	8	-	1	-	-
CORNFOEM	1	1	-	2	-	-	1	-	-	-	-	1	-	-	-	-	-	-
CORNRUGO	1	1	-	-	2	-	2	-	6	3	-	-	-	1	-	-	1	-
CORNSTOL	3	2	2	3	3	-	-	1	-	-	-	-	-	1	-	-	2	3
CORYCORN	3	1	-	-	-	-	3	-	7	4	-	-	-	-	-	-	-	1
CRAT_SP1	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT_SP2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT_SP3	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
CRAT__SP	1	1	1	-	-	-	1	-	2	-	-	-	-	-	-	-	-	2
CRYPCANA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CYPRCALC	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CYSTBULB	2	4	-	9	4	-	-	1	-	-	-	3	-	3	-	-	-	-
CYSTFRAG	2	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-
CYSTTENU	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DACTGLOM	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DANTSPIC	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
DAUCCARO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
DESMGLUT	4	-	-	-	-	-	2	-	1	1	-	-	-	-	-	-	-	1
DIANARME	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DICECANA	1	-	-	-	-	-	1	-	2	2	-	-	-	-	-	-	-	-
DICECUCU	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
DIERLONI	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
DIRCPALU	5	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
DRYOCART	5	1	-	4	2	-	2	2	1	1	-	1	9	1	-	5	-	-
DRYOCRIS	4	4	-	3	2	-	-	1	-	-	-	2	-	2	1	1	-	-
DRYOINTE	3	7	-	6	1	-	3	3	1	2	-	8	4	1	-	3	-	-
DRYOMARG	1	8	-	2	1	-	1	1	2	1	-	-	-	8	-	-	-	-
ECHILOBA	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
ELYMREPE	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ELYMVIRG	-	2	2	3	-	-	-	-	-	-	-	-	-	-	-	-	-	1
EPIFVIRG	3	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
EPILCILI	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1
EPILCOLO	-	4	-	4	1	1	-	1	1	-	-	4	-	2	-	-	-	-
EPILLEPT	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1
EPILPARV	-	1	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-
EPIPHELL	8	1	-	1	2	-	3	2	2	8	-	3	1	1	1	7	1	1
EQUIARVE	1	7	2	7	3	2	-	-	3	-	-	1	-	1	-	-	2	5
EQUIHYEM	5	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
EQUILAEV	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EQUISCIR	3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-
ERIGANNU	2	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
ERIGPHIL	1	8	1	3	-	-	-	-	5	-	-	-	-	1	1	-	1	1
ERIGSTRI	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
ERIG__SP	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ERYTAMER	8	4	-	1	-	-	1	2	1	6	1	1	-	-	-	7	2	-
EUPAMACU	-	4	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	1
EUPAPERF	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
EUPARUGO	9	2	-	5	5	-	-	-	-	-	-	2	-	-	-	-	-	-
EUTHGRAM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
FAGUGRAN	4	3	-	1	-	-	-	-	5	1	-	-	1	2	-	2	-	-
FESTARUN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FESTPRAT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
FESTRUBR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FESTSUBV	2	1	-	-	1	-	1	-	3	1	-	-	-	-	-	-	-	-
FRAGVESC	1	-	-	-	-	-	1	1	2	-	-	2	-	-	-	1	-	-
FRAGVIRG	3	1	1	4	-	-	1	-	-	-	-	1	1	4	-	-	1	4
FRAXAMER	7	3	-	1	1	-	4	-	1	5	-	1	-	1	1	5	-	2
FRAXNIGR	1	1	2	1	3	1	-	2	2	-	-	1	-	2	-	-	2	1
FRAXPENN	2	9	2	1	3	-	-	1	4	-	-	1	-	3	-	-	2	4
GALESPEC	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
GALETETR	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALIAPAR	8	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
GALIASPR	-	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
GALICIRC	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
GALILANC	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
GALIOBTU	1	3	2	1	3	-	-	-	-	-	-	-	-	1	-	-	1	3
GALIPALU	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
GALITRIF	5	9	1	6	2	-	4	1	1	2	-	6	-	7	1	3	1	3
GALI__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GENTANDR	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
GERAMACU	8	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
GERAROBE	1	1	-	1	4	-	1	3	4	1	-	8	2	5	-	-	-	-
GEUMALEP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GEUMCANA	3	2	-	2	-	-	-	1	-	-	-	-	-	1	-	-	-	-
GEUMLACI	4	7	-	2	-	-	1	1	1	-	-	1	-	1	-	-	-	-
GEUMRIVA	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-
GEUMURBA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GEUM__SP	5	7	1	2	-	-	1	-	-	-	-	-	-	1	-	-	-	-
GLYCSTRI	2	1	3	1	7	1	1	2	4	-	-	5	-	3	-	2	1	-
GYMNDRYO	1	3	-	1	-	1	-	-	5	2	-	1	1	8	-	-	-	-
HACKVIRG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
HEPAACUT	2	-	-	1	-	-	-	-	4	2	-	1	-	-	-	-	-	-
HIERAURA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HIERCAES	2	1	1	3	1	-	1	-	8	-	-	8	-	5	-	1	-	2
HYDRVIRG	9	-	-	-	1	-	-	-	3	1	-	-	-	1	-	2	1	-
HYPEPERF	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
HYSTPATU	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IMPACAPE	2	1	3	8	5	3	2	2	5	3	1	1	6	1	-	2	1	1
INULHELI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IRISVERS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IRIS_SP	-	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
JUNCTENU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LACTCANA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
LACTSERR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LACT_SP	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-
LAPOCANA	8	2	-	1	4	1	-	1	-	-	-	1	-	-	-	-	-	-
LEERORYZ	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
LEERVIRG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LEONCARD	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
LIPALOES	-	1	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
LOBEINFL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LOBE_SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LONICANA	2	-	-	-	-	-	1	-	4	3	-	-	-	2	-	-	-	-
LONIDIOI	1	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-
LONIHIRS	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LYCOAMER	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
LYCOANNO	5	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
LYCODEND	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
LYCOOBOB	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
LYCOTRIS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
LYCOUNIF	-	2	2	-	1	2	-	-	-	-	-	4	-	3	-	-	1	1
LYSICILI	-	4	2	2	1	1	-	-	-	-	-	-	-	-	-	-	1	3
LYSINUMM	1	1	2	1	2	3	-	-	-	-	-	1	-	-	-	-	-	-
LYSITERR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
MAIACANA	9	7	-	3	-	-	4	1	3	1	-	1	1	1	1	5	1	2
MAIARACE	7	6	-	1	1	-	2	-	2	6	-	3	1	7	-	5	-	-
MAIASTEL	4	2	-	1	-	-	1	-	2	1	-	-	-	-	-	-	-	-
MATTSTRU	9	4	1	2	1	1	-	-	2	-	-	-	-	-	-	-	-	1
MEDILUPU	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2
MELIALBA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
MELIOFFI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
MENICANA	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
MENTARVE	1	2	1	-	1	-	-	-	-	-	-	1	-	-	-	1	1	-
MILIEFFU	7	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
MITCREPE	1	-	-	-	-	-	-	-	2	3	-	-	-	-	-	1	-	-
MITEDIPH	1	2	-	1	-	-	-	-	1	1	-	4	-	3	-	-	-	-
MONAFIST	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
MONOHYPO	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MONOUNIF	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
MUHLFRON	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
MUHLMEXI	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
NEPECATA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ONOCSENS	9	8	3	6	6	2	1	1	1	-	-	1	-	-	-	1	2	2
ONOPACAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORYZASPE	4	-	-	-	-	-	2	-	1	3	-	-	-	-	-	3	-	-
OSMOCLAY	2	-	-	-	-	-	1	-	4	2	-	-	-	1	-	1	-	-
OSMUCLAY	4	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
OSMUREGA	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
OSTRVIRG	6	1	-	1	-	-	3	-	2	8	-	-	-	1	-	2	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
OXALSTRI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
OXAL__SP	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
PANAQUIN	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PANIACUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
PANICAPI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PANI__SP	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
PARTINSE	2	9	2	1	9	-	1	2	5	-	-	9	2	5	1	-	2	3
PHALARUN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
PHEGCONN	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PHLEPRAT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
PHLO__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PHRYLEPT	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
PICEGLAU	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
PILEPUMI	1	1	1	1	1	3	-	-	1	-	-	5	1	-	-	-	2	1
PINUSTRO	1	1	-	-	-	-	-	-	1	1	-	-	-	1	-	-	-	-
PLANLANC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
PLANMAJO	-	2	1	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-
PLANRUGE	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
POA_ALSO	1	2	1	-	3	-	-	-	2	1	-	-	-	1	-	-	-	-
POA_COMP	6	-	1	1	-	-	1	-	4	-	-	-	-	2	-	-	-	5
POA_PALU	1	7	2	4	1	1	-	-	-	-	-	2	-	-	-	-	2	1
POA_PRAT	6	2	1	-	-	-	1	-	-	-	-	-	-	-	-	1	1	3
POA_SALT	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
POA___SP	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
PODOPELT	2	-	-	-	-	-	2	-	1	-	-	-	-	-	-	1	-	-
POLYACRO	8	1	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-
POLYPAUC	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
POLYPERS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POLYPUBE	7	-	-	2	1	-	2	-	2	1	-	2	3	2	-	4	1	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
POPUBALS	4	3	-	2	-	-	-	1	-	-	-	-	-	1	-	-	-	1
POPUGRAN	1	-	-	-	-	-	-	-	3	2	-	-	-	-	-	1	-	-
POPUTREM	2	2	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	3
POTENORV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POTERECT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
PREN__SP	1	-	-	-	-	-	-	-	4	-	-	-	-	1	-	-	-	-
PRUNSERO	5	5	-	-	-	-	3	-	4	2	-	-	-	2	-	2	-	2
PRUNVIRG	9	6	2	3	2	-	3	2	1	6	-	-	-	4	1	4	1	3
PRUNVULG	2	3	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3
PTERAQUI	3	-	-	-	-	-	2	-	8	5	-	-	-	-	-	1	-	2
PYROELLI	1	-	-	-	-	-	1	-	4	1	-	-	-	2	-	-	-	-
QUERALBA	8	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
QUERMACR	8	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
QUERRUBR	6	-	-	-	-	-	2	-	7	3	-	-	1	-	-	4	-	1
QUER__SP	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
RANUABOR	2	4	1	3	1	-	-	1	1	1	-	2	1	1	-	5	-	-
RANUACRI	9	7	1	3	-	-	1	-	1	-	-	-	-	1	-	-	1	4
RANUHICA	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
RANURECU	3	6	-	1	4	-	3	1	4	-	-	1	-	2	-	-	1	-
RHAMALNI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHAMCATH	3	6	2	4	2	-	3	2	6	-	-	4	-	6	-	2	-	4
RHUSRADI	3	2	1	3	1	-	2	-	3	1	-	-	-	3	1	1	-	-
RHUSTYPH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIBEAMER	1	3	-	1	2	2	-	-	-	-	-	-	1	-	-	-	-	1
RIBECYNO	5	9	-	7	1	-	4	2	5	2	-	1	-	6	1	4	-	1
RIBEGLAN	1	1	-	2	-	2	-	-	-	-	-	2	-	1	-	-	-	-
RIBELACU	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-
RIBERUBR	2	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
RIBETRIS	6	8	1	6	1	-	1	1	1	-	-	-	-	-	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
RIBE_827	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
ROBIPSEU	1	-	2	-	-	-	1	-	1	1	-	-	-	-	-	1	1	-
ROSABLAN	1	1	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
ROSAPALU	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RUBUALLE	1	1	-	-	-	-	1	-	2	1	-	1	-	1	-	-	-	1
RUBUIDAE	1	7	-	5	1	-	4	2	2	-	-	8	2	3	-	1	-	2
RUBUOCCI	6	-	-	-	1	-	-	-	1	-	-	-	-	-	-	1	-	-
RUBUODOR	6	2	-	-	-	-	-	-	1	-	-	3	1	1	-	-	-	-
RUBUPUBE	1	1	2	8	2	-	-	1	1	-	-	9	3	8	-	-	-	2
RUBU_840	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
RUDBHIRT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
RUMEORBI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SALIBEBB	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
SALIDISC	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
SALIERIO	-	2	1	-	1	-	-	-	-	-	-	-	-	-	-	1	1	2
SALIPETI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SAMBCANA	2	-	-	2	-	2	-	1	-	-	-	-	-	1	-	-	-	-
SAMBRAPU	2	1	-	-	-	-	2	-	3	1	-	-	2	3	-	2	-	-
SANGCANA	9	-	-	-	-	-	-	-	4	3	-	-	-	-	-	1	1	-
SANIMARI	3	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
SANITRIF	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SANI__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCHIPURP	2	2	-	2	-	-	-	-	4	-	-	-	-	2	1	-	-	-
SCIRATRO	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
SCUTLATE	-	2	1	1	-	-	-	-	-	-	-	-	-	1	-	-	1	-
SICYANGU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SILEVULG	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
SISYMONT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
SIUMSUAV	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
SMILHERB	3	-	-	-	-	-	2	-	5	5	-	-	-	-	-	2	-	1
SMILHISP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SOLADULC	9	1	2	6	1	1	2	2	-	-	-	4	1	3	-	-	-	-
SOLIALTI	5	2	-	2	1	-	1	1	1	-	-	3	-	-	-	1	1	2
SOLICAES	9	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-
SOLICANA	2	5	1	3	1	-	2	1	7	-	-	6	1	7	-	2	-	3
SOLIFLEX	3	1	-	3	3	-	1	-	7	1	-	3	1	2	1	-	-	-
SOLIGIGA	-	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	2	2
SOLIJUNC	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
SOLINEMO	3	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2
SOLIRUGO	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
SONCARVE	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
SONCOLER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SPHEINTE	3	2	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-
STELLONG	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
STREROSE	7	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
SYMPALBU	5	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
TARAOFFI	4	1	2	3	2	-	2	1	1	1	-	9	2	1	-	2	1	3
TAXUCANA	1	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
THALDIOI	1	1	-	-	-	-	1	-	1	-	-	-	-	-	-	1	-	-
THALPUBE	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-
THELNOVE	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
THELPALU	1	1	-	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-
THUJOCCI	2	9	-	5	1	-	2	-	2	1	-	3	1	1	-	-	-	1
TIARCORD	2	1	-	6	2	1	2	2	8	-	-	2	6	1	-	1	-	-
TILIAMER	7	1	-	1	2	-	4	-	7	2	-	2	-	7	-	2	1	3
TRAGDUBI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
TRIEBORE	3	1	-	1	-	-	-	-	6	3	-	3	4	4	-	1	-	-
TRIFREPE	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
TRILEREC	3	3	-	1	2	-	-	1	9	1	-	1	-	1	-	1	-	-
TRILGRAN	1	2	-	3	1	-	5	-	2	1	-	-	-	5	1	8	-	1
TRIOAURA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TSUGCANA	3	8	-	1	-	-	-	-	4	-	-	6	1	6	-	-	-	-
TUSSFARF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
TYPHLATI	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ULMUAMER	2	7	1	1	8	1	-	2	1	-	-	4	1	5	-	1	1	2
UNKN_751	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UNKN_791	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
UNKN_822	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
URTIDIGR	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-
URTIDIOI	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UVULGRAN	9	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-
VACCANGU	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VERBHAST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VERBTHAP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VERBURTI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VEROOFFI	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VEROSERP	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIBUACER	3	-	-	-	-	-	1	-	5	4	-	-	-	-	-	-	-	1
VIBULENT	1	2	2	2	-	-	3	-	3	2	-	-	-	2	-	-	-	4
VIBUOPUL	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIBUTRIL	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VICICRAC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
VIOLAFFI	2	4	2	2	-	-	-	-	1	-	-	-	-	-	-	-	-	3
VIOLBLAN	1	1	-	1	1	-	1	-	2	-	-	3	-	2	-	-	-	-
VIOLCANA	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIOLCUCU	6	1	-	-	1	-	-	1	2	-	-	-	1	-	-	-	-	-
VIOLLABR	1	1	-	2	-	-	1	-	-	-	-	1	-	-	-	1	-	-

Appendix 6. Distribution of species by microhabitat: closed canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	dGAP	mGAP	MOUN	dPIT	mPIT	LOG	STMP	RMAT	STON	LANE	DITCH	F
VIOLPUBE	5	1	-	2	3	-	1	1	1	3	-	2	-	-	-	2	1	-
VIOLROST	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIOLSORO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
VIOL_788	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIOL__SP	2	1	-	-	-	1	1	-	1	-	-	1	-	1	-	-	1	1
VITIRIPA	3	6	1	4	2	-	3	-	8	-	-	1	-	1	-	1	1	5
WALDFRAG	1	1	-	-	-	-	1	-	5	5	-	1	-	-	-	-	-	-

APPENDIX 7

DISTRIBUTION OF SPECIES BY MICROHABITAT: OPEN CANOPY

Legend

Column Heading	Description	Unit
dFLR	seasonally dry forest floor	# quadrats
mFLR	seasonally moist forest floor	# quadrats
wFLR	seasonally wet forest floor	# quadrats
mDEP	seasonally moist depression	# quadrats
wDEP	seasonally wet depression	# quadrats
SEEP	seep	# quadrats
MOUN	tip-up mound	# quadrats
dPIT	seasonally dry tree pit	# quadrats
wPIT	seasonally wet tree pit	# quadrats
LOG	log on dry, moist or wet substrate	# quadrats
STMP	stump on dry, moist or wet substrate	# quadrats
RMAT	raised root mat on dry, moist or wet substrate	# quadrats
LANE	lane or access road	# quadrats
DITCH	ditch associated with lane/access road	# quadrats
RFLD	regenerating farm field	# quadrats
RMA	riparian marsh	# quadrats
RME	riparian meadow	# quadrats
RT	riparian thicket	# quadrats

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
ABIEBALS	3	2	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
ACERNEGU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACERRUBR	8	5	-	-	-	-	2	-	-	-	-	1	-	-	4	-	-	1
ACERSACC	.	3	-	-	-	-	5	3	-	1	1	4	4	1	1	-	-	-
ACERSACN	1	4	3	1	3	-	-	-	-	-	-	-	1	-	4	-	-	-
ACERSANI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ACERSPIC	3	6	1	2	1	-	-	-	-	4	-	5	-	-	-	-	-	-
ACHIMILL	-	1	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-
ACTAPACH	5	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
ACTARUBR	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
ACTA__SP	1	1	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
ADIAPEDA	1	-	1	-	-	-	1	-	-	-	-	1	-	-	-	-	1	-
AGRIGRYP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
AGROGIGA	-	1	1	-	-	-	-	-	-	-	-	-	2	1	3	3	3	-
AGROSTOL	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	1	-	-
ALLITRIC	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ALNUINCA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMBRARTE	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
AMELARBO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMELINTE	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMEL__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AMPHBRAC	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
ANEMCANA	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-
ANEMQUIN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ANEMVIRG	-	2	-	-	-	-	-	-	-	-	-	-	1	-	5	-	-	-
ANTENEGL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
APOCANDR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
AQUICANA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
ARALNUDI	4	2	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
ARCTMINU	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
ARISTRIP	.	9	4	3	3	1	1	1	-	1	1	4	1	-	-	-	2	-
ASARCANA	5	1	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-
ASCLINCA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
ASCLSYRI	5	1	-	-	-	-	-	-	-	-	-	-	2	-	4	-	-	-
ASTECILI	3	1	-	-	-	-	-	-	-	-	-	-	1	1	5	-	-	-
ASTECORD	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
ASTEERIC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
ASTELANC	-	1	1	-	1	-	-	-	-	-	-	-	2	1	1	-	1	-
ASTELATE	3	5	1	1	-	-	1	-	-	3	1	3	3	1	4	1	2	1
ASTEMACR	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ASTENOVE	1	1	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-
ASTEPUNI	-	2	1	-	-	-	-	-	-	1	1	1	3	1	3	2	3	1
ASTEUMBE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ATHYFILI	3	5	2	-	1	1	-	-	-	1	-	-	2	-	-	1	2	1
ATHYTHEL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BETUALLE	-	1	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	1
BETUPAPY	2	-	-	-	-	-	-	-	-	1	1	-	1	-	4	-	-	-
BIDEFRON	-	1	2	-	1	-	-	-	-	-	-	1	3	-	-	1	2	1
BOEHCYLI	1	4	3	1	2	1	-	-	-	1	-	2	2	-	-	3	3	1
BOTRMATR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
BOTRMULT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BOTRVIRG	4	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
BRACEREC	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BROMINER	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	-	-
CALTPALU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CALYSEPI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARDACAN	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARDDIPH	6	3	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
CARDNUTA	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
CARDPENS	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-
CAREALBU	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREALOP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
CAREARCT	6	1	-	-	-	-	1	-	-	1	-	1	2	-	-	-	-	-
CAREBACK	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
CAREBEBB	-	1	1	-	1	-	-	-	-	-	-	-	2	-	1	-	1	1
CAREBLAN	1	4	1	-	1	-	1	-	-	-	-	1	4	-	1	-	-	-
CAREBREV	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
CARECEPH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECOMM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARECRIN	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CARECRIS	1	1	1	1	1	1	-	-	-	-	-	-	-	-	2	-	-	-
CAREDEWE	.	4	1	-	1	-	-	-	-	2	1	1	-	-	3	-	-	-
CAREDIGI	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CAREGRAC	1	4	2	2	1	1	-	-	-	-	1	2	4	-	2	-	2	1
CAREGRAN	-	1	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	-
CAREHIRT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREHITC	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREINTU	1	4	3	1	3	1	-	-	-	1	-	-	1	-	-	-	-	-
CARELANU	-	1	-	-	-	-	-	-	-	-	-	-	1	-	4	-	-	-
CARELAXI	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
CAREPECK	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREPEDU	5	6	-	-	-	-	1	-	-	2	1	2	-	-	-	-	-	-
CAREPENS	.	1	-	-	-	-	2	-	-	-	-	1	2	-	2	-	-	-
CAREPLAN	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREPLAT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CAREPRAI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
CAREPROJ	-	-	1	-	-	1	-	-	-	-	-	-	1	-	1	-	1	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
CAREPSEU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARERADI	3	3	1	1	-	-	2	-	-	2	-	-	-	-	2	-	2	-
CARERETR	-	-	3	-	2	1	-	-	-	-	-	-	1	-	-	-	2	-
CAREROSE	4	1	1	-	-	-	1	-	-	-	1	-	1	-	-	-	1	-
CARESPAR	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARESTIP	-	2	2	-	1	-	-	-	-	-	-	-	1	-	2	2	3	1
CARETENE	-	2	-	-	-	1	-	-	-	-	-	-	2	1	4	-	-	-
CARETRIB	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-
CAREVULP	-	1	1	-	-	-	-	-	-	-	1	-	2	-	1	-	1	-
CAREWOOD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_719	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_868	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
CARE_870	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
CARE_879	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
CARE_OV	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CARE_SP	1	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
CARPCARO	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
CARYCORD	7	-	-	-	-	-	1	-	-	-	-	-	1	-	1	-	-	-
CAULTHAL	6	1	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
CEANAMER	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CELASCAN	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CERAFONT	1	1	-	-	-	-	-	-	-	-	-	-	2	-	3	-	-	-
CHIMUMBE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CHRYLEUC	-	1	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-
CICUBULB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CICUMACU	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1	-	-
CINNLATI	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
CIRCALPI	3	5	-	1	-	1	-	-	-	3	2	4	1	-	-	-	-	-
CIRCLUTE	.	8	1	3	-	-	2	1	-	1	-	6	5	-	-	1	2	1

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
CIRSARVE	2	-	-	-	-	-	1	-	-	-	-	-	3	-	3	-	-	-
CIRSVULG	3	-	-	-	-	-	1	1	-	-	-	1	1	-	2	-	-	-
CLAYCARO	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLEMVIRG	1	-	1	-	-	-	-	-	-	1	-	2	1	-	-	1	2	1
CLINBORE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CONYCANA	3	-	-	-	-	-	1	-	-	-	-	1	1	-	-	-	-	-
CORNALTE	4	5	-	1	-	-	-	-	-	-	-	2	-	1	-	-	-	-
CORNFOEM	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
CORNRUGO	4	-	2	-	1	-	1	-	-	-	-	-	2	-	1	1	2	-
CORNSTOL	-	3	1	1	-	-	-	-	-	-	-	1	2	1	4	3	3	1
CORYCORN	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT_SP1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT_SP2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT_SP3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CRAT__SP	3	2	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-
CRYPCANA	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CYPRCALC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CYSTBULB	2	2	1	2	-	-	-	-	-	1	-	1	1	-	-	2	2	-
CYSTFRAG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CYSTTENU	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
DACTGLOM	1	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
DANTSPIC	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
DAUCCARO	-	-	-	-	-	-	-	-	-	-	-	1	2	-	2	-	-	-
DESMGLUT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIANARME	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
DICECANA	6	-	-	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-
DICECUCU	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIERLONI	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
DIRCPALU	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
DRYOCART	9	6	1	1	-	-	1	1	-	2	3	4	4	-	-	-	2	-
DRYOCRIS	1	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
DRYOINTE	6	6	-	1	-	-	2	1	-	3	3	8	-	-	-	-	-	-
DRYOMARG	4	3	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-
ECHILOBA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ELYMREPE	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
ELYMVIRG	-	1	1	-	1	-	-	-	-	1	-	-	-	-	1	-	-	-
EPIFVIRG	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
EPILCILI	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
EPILCOLO	4	5	1	-	-	1	1	1	-	1	-	2	3	1	-	2	3	1
EPILLEPT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
EPILPARV	-	2	1	-	1	-	-	-	-	1	-	1	-	-	-	-	-	-
EPIPHELL	.	4	1	-	-	-	1	-	-	-	1	2	2	-	2	-	2	1
EQUIARVE	-	2	2	2	1	-	-	-	-	-	1	2	3	1	6	3	3	1
EQUIHYEM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
EQUILAEV	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
EQUISCIR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ERIGANNU	2	1	1	-	-	-	-	-	-	-	-	1	1	-	-	1	1	-
ERIGPHIL	6	-	-	1	-	-	-	-	-	-	1	1	3	-	2	-	-	1
ERIGSTRI	-	-	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-
ERIG__SP	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
ERYTAMER	.	5	-	1	-	-	1	1	-	-	-	-	5	1	-	-	-	-
EUPAMACU	-	3	1	-	-	1	-	1	-	-	-	1	2	-	2	3	3	1
EUPAPERF	1	-	1	-	-	-	-	-	-	-	-	-	1	-	1	1	2	-
EUPARUGO	2	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-
EUTHGRAM	-	1	-	-	-	-	1	-	-	-	-	-	-	-	4	-	-	-
FAGUGRAN	7	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-
FESTARUN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
FESTPRAT	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
FESTRUBR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
FESTSUBV	4	-	-	-	-	-	-	1	-	-	1	-	-	-	1	-	-	-
FRAGVESC	4	2	-	-	-	-	1	-	-	1	-	1	3	-	-	-	-	-
FRAGVIRG	-	4	-	-	-	-	-	-	-	1	1	2	3	-	6	-	-	-
FRAXAMER	.	2	-	-	-	-	5	1	-	-	-	-	1	1	2	-	-	-
FRAXNIGR	4	7	3	2	2	-	-	-	-	1	-	1	2	-	3	-	1	-
FRAXPENN	4	4	-	-	-	1	-	-	-	1	-	4	2	-	5	-	-	1
GALESPEC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALETETR	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALIAPAR	4	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
GALIASPR	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALICIRC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALILANC	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GALIOBTU	-	1	1	-	-	-	-	-	-	1	-	-	3	1	3	3	3	1
GALIPALU	-	-	2	1	2	-	-	-	-	1	-	-	-	-	-	-	-	-
GALITRIF	.	5	-	2	-	1	2	1	-	5	1	2	3	-	3	-	-	1
GALI_SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GENTANDR	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
GERAMACU	1	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-
GERAROBE	8	5	2	3	2	-	1	1	-	1	-	5	2	-	-	-	-	-
GEUMALEP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GEUMCANA	1	3	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	1
GEUMLACI	1	3	1	1	1	-	-	-	-	-	-	-	3	-	-	1	-	-
GEUMRIVA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GEUMURBA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GEUM_SP	-	2	1	-	-	-	-	-	-	-	-	1	3	-	1	-	1	1
GLYCSTRI	3	8	4	3	3	1	-	-	-	2	1	2	3	1	2	3	3	1
GYMNDRYO	2	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
HACKVIRG	3	-	-	-	-	-	1	1	-	-	-	-	1	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
HEPAACUT	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
HIERAURA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HIERCAES	6	2	-	-	-	-	-	-	-	2	2	3	4	-	4	-	-	-
HYDRVIRG	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HYPEPERF	-	-	-	-	-	-	-	-	-	-	-	-	3	-	5	-	1	-
HYSTPATU	1	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-
IMPACAPE	6	1	4	2	3	1	-	-	1	8	3	8	3	1	-	3	3	1
INULHELI	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
IRISVERS	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IRIS__SP	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-
JUNCTENU	1	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
LACTCANA	1	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-
LACTSERR	2	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-
LACT__SP	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
LAPOCANA	1	2	2	-	1	-	-	-	-	-	-	-	-	-	-	2	3	-
LEERORYZ	-	-	1	-	-	-	-	-	-	-	-	-	2	1	-	3	3	-
LEERVIRG	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LEONCARD	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
LIPALOES	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LOBEINFL	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LOBE__SP	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
LONICANA	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LONIDIOI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LONIHIRS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LYCOAMER	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
LYCOANNO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LYCODEND	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LYCOOBOB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LYCOTRIS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
LYCOUNIF	-	2	2	-	1	-	-	-	-	2	-	2	2	1	1	1	2	-
LYSICILI	-	1	1	-	-	-	-	-	-	-	-	-	2	-	3	-	1	-
LYSINUMM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
LYSITERR	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
MAIACANA	.	2	-	-	-	-	3	-	-	1	1	2	2	-	1	-	-	-
MAIARACE	8	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
MAIASTEL	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MATTSTRU	-	1	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	-
MEDILUPU	1	1	-	-	-	-	-	-	-	-	-	-	3	-	4	-	-	-
MELIALBA	1	-	-	-	-	-	-	-	-	-	-	-	1	-	3	-	-	-
MELIOFFI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
MENICANA	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
MENTARVE	-	1	1	-	-	-	-	-	-	-	-	1	1	1	1	1	2	-
MILIEFFU	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MITCREPE	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
MITEDIPH	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MONAFIST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MONOHYPO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MONOUNIF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MUHLFRON	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
MUHLMEXI	-	-	-	-	-	-	-	-	-	-	-	-	4	-	1	-	-	-
NEPECATA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ONOCSENS	1	6	1	1	1	1	-	-	-	-	-	2	3	-	3	2	1	-
ONOPACAN	3	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
ORYZASPE	7	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
OSMOCLAY	6	1	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
OSMUCLAY	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OSMUREGA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OSTRVIRG	7	-	-	-	-	-	2	-	-	1	-	-	2	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
OXALSTRI	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
OXAL__SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PANAQUIN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PANIACUM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
PANICAPI	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PANI__SP	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
PARTINSE	3	5	1	2	-	-	-	-	-	3	1	2	3	1	4	3	3	1
PHALARUN	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-
PHEGCONN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PHLEPRAT	-	1	-	-	-	-	-	-	-	-	-	-	2	-	2	-	-	-
PHLO__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PHRYLEPT	4	-	-	-	-	-	1	-	-	-	-	-	3	-	1	-	-	-
PICEGLAU	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
PILEPUMI	4	2	2	-	1	-	-	-	-	1	-	2	3	1	2	1	3	1
PINUSTRO	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PLANLANC	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-
PLANMAJO	-	1	-	-	-	-	-	-	-	-	-	-	4	-	1	-	-	-
PLANRUGE	1	1	-	-	-	-	-	-	-	-	-	-	4	-	2	-	-	-
POA_ALSO	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
POA_COMP	3	-	1	-	-	-	-	-	-	-	-	-	3	-	6	1	1	-
POA_PALU	2	1	1	1	-	-	-	-	-	-	-	-	3	1	2	3	3	1
POA_PRAT	4	1	1	-	-	-	1	-	-	-	-	2	4	-	6	-	3	1
POA_SALT	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POA___SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PODOPELT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POLYACRO	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POLYPAUC	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
POLYPERS	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-
POLYPUBE	6	1	-	-	-	-	3	1	-	-	-	-	1	1	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
POPUBALS	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
POPUGRAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POPUTREM	-	1	-	-	-	-	-	-	-	-	-	-	1	-	5	-	-	-
POTENORV	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
POTERECT	-	-	-	-	-	-	-	-	-	-	-	-	2	-	5	-	-	-
PREN__SP	4	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
PRUNSERO	7	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-
PRUNVIRG	8	4	-	1	-	-	1	1	-	1	-	1	3	-	5	-	-	-
PRUNVULG	-	1	1	-	-	-	-	-	-	-	-	-	3	-	4	-	1	-
PTERAQUI	5	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
PYROELLI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUERALBA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUERMACR	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
QUERRUBR	5	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-
QUER__SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RANUABOR	5	3	-	-	-	1	1	1	-	-	-	3	2	-	-	-	-	1
RANUACRI	3	2	1	1	-	-	-	-	-	-	-	2	3	1	5	-	2	1
RANUHICA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RANURECU	2	2	1	1	1	1	-	-	-	1	1	-	2	-	-	-	-	1
RHAMALNI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHAMCATH	9	5	2	1	2	-	2	-	-	-	-	1	2	-	5	-	-	-
RHUSRADI	4	1	1	-	-	-	-	-	-	-	-	1	2	-	-	-	1	-
RHUSTYPH	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
RIBEAMER	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-
RIBECYNO	4	-	1	-	-	-	-	-	-	-	-	2	1	-	1	-	2	-
RIBEGLAN	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIBELACU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIBERUBR	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
RIBETRIS	2	6	1	1	-	-	-	-	-	2	-	-	-	-	-	-	3	1

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
RIBE_827	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ROBIPSEU	2	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
ROSABLAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ROSAPALU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
RUBUALLE	3	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
RUBUIDAE	9	7	-	2	-	-	1	1	-	3	4	6	5	-	4	-	-	-
RUBUOCCI	7	-	1	-	-	-	1	1	-	-	-	1	2	-	-	-	1	-
RUBUODOR	-	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
RUBUPUBE	1	6	-	1	-	-	-	-	-	5	2	8	1	1	3	-	1	1
RUBU_840	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
RUDBHIRT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RUMEORBI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
SALIBEBB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
SALIDISC	-	1	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-
SALIERIO	-	1	1	-	-	-	-	-	-	-	-	-	1	1	4	-	1	-
SALIPETI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
SAMBCANA	-	3	1	1	1	-	-	-	-	-	-	1	-	-	-	-	-	-
SAMBRAPU	7	1	-	-	-	-	1	1	-	-	-	2	2	-	-	-	-	-
SANGCANA	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
SANIMARI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SANITRIF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SANI__SP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCHIPURP	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCIRATRO	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-
SCUTLATE	-	1	1	-	-	-	-	-	-	-	-	1	1	1	-	-	3	-
SICYANGU	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
SILEVULG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
SISYMONT	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
SIUMSUAV	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
SMILHERB	3	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-
SMILHISP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SOLADULC	7	4	3	2	3	1	1	1	-	-	-	2	2	-	-	1	1	1
SOLIALTI	4	3	-	-	-	-	-	-	-	1	-	2	4	-	4	1	-	-
SOLICAES	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SOLICANA	.	4	3	-	2	-	2	-	-	3	1	3	5	-	3	-	1	-
SOLIFLEX	3	1	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-
SOLIGIGA	1	3	1	-	-	-	-	-	-	1	-	-	3	1	3	2	3	-
SOLIJUNC	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
SOLINEMO	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
SOLIRUGO	1	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
SONCARVE	2	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
SONCOLER	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-
SPHEINTE	2	1	1	-	-	-	-	-	-	2	2	1	3	-	-	1	2	-
STELLONG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
STREROSE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SYMPALBU	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
TARAOFFI	.	3	1	1	1	-	1	1	-	2	1	2	6	-	5	-	-	1
TAXUCANA	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
THALDIOI	6	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
THALPUBE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
THELNOVE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
THELPALU	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
THUJOCCI	4	2	1	-	-	-	-	-	-	-	-	1	-	-	1	-	1	-
TIARCORD	5	9	-	1	-	1	-	-	-	7	3	7	3	-	-	-	1	-
TILIAMER	.	5	1	-	1	-	3	-	-	-	-	2	-	-	1	-	1	-
TRAGDUBI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
TRIEBORE	4	2	-	-	-	-	-	-	-	2	-	2	-	-	-	-	-	-
TRIFREPE	2	-	-	-	-	-	1	-	-	-	-	-	3	-	1	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
TRILEREC	7	1	-	-	-	-	-	-	-	-	-	3	1	-	-	-	-	-
TRILGRAN	.	1	-	-	-	-	4	-	-	-	-	1	4	-	-	-	-	-
TRIOAURA	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TSUGCANA	5	1	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-
TUSSFARF	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-
TYPHLATI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ULMUAMER	4	7	3	1	2	-	-	-	-	1	-	1	2	-	2	-	2	-
UNKN_751	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UNKN_791	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UNKN_822	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
URTIDIGR	2	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-
URTIDIOI	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
UVULGRAN	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VACCANGU	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VERBHAST	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
VERBTHAP	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
VERBURTI	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
VEROOFFI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VEROSERP	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
VIBUACER	4	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
VIBULENT	2	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
VIBUOPUL	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIBUTRIL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
VICICRAC	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-
VIOLAFFI	-	1	-	-	-	-	-	-	-	1	-	-	3	-	4	-	2	1
VIOLBLAN	1	2	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-
VIOLCANA	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
VIOLCUCU	-	2	1	-	1	-	-	-	-	1	-	-	1	-	-	1	1	-
VIOLLABR	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-

Appendix 7. Distribution of species by microhabitat: open canopy.

SPECIES	dFLR	mFLR	wFLR	mDEP	wDEP	SEEP	MOUN	dPIT	wPIT	LOG	STMP	RMAT	LANE	DITCH	RFLD	RMA	RME	RT
VIOLPUBE	8	2	-	-	-	-	2	-	-	-	-	-	1	-	-	-	-	-
VIOLROST	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIOLSORO	1	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-
VIOL_788	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
VIOL__SP	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-
VITIRIPA	7	2	1	-	-	-	-	-	-	-	-	1	3	-	5	1	1	-
WALDFRAG	4	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-

APPENDIX 8

ENVIRONMENTAL DATA SUMMARY BY QUADRAT (I)

Legend

Column Heading	Description	Unit/Label
PA#	patch number (label)	numeric label
Q#	quadrat number (label)	numeric label
# SPP	# species recorded in quadrat	number
# MH	# microhabitats recorded in quadrat	number
SPM	soil parent material class:	
	glacio-fluvial parent material	1
	calcareous till parent material	2
	lacustrine parent material	3
	calcareous outwash parent material	4
SO	soil order class:	
	brunisol	1
	gleyed brunisol	2
	luvisol	3
	gleyed luvisol	4
	gleysol	5
MOIS	soil moisture class	
	seasonally wet depressions present	1
	seasonally moist depressions present	2
	all depression seasonally dry	3
SOM	% soil organic matter	percentage
pH	soil pH	value
CALC	available calcium	cmol/kg
Ca:Mg	calcium:magnesium ratio	value
K:Mg	potassium:magnesium ratio	value
OMH	open microhabitat class	Y (yes)
		N (no)
SEEP	seep	Y (yes)
		N (no)
DIST	disturbance class:	
	regenerating field	F
	canopy gap	G
	trail/lane/access road	T
	no disturbance features present	N
PA	patch area	hectares
FC	% forest cover in 5km x 5km square centered on quadrat	percentage
PI	patch isolation: mean distance to nearest 8 woodlots, measured in 45 degree arcs	metres

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
1	1	57	2	4	3	3	3.1	6.2	2.1	0.8	0.5	Y	N	F	183	49	228
1	2	53	2	4	3	3	3.9	6.7	2.4	1.2	0.9	N	N	F	183	49	228
1	3	44	4	4	3	3	7.8	7.1	7.3	14.3	5.9	Y	N	G	183	49	228
1	4	55	2	4	3	3	6.4	7.0	5.3	1.5	0.5	Y	N	G	183	49	228
1	5	32	1	4	3	3	6.6	7.2	5.9	5.7	1.9	N	N	N	183	49	228
1	6	38	3	4	3	3	6.1	7.3	7.0	2.7	1.0	N	N	N	183	49	228
1	7	41	1	4	3	3	7.4	7.2	6.7	1.9	0.8	N	N	N	183	49	228
1	8	44	3	4	3	3	10.3	7.5	14.9	2.4	0.4	N	N	N	183	49	228
2	9	63	3	2	2	2	14.5	7.5	21.8	2.5	0.3	N	N	N	53	41	50
2	10	58	4	2	2	1	19.6	7.4	12.4	2.4	0.5	N	N	N	53	41	50
2	11	56	4	2	2	2	11.0	7.7	19.9	3.0	0.4	N	N	N	53	41	50
2	12	59	4	2	2	2	14.0	7.8	18.0	2.7	0.4	N	N	N	53	41	50
2	13	58	4	2	2	2	15.8	7.8	17.0	3.0	0.4	N	N	N	53	41	50
2	14	62	4	2	2	2	12.8	7.5	19.1	2.1	0.3	N	N	N	53	41	50
2	15	37	2	2	2	3	12.0	7.4	11.3	3.1	0.8	N	N	N	53	41	50
2	16	57	4	2	2	1	16.5	7.5	19.0	1.1	0.2	N	N	N	53	41	50
3	17	42	4	4	3	3	8.4	5.6	2.0	2.0	1.1	N	N	T	42	43	415
3	18	51	7	4	3	3	10.5	5.5	1.4	0.4	0.3	Y	N	TG	42	43	415
3	19	49	3	4	4	1	9.4	5.9	2.2	4.3	2.7	Y	Y	G	42	43	415
3	20	36	4	4	3	1	10.8	5.7	1.1	0.3	0.2	N	N	N	42	43	415
3	21	47	3	4	3	1	8.6	5.7	3.1	6.0	2.1	N	N	N	42	43	415
3	22	56	4	4	3	3	8.1	5.9	2.4	0.4	0.2	Y	N	TG	42	43	415
3	23	35	3	4	4	1	19.8	6.7	13.7	0.8	0.1	N	Y	N	42	43	415
3	24	30	3	4	4	1	19.1	6.9	0.2	0.0	0.1	N	N	N	42	43	415
4	25	107	3	2	2	2	15.4	-	-	-	-	Y	N	T	78	30	450
4	26	113	4	2	2	2	15.5	-	-	-	-	Y	N	T	78	30	450
4	27	49	2	2	2	2	13.0	-	-	-	-	N	N	N	78	30	450

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
4	28	59	2	2	2	2	16.6	-	-	-	-	N	N	N	78	30	450
4	29	37	4	2	2	2	14.3	-	-	-	-	N	N	N	78	30	450
4	30	86	4	2	2	1	18.0	-	-	-	-	Y	N	G	78	30	450
4	31	76	4	2	2	1	17.6	-	-	-	-	Y	N	G	78	30	450
4	32	72	7	2	2	2	20.8	-	-	-	-	Y	N	N	78	30	450
5	33	52	4	2	1	3	10.9	7.6	16.4	3.2	-	Y	N	G	98	41	356
5	34	40	4	2	1	3	11.3	7.8	18.6	2.3	0.4	N	N	N	98	41	356
5	35	45	3	2	1	3	11.8	7.8	19.8	3.2	0.9	N	N	N	98	41	356
5	36	39	2	2	1	3	10.3	7.8	15.3	5.0	1.5	N	N	N	98	41	356
5	37	29	1	2	1	3	7.7	7.6	18.3	2.1	0.6	N	N	N	98	41	356
5	38	47	1	2	1	3	12.9	7.5	15.4	4.3	0.9	N	N	N	98	41	356
5	39	31	1	2	1	3	8.5	7.9	20.2	2.6	0.6	N	N	N	98	41	356
5	40	38	3	2	1	3	10.3	7.8	19.9	2.3	0.7	N	N	N	98	41	356
6	41	25	2	2	1	3	9.5	-	-	-	-	N	N	T	12	30	487
6	42	50	5	2	2	2	12.7	-	-	-	-	N	N	N	12	30	487
6	43	56	5	2	2	2	14.0	-	-	-	-	Y	N	G	12	30	487
6	44	58	3	2	2	2	14.0	-	-	-	-	N	N	N	12	30	487
6	45	53	3	2	2	2	11.0	-	-	-	-	N	N	N	12	30	487
6	46	44	3	2	1	3	11.3	-	-	-	-	N	N	N	12	30	487
6	47	64	4	2	2	2	13.9	-	-	-	-	N	N	N	12	30	487
6	48	66	3	2	2	2	12.1	-	-	-	-	N	N	N	12	30	487
7	49	48	3	2	1	3	7.4	7.2	7.1	2.8	1.1	N	N	N	68	55	300
7	50	59	2	2	1	3	5.3	7.0	4.7	1.5	0.7	Y	N	G	68	55	300
7	51	70	4	2	1	3	6.7	7.3	5.8	2.8	1.1	Y	N	G	68	55	300
7	52	33	1	2	1	3	6.4	7.2	5.7	1.3	0.5	N	N	N	68	55	300
7	53	46	3	2	1	3	5.6	7.2	8.0	3.9	1.3	N	N	N	68	55	300
7	54	67	1	2	1	3	6.0	7.0	6.0	1.9	0.8	N	N	G	68	55	300

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
7	55	50	2	2	1	3	6.1	6.8	4.4	1.2	0.6	N	N	N	68	55	300
7	56	48	5	2	1	3	7.4	7.1	6.1	2.0	0.7	Y	N	G	68	55	300
8	57	30	5	2	3	3	6.1	-	-	-	-	Y	N	G	101	31	431
8	58	16	3	2	3	3	6.8	-	-	-	-	N	N	N	101	31	431
8	59	14	3	2	3	3	8.2	-	-	-	-	N	N	N	101	31	431
8	60	21	2	2	3	3	8.9	-	-	-	-	N	N	N	101	31	431
8	61	17	2	2	3	3	7.3	5.9	4.5	33.9	12.0	N	N	N	101	31	431
8	62	21	1	2	3	3	6.1	5.8	3.0	37.0	23.7	N	N	N	101	31	431
8	63	21	3	2	3	3	6.6	5.9	2.6	64.0	42.6	N	N	N	101	31	431
8	64	25	2	2	3	3	9.1	5.9	4.0	43.0	27.1	N	N	N	101	31	431
9	65	33	1	2	1	3	5.9	6.6	4.6	221.3	62.8	N	N	N	267	45	337
9	66	34	2	2	1	3	5.6	6.1	2.4	116.7	88.9	N	N	N	267	45	337
9	67	35	1	2	1	3	5.9	5.6	1.3	128.8	180.9	N	N	N	267	45	337
9	68	37	1	2	1	3	6.2	6.2	4.1	78.8	29.2	N	N	N	267	45	337
9	69	46	1	2	1	3	5.0	6.2	0.7	0.5	0.3	N	N	N	267	45	337
9	70	34	1	2	1	3	5.1	6.5	5.1	70.6	44.8	N	N	N	267	45	337
9	71	37	1	2	1	3	8.1	5.6	1.1	0.6	0.8	N	N	N	267	45	337
9	72	42	2	2	1	3	6.4	5.9	0.3	0.2	0.5	N	N	G	267	45	337
10	73	53	1	4	3	3	8.3	6.5	6.1	117.9	16.4	Y	N	G	82	39	294
10	74	48	4	4	3	3	6.1	6.7	8.5	91.6	26.5	Y	N	G	82	39	294
10	75	28	3	4	3	3	8.2	6.4	4.4	216.0	33.9	N	N	G	82	39	294
10	76	35	4	4	3	3	10.2	6.8	9.5	77.3	11.8	N	N	N	82	39	294
10	77	34	3	4	3	3	8.0	6.6	7.6	73.8	12.5	N	N	N	82	39	294
10	78	60	1	4	3	3	8.4	6.3	4.1	1.4	0.2	N	N	N	82	39	294
10	79	47	4	4	3	3	8.9	7.4	12.8	88.7	18.3	Y	N	N	82	39	294
10	80	41	1	4	3	3	10.5	7.2	13.5	65.5	12.7	N	N	N	82	39	294
11	81	96	4	4	1	1	5.1	7.7	11.7	113.2	13.1	Y	N	TF	34	41	244

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
11	82	85	3	4	1	1	3.9	7.9	9.4	455.5	43.8	Y	N	TF	34	41	244
11	83	76	2	4	1	1	4.0	8.0	10.5	1021.6	77.1	Y	N	F	34	41	244
11	84	84	2	4	1	3	7.1	7.7	14.3	154.1	18.0	Y	N	F	34	41	244
11	85	79	1	4	2	2	10.1	7.8	18.6	62.4	6.5	Y	N	G	34	41	244
11	86	91	2	4	2	1	12.1	7.6	19.8	48.1	4.9	N	N	N	34	41	244
11	87	89	1	4	2	2	8.8	7.6	12.8	113.3	15.1	N	N	N	34	41	244
11	88	88	3	4	2	1	8.6	7.7	8.2	2.4	0.1	N	N	N	34	41	244
12	89	57	5	4	3	1	18.5	5.9	5.9	2.2	0.2	N	N	N	42	42	394
12	90	58	5	4	4	1	18.3	6.5	6.4	2.4	0.3	N	N	N	42	42	394
12	91	62	4	4	3	1	12.6	5.6	6.4	104.3	26.4	N	N	N	42	42	394
12	92	58	4	4	3	1	16.7	6.0	9.2	74.4	8.2	N	N	N	42	42	394
12	93	58	3	4	3	3	17.2	5.6	4.0	1.9	0.2	N	N	N	42	42	394
12	94	54	2	4	4	1	14.6	6.2	10.9	96.2	9.6	N	N	N	42	42	394
12	95	60	3	4	4	1	17.6	6.5	14.6	59.1	6.1	N	N	N	42	42	394
12	96	55	4	4	4	1	15.1	6.4	12.5	121.4	9.5	N	N	N	42	42	394
13	97	21	3	1	1	3	5.2	7.0	10.4	252.8	27.0	N	N	T	64	67	106
13	98	21	3	1	1	3	5.7	7.1	8.2	2.7	0.1	N	N	T	64	67	106
13	99	20	3	1	1	3	7.3	6.4	10.1	109.1	16.3	N	N	N	64	67	106
13	100	17	4	1	1	3	7.6	6.3	8.2	2.2	0.2	N	N	N	64	67	106
13	101	23	3	1	1	3	7.8	6.4	8.8	2.6	0.1	N	N	G	64	67	106
13	102	17	2	1	1	3	6.6	6.9	11.3	1100.4	33.6	N	N	N	64	67	106
13	103	18	3	1	1	3	8.2	6.0	2.5	1.4	0.2	N	N	N	64	67	106
13	104	21	5	1	1	3	4.7	6.8	38.6	70.7	0.5	Y	N	TG	64	67	106
14	105	16	2	2	3	3	8.7	6.9	10.5	203.1	26.1	N	N	T	10	38	647
14	106	28	4	2	3	3	7.7	6.8	8.0	194.4	35.6	N	N	T	10	38	647
14	107	24	3	2	3	3	7.7	6.6	5.6	1.4	0.3	N	N	N	10	38	647
14	108	13	1	2	3	3	8.5	6.5	9.5	116.0	20.0	N	N	N	10	38	647

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
14	109	15	1	2	3	3	10.8	6.6	8.6	838.2	160.3	N	N	N	10	38	647
14	110	14	3	2	3	3	11.6	7.0	13.2	127.8	16.4	N	N	N	10	38	647
14	111	19	1	2	3	3	8.6	6.6	8.8	286.5	60.1	N	N	N	10	38	647
14	112	16	3	2	3	3	11.7	6.5	10.4	201.9	36.2	N	N	N	10	38	647
15	113	30	4	1	1	3	5.6	5.5	1.8	178.9	158.5	N	N	N	325	61	332
15	114	29	3	1	1	3	4.5	5.1	0.6	0.2	0.5	N	N	N	325	61	332
15	115	24	1	1	1	3	4.1	5.2	0.7	0.3	0.5	N	N	N	325	61	332
15	116	25	1	1	1	3	4.3	5.1	0.9	0.3	0.4	N	N	N	325	61	332
15	117	23	3	1	1	3	3.9	5.3	0.8	1.6	0.8	N	N	N	325	61	332
15	118	26	1	1	1	3	4.0	5.2	0.7	0.3	0.6	N	N	N	325	61	332
15	119	30	2	1	1	3	4.0	5.3	0.1	0.2	0.6	N	N	N	325	61	332
15	120	25	2	1	1	3	4.5	5.1	0.1	0.1	0.2	N	N	N	325	61	332
16	121	43	4	2	4	2	45.9	6.8	45.9	120.7	4.6	Y	N	G	547	46	422
16	122	39	4	2	4	2	23.1	6.8	26.8	123.9	5.1	N	N	N	547	46	422
16	123	26	4	2	4	2	25.0	7.0	27.2	330.8	10.3	Y	N	G	547	46	422
16	124	39	4	2	4	2	20.7	5.6	13.7	102.1	6.3	N	N	N	547	46	422
16	125	40	5	2	4	2	33.7	7.0	33.2	129.1	4.3	Y	N	G	547	46	422
16	126	39	2	2	4	2	36.8	6.4	33.0	94.4	4.9	N	N	N	547	46	422
16	127	40	4	2	4	2	28.1	7.3	25.1	152.3	4.7	N	N	G	547	46	422
16	128	38	4	2	4	2	13.6	6.6	15.7	58.8	3.1	N	N	N	547	46	422
17	129	14	1	2	3	3	7.3	6.0	5.3	3.5	0.9	N	N	N	101	30	1378
17	130	28	6	2	3	3	6.7	6.0	3.5	1.2	0.4	N	N	N	101	30	1378
17	131	15	2	2	3	3	6.8	7.0	8.1	2.4	0.2	N	N	N	101	30	1378
17	132	20	2	2	3	3	7.3	6.5	6.2	100.8	21.4	N	N	N	101	30	1378
17	133	58	2	2	3	3	7.3	6.4	0.7	0.5	0.4	Y	N	TG	101	30	1378
17	134	63	1	2	3	3	7.6	6.1	4.6	149.6	40.8	Y	N	TG	101	30	1378
17	135	32	2	2	3	3	5.7	6.0	3.7	60.4	16.9	Y	N	G	101	30	1378

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
17	136	57	3	2	3	3	6.4	6.8	3.2	1.5	0.2	Y	N	G	101	30	1378
18	137	32	1	1	1	3	6.1	5.6	1.4	65.9	60.9	N	N	N	94	52	291
18	138	21	4	1	1	3	5.7	5.6	1.0	0.3	0.3	N	N	T	94	52	291
18	139	22	2	1	1	3	5.3	5.3	0.8	0.3	0.4	N	N	G	94	52	291
18	140	22	1	1	1	3	4.9	5.7	3.4	83.4	23.2	N	N	N	94	52	291
18	141	29	1	1	1	3	6.2	5.3	0.6	0.1	0.4	N	N	N	94	52	291
18	142	18	3	1	1	3	6.5	6.0	6.0	65.0	16.7	N	N	N	94	52	291
18	143	30	2	1	1	3	5.3	5.6	1.3	60.6	65.3	N	N	t	94	52	291
18	144	27	1	1	1	3	5.2	5.4	0.9	0.3	0.3	N	N	N	94	52	291
19	145	57	1	2	3	3	12.1	6.6	5.5	1.5	0.3	N	N	N	37	28	663
19	146	41	3	2	3	3	8.4	6.0	6.6	64.0	13.4	N	N	N	37	28	663
19	147	59	2	2	3	3	11.0	6.4	9.3	47.6	5.6	N	N	N	37	28	663
19	148	40	4	2	3	3	8.8	6.1	2.3	0.8	0.3	Y	N	G	37	28	663
19	149	76	8	2	4	1	14.0	6.8	8.1	130.6	14.2	N	Y	N	37	28	663
19	150	58	5	2	4	2	17.5	6.9	12.3	79.4	8.6	Y	Y	N	37	28	663
19	151	58	4	2	4	1	40.9	6.7	27.5	86.3	7.0	Y	N	N	37	28	663
19	152	66	3	2	4	2	19.0	6.7	11.5	101.7	10.4	Y	N	G	37	28	663
20	153	41	3	2	5	1	42.6	7.1	52.6	21.8	1.8	Y	N	G	60	26	644
20	154	28	2	2	5	2	13.2	7.7	19.7	42.6	4.1	N	N	N	60	26	644
20	155	55	10	2	5	2	29.9	7.3	29.2	34.6	3.2	Y	N	G	60	26	644
20	156	40	4	2	5	1	69.2	6.7	50.7	11.4	1.7	N	N	N	60	26	644
20	157	32	3	2	5	2	13.5	7.7	21.5	1.2	0.1	N	N	G	60	26	644
20	158	25	3	2	5	2	16.8	7.6	24.8	0.8	0.1	N	N	N	60	26	644
20	159	37	4	2	5	1	74.0	6.7	50.7	11.3	1.3	N	N	N	60	26	644
20	160	14	4	2	5	1	68.7	6.7	50.1	14.7	1.7	N	N	N	60	26	644
21	161	27	4	2	3	2	11.4	6.5	6.2	3.0	0.8	N	N	N	12	31	653
21	162	27	4	2	3	3	13.6	7.0	13.2	2.0	0.3	Y	N	G	12	31	653

Appendix 8. Environmental data summary by quadrat (I).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
21	163	30	4	2	3	3	11.1	6.7	8.1	3.2	0.6	N	N	N	12	31	653
21	164	50	6	2	4	1	12.8	6.9	12.7	1.5	0.3	Y	N	G	12	31	653
21	165	50	6	2	4	1	19.9	6.9	25.0	1.4	0.1	Y	N	G	12	31	653
21	166	32	2	2	3	1	12.8	6.8	13.2	2.1	0.2	N	N	N	12	31	653
21	167	34	4	2	4	1	9.6	7.3	13.7	3.3	0.4	N	N	N	12	31	653
21	168	51	5	2	4	1	15.2	6.9	12.0	2.9	0.6	N	N	N	12	31	653
22	169	42	4	1	1	3	5.9	6.5	11.0	2.4	0.4	N	N	N	125	65	41
22	170	36	1	1	1	3	4.8	5.5	1.0	0.8	0.9	N	N	N	125	65	41
22	171	40	3	1	1	3	5.6	6.5	7.4	5.8	1.8	N	N	N	125	65	41
22	172	36	4	1	1	3	6.0	6.7	7.2	4.7	1.3	N	N	N	125	65	41
22	173	37	1	1	1	3	5.0	6.4	8.6	4.2	0.9	N	N	N	125	65	41
22	174	44	2	1	1	3	4.5	5.9	1.8	1.4	1.4	Y	N	G	125	65	41
22	175	35	3	1	1	3	5.1	5.5	1.5	1.0	1.0	N	N	N	125	65	41
22	176	45	2	1	1	3	4.3	5.5	0.7	1.3	2.8	Y	N	G	125	65	41
23	177	35	5	1	1	3	4.9	7.0	9.8	1.7	0.0	N	N	T	113	68	113
23	178	26	4	1	1	3	5.1	6.8	7.4	14.3	1.9	N	N	T	113	68	113
23	179	25	3	1	1	3	5.9	5.8	3.6	2.8	0.6	N	N	N	113	68	113
23	180	34	3	1	1	3	5.0	6.0	3.1	3.0	0.8	Y	N	G	113	68	113
23	181	32	3	1	1	3	6.2	6.3	4.0	3.9	1.0	N	N	N	113	68	113
23	182	18	3	1	1	3	6.0	6.1	9.6	3.8	0.4	N	N	N	113	68	113
23	183	26	3	1	1	3	6.0	6.4	6.9	13.5	1.9	N	N	N	113	68	113
23	184	30	1	1	1	3	5.6	5.8	1.8	1.9	0.5	N	N	N	113	68	113
24	185	24	2	3	4	2	75.5	6.2	54.4	0.4	0.1	N	N	N	154	34	131
24	186	58	4	3	4	2	76.7	7.0	55.5	0.6	0.0	N	N	N	154	34	131
24	187	61	4	3	4	2	62.7	7.2	62.1	0.6	0.1	N	N	N	154	34	131
24	188	44	4	3	4	2	69.4	7.0	60.6	0.7	0.0	Y	N	G	154	34	131
24	189	59	4	3	4	2	62.9	7.2	56.2	0.6	0.0	N	N	N	154	34	131

Appendix 8. Environmental data summary by quadrat (1).

PA#	Q#	#SPP	#MH	SPM	SO	MOIS	SOM	pH	CALC	Ca:Mg	K:Mg	OMH	SEEP	DIST	PA	FC	PI
24	190	44	7	3	4	2	74.9	6.8	69.8	0.4	0.0	Y	N	G	154	34	131
24	191	51	5	3	4	2	64.1	7.0	59.2	0.6	0.0	Y	N	G	154	34	131
24	192	47	4	3	4	2	67.0	7.0	50.2	0.7	0.1	N	N	N	154	34	131

APPENDIX 9

ENVIRONMENTAL DATA SUMMARY BY QUADRAT (II)

Legend

Column Heading	Description	Unit/Label
PA#	patch number (label)	numeric label
Q#	quadrat number (label)	numeric label
#SPP	# species recorded in quadrat	number
#GEN	# genera recorded in quadrat	number
#FAM	# families recorded in quadrat	number
#ANN	# annual species recorded in quadrat	number
#BIE	# biennial species recorded in quadrat	number
#PER	# perennial species recorded in quadrat	number
#NAT	# native species recorded in quadrat	number
#ALI	# alien species recorded in quadrat	number
#F	# species with affinity for forest habitats	number
#FO	# species with affinity for forest + open habitats	number
#OF	# species with affinity for open + forest habitats	number
#O	# species with affinity for open habittats	number
CT	cover type class:	
	red/white oak (no sugar maple)	1
	red/white oak + sugar maple	2
	sugar maple (no red/white oak: no wet-mesic, wet species)	3
	sugar maple + wet-mesic or wet species	4
	wet-mesic or wet species (no sugar maple)	5
#LTS	# live tree stems (all diameter size classes)	number
#0-4	# live tree stems 0-4 cm dbh	number
#4-10	# live tree stems 4-10 cm dbh	number
#10-30	# live tree stems 10-30 cm dbh	number
#>30	# live tree stems >30 cm dbh	number

NOTE: species attributes may not sum to species total since unclassified species not included in summary.

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
1	1	57	49	30	0	3	54	48	9	2	6	29	8	1	16	12	4	0	0
1	2	53	45	31	0	2	51	45	8	2	10	24	4	2	108	100	3	5	0
1	3	44	37	26	0	0	44	41	3	13	8	15	0	2	32	22	3	5	2
1	4	55	41	30	1	0	54	51	4	10	13	18	0	2	56	51	2	3	0
1	5	32	26	22	0	0	32	28	4	7	6	9	2	2	43	27	10	5	1
1	6	38	32	25	0	0	38	37	1	6	10	10	1	3	29	15	7	7	0
1	7	41	33	26	0	0	41	38	3	7	12	10	1	3	57	39	14	3	1
1	8	44	34	25	0	0	44	41	3	11	11	12	1	3	38	27	2	3	6
2	9	63	47	31	0	2	61	58	5	16	24	8	3	4	80	60	13	7	0
2	10	58	45	29	0	1	57	53	5	16	19	9	2	4	108	97	8	3	0
2	11	56	44	28	0	1	55	50	6	15	19	7	4	4	109	78	21	10	0
2	12	59	41	28	0	2	57	53	6	13	21	8	3	4	84	57	20	7	0
2	13	58	47	30	1	1	56	53	5	16	22	9	1	3	89	70	13	6	0
2	14	62	47	31	0	2	60	54	8	18	22	12	3	4	94	74	13	7	0
2	15	37	30	24	0	0	37	34	3	11	10	6	1	3	78	68	4	6	0
2	16	57	42	29	0	1	56	52	4	16	21	7	2	4	100	72	26	2	0
3	17	42	31	24	1	0	41	39	2	9	18	9	0	3	168	160	2	5	1
3	18	51	37	27	1	1	49	48	3	13	16	11	2	3	35	32	1	0	2
3	19	49	34	28	1	0	48	47	2	10	20	11	0	4	55	52	3	0	0
3	20	36	29	23	1	0	35	34	2	11	13	4	0	3	101	97	1	3	0
3	21	47	34	27	1	1	45	43	4	17	12	9	0	3	95	91	1	3	0
3	22	56	39	26	1	2	53	52	4	11	18	18	4	3	137	135	0	2	0
3	23	35	29	20	2	1	31	32	2	12	13	6	1	4	9	6	1	1	1
3	24	30	27	21	1	1	28	29	1	12	11	4	0	3	24	13	6	5	0
4	25	107	77	39	4	4	99	84	22	11	24	44	16	3	75	59	13	2	1
4	26	113	79	42	5	6	101	84	27	8	24	51	18	4	34	28	3	3	0
4	27	49	37	26	0	2	47	41	8	9	17	14	2	4	90	65	20	4	1
4	28	59	45	29	1	0	58	53	6	15	21	11	3	4	79	62	8	8	1
4	29	37	32	23	1	0	36	34	3	9	12	7	1	3	115	96	16	2	1
4	30	86	61	34	4	2	80	75	10	12	24	33	8	4	48	42	6	0	0

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
4	31	76	54	31	4	4	67	64	9	11	22	23	8	4	54	38	14	2	0
4	32	72	50	28	3	1	69	65	7	13	23	24	4	4	78	51	21	6	0
5	33	52	38	22	1	1	50	45	7	14	11	15	4	3	63	35	17	11	0
5	34	40	32	19	1	0	38	38	2	16	9	5	0	3	53	21	25	6	1
5	35	45	36	22	0	0	45	39	6	12	12	11	2	3	56	23	19	14	0
5	36	39	31	21	0	1	38	35	4	14	9	6	1	3	53	25	20	8	0
5	37	29	25	15	1	0	28	27	2	11	7	5	0	3	46	11	26	9	0
5	38	47	37	22	1	2	44	41	6	11	11	13	3	2	77	55	11	11	0
5	39	31	26	20	0	0	31	29	2	13	6	3	1	3	43	14	17	12	0
5	40	38	31	20	0	0	38	35	3	12	8	11	1	3	60	31	21	8	0
6	41	25	21	18	0	0	25	21	4	3	9	7	0	4	58	46	9	2	1
6	42	50	43	32	0	1	49	45	5	14	14	10	0	4	79	54	17	8	0
6	43	56	43	29	0	1	55	48	8	12	19	11	5	5	47	27	13	7	0
6	44	58	46	27	0	1	57	50	7	15	12	14	3	4	109	77	24	7	1
6	45	53	44	29	0	1	52	48	5	13	15	11	1	4	93	63	25	5	0
6	46	44	35	24	0	0	44	39	5	13	11	7	1	4	55	34	13	7	1
6	47	64	49	33	0	2	62	56	8	15	16	13	4	4	93	60	22	11	0
6	48	66	47	31	1	2	63	60	6	17	17	16	5	4	81	58	12	11	0
7	49	48	38	25	0	0	48	44	4	13	10	15	0	2	44	30	5	7	2
7	50	59	43	24	0	1	58	52	7	11	12	22	2	2	66	59	5	2	0
7	51	70	49	30	0	0	70	65	5	19	18	19	1	2	99	95	2	2	0
7	52	33	27	22	0	0	33	32	1	5	12	6	0	2	41	27	7	6	1
7	53	46	37	25	0	0	46	43	3	7	12	14	3	3	53	42	9	0	2
7	54	67	46	28	0	0	66	59	7	15	15	23	2	2	86	77	5	3	1
7	55	50	40	30	0	0	50	46	3	11	16	12	0	2	82	73	5	2	2
7	56	48	34	21	0	0	48	44	4	12	12	13	1	2	63	55	3	1	4
8	57	30	25	19	0	0	30	29	1	8	9	3	0	3	131	126	4	0	1
8	58	16	15	12	0	0	16	14	2	3	4	2	0	2	66	52	9	3	2
8	59	14	14	11	0	0	14	13	1	3	2	2	0	2	41	34	2	3	2
8	60	21	19	15	0	0	21	20	1	7	6	0	0	3	49	39	6	4	0

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
8	61	17	15	11	0	0	17	16	1	4	3	0	0	2	58	42	11	3	2
8	62	21	19	15	0	0	21	20	1	5	6	2	0	3	46	31	11	4	0
8	63	21	17	13	0	0	21	20	1	6	5	2	0	2	26	13	9	3	1
8	64	25	19	15	1	0	24	23	2	6	5	3	0	2	29	20	7	1	1
9	65	33	30	23	0	0	33	31	2	6	7	12	2	2	117	106	4	5	2
9	66	34	29	24	1	0	33	33	1	2	12	10	1	2	58	50	3	4	1
9	67	35	28	21	0	0	35	35	0	4	7	13	2	2	94	85	5	3	1
9	68	37	29	23	0	0	37	36	1	7	7	12	0	2	66	63	0	3	1
9	69	46	38	28	0	0	46	42	3	8	13	13	0	3	67	61	1	5	0
9	70	34	27	22	0	0	34	32	2	4	4	14	1	2	86	75	5	6	0
9	71	37	30	25	0	0	37	34	3	7	7	12	1	2	112	98	7	4	3
9	72	42	35	24	0	0	42	39	3	7	13	17	0	2	116	109	4	3	0
10	73	53	46	33	2	1	50	47	6	23	12	8	2	3	30	25	2	2	1
10	74	48	40	33	2	1	45	43	5	20	13	6	0	3	102	94	6	1	1
10	75	28	26	21	1	0	27	27	1	13	8	3	0	3	79	70	7	2	0
10	76	35	30	22	2	0	33	34	1	15	10	5	0	3	71	58	4	8	1
10	77	34	29	24	2	0	32	34	0	18	8	3	0	3	56	49	3	3	1
10	78	60	40	31	2	1	57	57	3	22	19	7	0	3	91	89	0	0	2
10	79	47	39	29	2	1	44	44	3	20	14	7	0	3	83	76	3	4	0
10	80	41	32	27	1	0	40	40	1	24	9	3	0	3	32	27	1	3	1
11	81	96	62	31	2	5	88	74	20	5	14	43	22	5	66	56	9	1	0
11	82	85	60	32	1	3	82	64	21	4	17	37	19	5	30	26	3	0	1
11	83	76	53	29	2	5	69	59	17	1	11	38	17	5	55	48	7	0	0
11	84	84	59	31	1	4	79	65	19	4	8	40	18	5	104	94	9	1	0
11	85	79	56	33	2	2	75	62	16	4	17	38	12	5	92	86	4	2	0
11	86	91	61	34	2	0	89	78	12	5	29	40	7	5	181	168	11	1	1
11	87	89	59	36	3	2	83	77	11	5	19	45	10	4	152	137	12	3	0
11	88	88	54	32	2	0	86	74	12	4	22	46	7	5	114	94	18	2	0
12	89	57	45	28	1	0	56	55	2	21	20	6	0	4	45	35	3	5	2
12	90	58	45	29	0	0	58	57	1	26	23	3	0	4	31	15	8	6	2

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
12	91	62	51	34	0	0	63	59	4	20	19	9	0	4	141	135	2	3	1
12	92	58	47	29	2	1	55	53	5	19	17	10	1	3	28	14	8	5	1
12	93	58	45	29	1	0	57	56	2	19	19	10	0	4	39	35	0	3	1
12	94	54	42	32	2	1	51	49	5	21	17	8	0	4	76	53	12	11	0
12	95	60	47	31	1	1	58	57	3	23	18	10	1	4	24	15	2	5	2
12	96	55	50	33	2	1	52	49	6	19	18	7	1	3	35	24	4	6	1
13	97	21	18	15	0	0	21	20	1	9	8	1	0	3	24	17	7	0	0
13	98	21	19	14	0	0	21	20	1	5	9	1	0	3	17	14	0	2	1
13	99	20	16	12	0	0	20	20	0	7	6	2	0	2	22	17	3	0	2
13	100	17	15	11	0	0	17	17	0	6	7	2	0	3	19	17	0	1	1
13	101	23	22	15	0	0	23	22	1	5	8	4	1	2	53	45	1	5	2
13	102	17	16	13	0	0	17	17	0	5	7	1	0	3	22	9	12	1	0
13	103	18	17	13	0	0	18	18	0	5	8	1	0	2	25	16	6	2	1
13	104	21	21	15	0	0	21	21	0	7	5	2	0	2	98	96	0	0	2
14	105	16	15	13	0	0	16	14	2	3	7	1	0	3	26	8	13	4	1
14	106	28	25	19	0	1	27	25	3	5	10	7	1	3	57	45	9	2	1
14	107	24	24	21	0	1	23	21	3	6	9	4	0	3	31	5	19	7	0
14	108	13	13	11	0	0	13	13	0	5	3	1	0	3	20	5	13	2	0
14	109	15	14	13	0	0	15	14	1	4	5	3	0	3	34	23	8	2	1
14	110	14	13	11	0	0	14	13	1	3	5	3	0	3	39	25	9	5	0
14	111	19	16	13	0	0	19	18	1	4	7	3	0	3	32	19	8	3	2
14	112	16	14	13	0	0	16	16	0	6	4	1	0	3	25	9	12	3	1
15	113	30	25	17	0	0	30	29	1	5	7	7	1	2	60	46	6	5	3
15	114	29	26	17	0	0	29	27	2	8	8	6	0	2	21	16	2	3	0
15	115	24	21	15	0	0	24	23	1	6	6	6	0	2	25	12	5	5	3
15	116	25	22	15	0	0	25	25	0	5	6	7	0	2	9	4	0	5	0
15	117	23	21	13	0	0	23	23	0	5	4	5	1	2	31	23	1	7	0
15	118	26	23	18	0	0	26	26	0	8	6	5	0	2	23	14	3	4	2
15	119	30	28	18	0	0	30	30	0	5	6	10	1	3	54	48	0	6	0
15	120	25	22	14	0	0	25	25	0	7	5	5	0	3	23	13	5	4	1

Appendix 9. Environmental data summary by quadrat (11).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
16	121	43	30	24	2	0	41	40	3	12	17	6	0	3	13	10	2	0	1
16	122	39	31	27	1	1	37	34	5	10	13	7	0	3	32	18	10	4	0
16	123	26	21	20	1	1	24	23	3	9	7	4	0	3	22	21	0	1	0
16	124	39	29	25	1	1	37	36	3	12	15	6	0	4	23	14	4	4	1
16	125	40	30	22	1	1	38	35	5	10	14	9	1	4	42	38	1	3	0
16	126	39	27	23	1	1	37	35	4	11	16	7	0	4	56	49	3	2	2
16	127	40	27	20	1	1	38	36	4	13	14	7	0	3	17	11	3	2	1
16	128	38	31	25	1	1	35	32	5	9	13	7	0	3	24	17	3	2	2
17	129	14	13	9	0	0	14	13	1	8	4	1	0	3	37	20	13	2	2
17	130	28	25	21	0	0	28	24	4	12	6	7	0	3	16	5	7	3	1
17	131	15	14	12	0	0	15	13	2	7	4	2	0	3	29	24	0	1	4
17	132	20	18	14	0	0	20	19	1	10	6	1	0	3	40	35	0	0	5
17	133	58	50	32	3	6	47	41	16	10	16	16	11	3	13	12	0	1	0
17	134	63	51	34	4	9	50	47	16	12	13	16	15	3	10	6	1	3	0
17	135	32	27	19	0	3	29	25	7	7	7	11	5	3	42	37	5	0	0
17	136	57	50	30	3	6	48	41	16	15	11	16	11	3	9	5	2	0	2
18	137	32	27	20	0	0	32	31	1	14	8	4	0	2	63	27	24	12	0
18	138	21	17	12	0	0	21	20	1	6	5	4	0	2	52	25	18	9	0
18	139	22	18	14	0	0	22	21	1	6	7	4	0	2	36	19	11	6	0
18	140	22	19	13	0	0	22	21	1	8	3	5	0	2	42	9	25	8	0
18	141	29	25	17	0	0	29	28	1	10	6	7	1	2	47	15	19	13	0
18	142	18	16	11	0	0	18	17	1	6	4	3	0	2	39	17	18	3	1
18	143	30	26	19	0	0	30	29	1	9	9	6	0	2	40	18	16	5	1
18	144	27	23	17	0	0	27	26	1	11	7	6	0	2	28	9	11	8	0
19	145	57	44	29	1	0	56	53	4	18	16	10	0	3	44	34	7	3	0
19	146	41	31	26	0	0	41	38	3	12	11	7	0	3	79	68	8	2	1
19	147	59	41	27	0	0	59	54	5	20	18	8	2	3	49	40	4	5	0
19	148	40	30	24	0	0	40	39	1	14	13	5	0	3	46	30	12	4	0
19	149	76	50	36	2	1	73	70	6	16	31	16	1	4	53	43	4	6	0
19	150	58	48	33	2	1	55	53	5	14	18	14	1	4	66	56	4	6	0

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
19	151	58	45	32	3	0	55	54	4	14	19	15	3	4	36	25	6	5	0
19	152	66	47	33	2	0	64	62	4	19	23	15	1	4	89	77	5	5	2
20	153	41	36	25	4	4	33	32	8	8	13	10	4	5	26	21	4	1	0
20	154	28	23	19	0	1	27	23	5	8	10	5	0	4	21	12	2	4	3
20	155	55	40	29	1	1	53	47	7	9	19	16	2	4	25	15	3	6	1
20	156	40	31	23	4	0	36	36	3	4	17	11	1	5	12	9	0	1	2
20	157	32	25	21	1	1	30	27	5	8	11	8	0	4	20	14	4	2	0
20	158	25	22	19	0	1	24	18	6	5	9	7	0	4	26	7	5	11	3
20	159	37	30	21	3	0	34	33	4	3	17	13	1	5	26	23	0	1	2
20	160	14	14	12	3	0	11	12	2	1	6	5	0	5	9	7	2	0	0
21	161	27	24	21	0	0	27	27	0	11	9	3	0	3	25	19	1	5	0
21	162	27	24	20	0	0	27	24	3	11	7	4	0	3	35	33	1	0	1
21	163	30	25	18	0	0	30	30	0	11	10	2	0	3	13	5	2	6	0
21	164	50	38	25	3	2	45	41	8	8	14	20	1	4	67	64	3	0	0
21	165	50	39	27	1	1	48	42	8	14	15	11	2	4	96	89	0	6	1
21	166	32	29	23	0	1	31	30	2	16	8	5	0	4	47	42	1	1	3
21	167	34	29	22	0	0	34	32	2	9	13	6	0	4	45	35	6	2	2
21	168	51	39	27	2	1	48	43	8	12	15	17	0	4	42	38	2	1	1
22	169	42	36	22	0	0	42	40	2	13	9	12	1	3	34	27	1	5	1
22	170	36	28	18	0	0	36	35	1	10	11	8	1	2	65	45	11	8	1
22	171	40	35	24	0	0	40	39	1	9	11	11	1	2	25	11	3	11	0
22	172	36	31	20	0	0	36	35	1	6	10	11	2	2	48	33	2	12	1
22	173	37	30	22	0	0	37	36	1	9	12	8	2	2	45	32	5	8	0
22	174	44	37	24	0	0	44	43	1	8	14	10	1	2	121	104	12	4	1
22	175	35	29	20	0	0	35	34	1	9	10	9	0	2	120	106	7	7	0
22	176	45	33	22	0	0	45	44	1	12	13	10	2	2	63	46	12	4	1
23	177	35	31	22	0	0	35	34	1	12	9	7	0	2	16	5	9	2	0
23	178	26	22	16	0	0	26	24	2	6	5	9	1	3	18	12	4	2	1
23	179	25	21	17	0	0	25	24	1	8	4	7	0	2	24	10	3	11	0
23	180	34	27	20	0	0	34	33	1	10	9	9	0	3	86	80	5	1	0

Appendix 9. Environmental data summary by quadrat (II).

PA#	Q#	#SPP	#GEN	#FAM	#ANN	#BIE	#PER	#NAT	#ALI	#F	#FO	#OF	#O	CT	#LTS	#0-4	#4-10	#10-30	#>30
23	181	32	26	21	0	0	32	31	1	8	9	8	0	2	32	10	13	8	1
23	182	18	17	12	0	0	18	18	0	6	3	4	0	3	49	45	0	3	1
23	183	26	21	15	0	0	26	25	1	9	6	6	0	2	23	15	2	5	1
23	184	30	27	20	0	0	30	29	1	10	8	5	0	2	31	25	1	3	2
24	185	24	17	16	0	1	23	21	3	6	8	2	0	3	54	39	10	4	1
24	186	58	40	25	1	2	55	50	8	14	14	14	3	4	65	43	17	4	1
24	187	61	46	30	1	1	59	54	6	13	19	17	0	4	103	95	3	3	2
24	188	44	30	20	1	1	42	37	6	11	9	16	2	5	17	15	2	0	0
24	189	59	41	30	1	1	57	51	7	13	15	16	1	4	143	129	6	7	1
24	190	44	31	25	1	1	42	36	7	8	13	10	1	4	51	27	20	4	0
24	191	51	40	28	1	1	49	44	6	11	17	12	0	4	92	85	3	1	3
24	192	47	35	27	1	1	45	40	6	11	13	10	1	4	47	39	3	4	1

APPENDIX 10

ENVIRONMENTAL DATA SUMMARY BY QUADRAT (III)

Legend

Column Heading	Description	Unit/Label
PA#	patch number (label)	numeric label
Q#	quadrat number (label)	numeric label
#SPP	# species recorded in quadrat	number
#TRE	# tree species recorded in quadrat	number
#SHR	# shrub species recorded in quadrat	number
#VIN	# vine species recorded in quadrat	number
#FRN	# fern species recorded in quadrat	number
#FA	# fern ally species recorded in quadrat	number
#GRA	# grass species recorded in quadrat	number
#HRB	# herb species recorded in quadrat	number
#INH	# herb species dispersed by animal ingestion	number
#ADH	# herb species dispersed by animal adhesion	number
#ANH	# herb species dispersed by ants	number
#WIH	# herb species dispersed by wind	number
#PDH	# herb species dispersed by prolonged dormancy	number
#MEH	# herb species dispersed by mechanical expulsion	number
#NFH	# herb species dispersed by propagules with no facilitating morphology	number
#MUH	# herb species dispersed by multiple modes	number
#VEH	# herb species dispersed by vegetative expansion	number

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
1	1	57	12	6	3	3	3	5	25	2	2	3	12	7	4	2	7	12
1	2	53	12	11	3	2	1	3	21	2	3	3	9	6	1	1	4	10
1	3	44	8	8	4	2	0	2	20	5	4	3	5	1	0	3	1	10
1	4	55	14	10	3	2	0	2	24	3	6	6	9	2	0	2	4	11
1	5	32	8	6	2	2	0	1	13	3	1	3	3	2	0	2	1	6
1	6	38	11	4	4	3	0	1	15	1	2	3	5	0	0	5	1	6
1	7	41	11	9	3	2	0	0	16	2	2	4	5	0	0	3	0	8
1	8	44	9	10	2	1	0	2	20	4	4	3	4	1	0	6	2	7
2	9	63	11	4	2	4	1	3	38	6	5	7	10	7	4	8	9	19
2	10	58	10	9	3	5	1	3	27	5	3	5	9	4	2	5	6	12
2	11	56	9	5	1	6	1	5	29	4	2	4	9	6	1	9	6	12
2	12	59	13	5	2	3	1	3	32	3	3	8	8	7	2	8	7	14
2	13	58	10	4	3	7	0	3	31	5	2	6	8	5	4	7	6	16
2	14	62	7	5	3	6	1	1	39	6	5	8	8	7	3	9	7	19
2	15	37	9	4	1	2	0	1	20	4	1	5	3	2	0	6	1	11
2	16	57	9	4	2	9	1	2	30	3	5	6	7	3	3	8	5	12
3	17	42	5	2	0	4	0	2	29	2	5	7	5	2	2	9	3	14
3	18	51	9	6	1	4	0	1	30	4	6	7	6	4	2	8	5	16
3	19	49	8	3	2	5	0	1	30	2	5	5	6	1	3	11	3	14
3	20	36	8	1	1	5	1	0	20	4	3	7	2	0	2	2	0	13
3	21	47	8	3	1	4	0	0	31	4	5	9	3	1	4	7	2	15
3	22	56	4	3	3	4	0	5	37	2	5	6	11	6	5	10	8	14
3	23	35	2	1	1	9	0	2	20	2	3	3	2	2	4	6	2	9
3	24	30	3	1	1	6	0	0	19	2	4	4	1	1	5	4	2	10
4	25	107	10	7	3	5	2	15	65	3	11	9	19	22	1	15	14	26
4	26	113	8	9	4	4	2	13	73	3	10	6	23	23	2	21	14	28
4	27	49	6	3	3	3	0	2	32	4	4	6	7	8	0	7	4	14
4	28	59	9	5	3	2	0	3	37	5	2	9	9	6	2	7	3	17
4	29	37	8	3	1	1	0	1	23	5	3	3	6	2	1	5	2	12

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
4	30	86	8	11	4	6	1	8	48	3	7	1	19	10	2	14	8	15
4	31	76	8	5	3	5	1	4	49	3	8	1	17	10	3	13	6	15
4	32	72	7	7	2	6	1	7	43	3	7	9	11	5	4	10	6	19
5	33	52	8	1	2	1	0	6	34	2	3	9	15	6	1	5	7	16
5	34	40	9	1	0	1	0	3	26	3	5	7	6	2	0	6	3	11
5	35	45	8	5	1	1	0	5	25	3	1	5	8	3	1	7	3	13
5	36	39	9	2	1	1	0	3	23	3	3	8	5	3	0	3	2	9
5	37	29	6	0	1	1	0	4	17	3	1	5	5	2	1	2	2	10
5	38	47	9	2	1	1	0	5	29	4	3	8	10	4	1	4	5	13
5	39	31	8	1	0	1	0	1	20	2	3	6	7	3	0	2	3	10
5	40	38	6	3	1	1	0	3	24	3	3	6	8	3	1	3	3	14
6	41	25	5	3	1	1	1	0	14	3	1	3	4	1	0	3	1	8
6	42	50	11	6	1	7	0	1	24	6	1	6	5	2	1	5	2	14
6	43	56	9	5	3	3	1	3	32	6	2	4	9	5	1	8	3	17
6	44	58	13	8	2	4	0	4	27	5	2	4	8	3	1	6	2	12
6	45	53	13	7	2	7	1	3	20	5	1	3	6	2	1	4	2	11
6	46	44	12	4	1	5	0	2	20	6	0	4	5	2	0	4	1	9
6	47	64	15	8	3	3	1	3	31	4	2	4	9	6	2	8	4	14
6	48	66	11	7	2	3	0	6	37	7	2	6	7	5	3	10	3	18
7	49	48	10	10	1	3	0	4	20	4	2	2	8	2	0	4	2	11
7	50	59	12	12	2	1	0	6	26	6	3	2	8	5	0	5	3	14
7	51	70	12	15	2	6	0	5	30	6	3	4	9	3	1	6	2	16
7	52	33	9	12	0	1	0	1	10	2	1	3	3	0	0	1	0	5
7	53	46	10	11	1	2	0	1	21	3	1	3	8	2	1	5	2	9
7	54	67	9	15	2	1	0	5	35	7	3	4	9	5	1	9	3	18
7	55	50	10	13	1	1	1	2	22	6	3	4	6	2	0	3	2	13
7	56	48	10	11	1	1	0	5	20	4	3	3	4	1	1	4	0	10
8	57	30	10	6	0	1	0	1	12	3	0	4	1	0	0	4	0	7

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
8	58	16	7	2	0	0	0	0	7	2	0	2	2	1	0	1	1	4
8	59	14	7	1	0	0	0	0	6	2	0	1	2	0	0	1	0	4
8	60	21	8	5	0	1	0	0	7	4	0	1	1	0	0	1	0	4
8	61	17	10	2	0	0	0	0	5	2	0	1	1	0	0	1	0	3
8	62	21	8	2	0	0	0	0	11	3	0	4	2	1	0	2	1	9
8	63	21	7	4	0	0	0	0	10	3	0	3	1	0	0	3	0	6
8	64	25	10	3	0	1	0	0	11	3	0	2	2	1	1	3	1	5
9	65	33	6	10	3	1	2	0	11	4	2	1	2	0	1	1	0	5
9	66	34	9	8	4	1	2	0	10	1	1	2	1	0	2	3	0	4
9	67	35	9	8	3	2	1	0	12	4	1	2	1	0	1	3	0	8
9	68	37	11	9	2	1	1	0	13	4	3	2	1	0	1	2	0	9
9	69	46	11	12	3	3	2	0	15	3	3	1	3	1	0	5	1	7
9	70	34	11	10	1	1	1	0	10	3	0	2	2	0	1	2	0	8
9	71	37	10	10	1	1	0	0	15	2	2	2	3	2	1	4	1	8
9	72	42	5	12	3	3	0	0	19	7	3	2	3	0	1	3	0	11
10	73	53	7	3	2	2	0	7	32	5	5	10	5	3	2	7	5	12
10	74	48	8	4	2	3	0	3	28	4	4	11	3	3	2	5	4	9
10	75	28	4	4	1	6	0	0	13	2	0	5	1	0	1	4	0	7
10	76	35	5	2	1	4	0	2	21	4	3	8	1	1	1	5	2	7
10	77	34	5	2	0	5	0	0	22	3	3	9	0	0	1	7	1	7
10	78	60	10	7	2	3	0	0	38	5	7	13	2	1	1	11	2	13
10	79	47	5	3	3	2	0	2	32	6	8	9	1	2	2	7	3	12
10	80	41	5	3	1	4	0	2	26	5	4	8	0	0	1	9	1	7
11	81	96	8	10	2	1	1	9	64	1	5	3	25	16	4	20	10	23
11	82	85	8	12	2	1	1	8	54	2	5	2	20	13	0	20	7	22
11	83	76	8	8	2	2	1	8	47	1	5	3	22	14	2	12	10	19
11	84	84	13	11	2	0	1	9	48	1	5	3	19	15	1	15	9	19
11	85	79	7	9	3	1	1	5	53	1	3	2	23	13	3	17	9	23

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
11	86	91	9	10	3	2	1	7	59	2	7	2	20	12	2	20	6	20
11	87	89	9	15	3	1	1	7	53	2	5	1	19	12	2	18	6	17
11	88	88	7	12	3	2	1	8	55	1	5	1	19	10	2	22	5	22
12	89	57	10	4	0	8	0	1	34	5	3	11	5	1	3	8	2	20
12	90	58	6	3	1	8	0	4	36	6	3	10	3	1	3	12	2	20
12	91	62	15	6	2	9	0	2	29	4	5	7	5	1	2	8	3	16
12	92	58	11	1	4	8	0	2	32	5	3	9	5	4	5	7	6	15
12	93	58	10	5	1	5	0	1	36	6	5	10	4	3	4	9	5	22
12	94	54	8	1	2	7	0	2	34	2	6	6	8	4	5	8	5	15
12	95	60	8	3	2	9	0	4	34	6	2	6	9	4	4	7	4	19
12	96	55	10	3	2	9	0	4	27	4	4	5	4	3	4	6	3	13
13	97	21	3	1	0	2	0	0	15	3	2	6	1	0	0	3	0	9
13	98	21	6	0	1	2	0	0	12	4	0	4	1	0	1	2	0	9
13	99	20	5	0	1	3	0	1	10	4	0	3	2	1	1	0	1	9
13	100	17	2	1	0	2	0	0	12	4	1	5	0	0	0	2	0	8
13	101	23	5	4	1	1	0	0	12	3	0	6	1	0	0	2	0	10
13	102	17	4	0	1	3	0	0	9	1	0	6	1	0	0	1	0	7
13	103	18	4	1	0	3	0	0	10	3	0	4	2	0	0	1	0	10
13	104	21	7	2	0	1	0	0	11	3	1	4	0	0	1	2	0	10
14	105	16	5	3	0	1	0	0	7	3	1	2	1	0	0	0	0	3
14	106	28	4	6	0	5	0	0	13	3	1	3	4	3	2	0	3	6
14	107	24	5	4	0	3	0	0	12	3	1	4	1	1	1	2	1	5
14	108	13	4	1	0	1	0	0	7	4	1	2	0	0	0	0	0	4
14	109	15	3	4	1	1	0	0	6	2	1	3	0	0	0	0	0	4
14	110	14	3	3	0	3	0	0	5	2	1	2	0	0	0	0	0	3
14	111	19	5	3	0	4	0	0	7	3	1	2	1	0	0	0	0	4
14	112	16	5	3	0	0	0	0	8	3	1	2	0	0	0	2	0	3
15	113	30	10	6	2	1	0	1	10	4	0	3	1	0	0	2	0	8

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
15	114	29	7	7	0	1	1	2	11	5	0	2	3	1	0	1	1	8
15	115	24	6	5	1	1	1	1	9	3	1	2	1	0	0	2	0	6
15	116	25	7	4	1	2	0	1	10	4	0	3	0	1	1	2	1	9
15	117	23	8	6	0	1	0	1	7	3	0	2	0	0	0	2	0	6
15	118	26	7	5	1	2	1	1	9	5	0	2	1	0	0	1	0	7
15	119	30	8	8	1	1	0	2	10	5	0	2	0	2	1	1	1	9
15	120	25	8	6	2	1	1	1	6	4	0	1	0	0	0	1	0	6
16	121	43	6	8	0	3	0	1	25	4	4	3	4	2	2	8	2	12
16	122	39	7	7	0	3	0	1	21	5	3	5	2	2	3	3	2	12
16	123	26	5	6	0	2	0	1	12	1	3	2	0	1	3	3	1	7
16	124	39	5	8	0	2	0	1	23	5	4	2	2	1	3	7	1	10
16	125	40	5	7	2	3	0	1	22	3	5	3	5	4	3	3	4	11
16	126	39	4	7	0	5	0	1	22	5	4	5	1	2	3	4	2	13
16	127	40	5	8	0	3	0	2	22	4	4	3	1	2	3	7	2	9
16	128	38	7	6	0	3	0	0	21	2	3	4	4	3	2	6	3	11
17	129	14	1	1	0	2	0	0	10	4	1	4	0	0	0	1	0	6
17	130	28	3	5	2	1	0	0	17	3	2	7	2	2	0	3	2	8
17	131	15	2	2	0	1	0	0	10	2	0	6	0	0	0	2	0	5
17	132	20	3	1	1	3	0	0	12	5	0	4	1	0	0	2	0	6
17	133	58	3	4	1	3	0	3	44	2	11	6	13	14	2	9	12	16
17	134	63	7	6	2	2	0	2	44	2	8	5	13	17	4	12	14	13
17	135	32	2	6	1	1	0	0	22	1	4	5	10	7	1	2	7	9
17	136	57	4	4	2	3	0	1	43	4	9	4	16	15	1	9	13	14
18	137	32	6	8	2	2	0	1	13	5	1	4	2	0	0	1	0	10
18	138	21	6	4	1	0	0	1	9	4	0	3	1	0	0	1	0	8
18	139	22	5	6	1	0	1	1	8	4	0	2	1	0	0	1	0	7
18	140	22	6	5	1	1	0	1	8	4	0	3	1	0	0	0	0	6
18	141	29	5	7	2	1	0	1	13	6	1	3	1	0	0	2	0	10

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
18	142	18	5	3	1	0	0	1	8	4	0	2	2	0	0	0	0	6
18	143	30	6	7	2	1	2	2	10	4	1	2	1	0	0	2	0	7
18	144	27	3	7	2	2	0	1	12	5	1	3	1	0	0	2	0	8
19	145	57	12	5	0	5	1	1	33	9	3	8	6	2	2	5	2	19
19	146	41	10	5	0	3	2	0	21	6	1	10	3	1	1	1	2	13
19	147	59	10	7	1	5	0	3	33	7	3	9	5	2	2	7	2	19
19	148	40	7	7	0	3	1	1	21	7	0	7	4	0	1	2	0	13
19	149	76	9	10	1	9	1	1	45	6	5	9	6	4	5	15	5	21
19	150	58	7	8	3	6	1	2	31	4	3	4	4	4	4	11	3	14
19	151	58	6	9	1	8	1	3	30	5	2	6	5	3	4	8	3	15
19	152	66	7	12	0	6	1	3	37	5	4	9	5	2	5	11	4	22
20	153	41	4	4	1	3	0	3	26	2	6	1	9	7	4	7	9	8
20	154	28	4	8	1	4	0	1	10	3	2	1	1	1	2	1	1	4
20	155	55	7	7	2	6	1	3	29	3	6	3	9	5	3	5	5	12
20	156	40	5	6	1	2	0	2	24	1	7	1	6	5	3	7	6	5
20	157	32	4	6	2	6	0	1	13	2	3	1	1	1	3	3	1	4
20	158	25	2	7	1	2	0	1	12	2	2	3	3	3	2	0	3	7
20	159	37	3	6	3	3	0	3	19	1	5	0	7	4	1	6	5	6
20	160	14	2	0	1	2	0	1	8	0	2	0	4	2	1	2	3	1
21	161	27	4	4	0	3	0	0	16	2	1	6	3	1	1	3	1	9
21	162	27	5	3	2	4	0	0	13	3	1	6	0	0	0	3	0	8
21	163	30	7	3	0	3	0	0	17	4	1	5	0	1	2	5	1	10
21	164	50	6	7	2	5	0	1	29	2	5	4	12	4	4	4	6	14
21	165	50	8	3	1	4	0	2	32	3	3	6	8	4	4	9	5	14
21	166	32	3	3	0	3	1	0	22	4	2	9	0	1	2	5	1	12
21	167	34	6	5	2	4	0	0	17	3	1	4	3	1	1	5	1	11
21	168	51	7	5	3	4	0	1	31	3	5	5	7	5	4	7	5	15
22	169	42	7	9	2	1	0	2	21	5	2	5	4	1	2	3	1	15

Appendix 10. Environmental data summary by quadrat (III).

PA#	Q#	#SPP	#TRE	#SHR	#VIN	#FRN	#FA	#GRA	#HRB	#INH	#ADH	#ANH	#WIH	#PDH	#MEH	#NFH	#MUH	#VEH
22	170	36	6	9	2	2	0	1	16	4	2	5	2	0	1	3	1	11
22	171	40	8	10	3	1	0	2	16	5	1	4	3	0	1	2	0	13
22	172	36	7	12	1	1	0	1	14	4	1	4	3	0	0	2	0	10
22	173	37	6	9	2	1	1	1	17	4	2	3	4	0	1	3	0	12
22	174	44	11	13	2	1	0	1	16	7	1	3	3	0	0	2	0	11
22	175	35	7	9	3	1	0	1	14	6	2	3	2	1	1	1	2	11
22	176	45	8	14	2	1	1	1	18	7	2	2	3	2	1	3	2	12
23	177	35	7	7	2	1	0	2	16	4	1	5	1	1	1	3	0	9
23	178	26	5	5	2	0	0	1	13	3	0	4	2	2	1	3	2	9
23	179	25	6	3	3	1	0	2	10	3	0	3	1	0	1	2	0	7
23	180	34	6	6	5	2	0	2	13	3	1	4	1	0	1	3	0	9
23	181	32	7	7	4	2	0	2	10	4	0	4	1	1	1	0	1	9
23	182	18	5	3	1	1	0	2	6	2	1	2	0	0	0	1	0	4
23	183	26	5	6	3	0	0	2	10	3	1	3	1	0	0	2	0	6
23	184	30	7	6	2	1	0	1	13	3	1	4	1	0	1	3	0	9
24	185	24	7	4	1	3	0	0	9	2	1	1	2	1	1	2	1	4
24	186	58	12	7	3	5	0	3	28	5	7	1	6	5	3	7	5	12
24	187	61	10	11	3	6	0	2	29	6	4	4	6	3	3	6	3	15
24	188	44	4	8	0	6	0	2	24	2	4	0	10	3	3	4	2	10
24	189	59	12	9	3	6	0	1	28	4	4	2	9	3	3	6	3	15
24	190	44	10	7	1	4	0	1	21	3	4	1	5	3	3	5	3	9
24	191	51	9	6	2	5	0	3	26	4	5	2	7	3	3	5	3	14
24	192	47	10	7	1	6	0	2	21	3	3	1	6	3	3	5	3	11

APPENDIX 11

REPRESENTATIVE SEED DISPERSAL DISTANCES OF NATIVE AND ALIEN SPECIES IN NORTH AMERICA

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Selected references to species from other continents are cited by country and enclosed in brackets. Methodologies vary: direct observation, experimental treatments (indoor, outdoor), estimated lateral dispersal distance based on terminal velocity values or mathematical models, and, measured parent-seedling distances (rarely). Legend: mtd = maximum trap distance. References: (1) Andersen 1988, (2) Andersen 1991, (3) Arnold 1981, (4) Antonovics and Ellstrand 1985, (5) Baker and O'Dowd 1982, (6) Bakker 1960, (7) Beattie and Lyons 1975, (8) Beer and Swaine 1977, (9) Berg 1966, (10) Berg 1969, (11) Boyd 1996, (12) Brodie 1951, (13) Brodie 1955, (14) Bullock 1989, (15) Bullock and Primack 1977, (16) Bulow-Olsen 1984, (17) Burton 1989, (18) Cain *et al.* 1998, (19) Campbell 1983, (20) Carey and Watkinson 1993, (21) Caspar 1987, (22) Clark *et al.* 1998, (23) Culver and Beattie 1978, (24) Davidson and Morton 1981, (25) Darley-Hill and Johnson 1981, (26) Evans *et al.* 1987, (27) Fenster 1991, (28) Gashwiler 1969, (29) Geiger 1950, (30) Greene and Johnson 1989, (31) Greene and Johnson 1995, (32) Greene and Johnson 1996, (33) Gross 1986, (34) Gross and Werner 1982, (35) Hinds and Hawksworth 1965, (36) Hoppes 1988, (37) Howard 1970, (38) Hughes and Westoby 1992ab, (39) Hughes *et al.* 1994, (40) Johnson 1996, (41) Johnson and Adkisson 1985, (42) Johnson and Patterson unpubl., (43) Jules 1996, (44) Kalisz unpubl., (45) Klinkenhamer *et al.* 1988, (46) Kjellsson 1985, (47) Kohlermann 1950, (48) Lee 1984, (49) Levin and Kerster 1969, (50) Levin and Kerster 1974, (51) Matlack 1987, (52) McCaughey *et al.* 1986, (53) McDonnell and Stiles 1983, (54) McEvoy and Cox 1987, (55) Meagher and Thompson 1987, (56) Mesler and Lu 1983, (57) Meyer and Schmid 1999, (58) Morse and Schmitt 1985, (59) Muller 1955, (60) O'Dowd and Hay 1980, (61) Ohara and Higashi 1987, (62) Okbo and Levin 1989, (63) Olivieri and Gouyon 1985, (64) Parra *et al.* 1993, (65) Pemberton 1988, (66) Platt 1976, (67) Platt and Weiss 1977, (68) Pudlo *et al.* 1980, (69) Rabinowitz and Rapp 1979, (70) Sacchi 1987, (71) Savile 1953, (72) Schaal 1980, (73) Schemske 1978, (74) Schmitt *et al.* 1985, (75) Sheldon and Burrows 1973, (76) Smith 1975, (77) Smith 1989, (78) Smith and Kok 1984, (79) Stamp 1989, (80) Stamp and Lucas 1983, (81) Stamp and Lucas 1990, (82) Stapanian and Smith 1978, (83) Stergios 1976, (84) Stratton 1994, (85) Thiede and Augspurger 1996, (86) Tomback and Linhart 1990, (87) Trapp 1988, (88) Vander Wall and Balda 1977, (89) Venable and Levin 1985, (90) Vickery *et al.* 1986, (91) Waller 1980, (92)Watkinson 1978, (93) Webb and Willson 1985, (94) Weiblen and Thomson 1995, (95) Werner 1975, (96)Werner and Platt 1976, (97) Westlaken and Maun 1985, (98) Westoby and Rice 1981, (99) Willson *et al.* 1990.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
ANIMAL DISPERSED						
Fleshy Fruits						
trees, shrubs, vines, herbs (n=13 spp)			170			53
Trees (n=1)						
Prunus serotina		 1	25 35 9			76 53 36
Shrubs (n=3)						

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Prunus virginiana			10 (mtd)			93
Prunus avium			10 (mtd)			93
Vines (n=2)						
Parthenocissus quinquefolia		9				36
Toxicodendron radicans			33 (mtd)			36
Vitis vulpina		0.5-6 (mode)				36
Herbs (n=1)						
Phytolacca americana			33 (mtd)			36
Nut Fruits						
Trees (n=3)						
Fagus grandifolia			4 km			41
Juglans nigra	38.1					82
Quercus palustris	1.1 km		1.9 km 5 km	0.1-1.9 km		25 42 (25)
Adhesive Fruits						
Herbs (n=4)						
Achyranthes aspera (Costa Rica)	24.7m - 2.4 km					15
Bidens sp. (Costa Rica)	12.4-108.8					15
Daucus carota			15			34
Petiveria alliacea (Costa Rica)	32.9-156.6					15
Elaiosome Seeds/Fruits						
Trees (n=2)						
Acacia suaveolens (Australia)	2.0-6.5		10.9	0.4-10.9		1

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Acacia terminalis (Australia)	1.1		1.9	0.2-1.9		38
Shrubs (n=4)						
Dendromecon harfordii	3.6		5.1			9
Dendromecon rigida	2.7		4.8 >10			9 14
Dillwynia retorta (Australia)	1.2		11.0	0.1-11.0		38
Fremontodendron decumbens			12	60% 6-8		11
Herbs (n=18)						
Asarum canadense	1.5			0.1-35.0		18
Carex pilulifera (Denmark)				0-1.4		46
Crotalaria rotundifolia	2.2					81
Datura discolor	2.3		39			60
Dicentra formosa			56			10
Erythronium grandiflorum		0.3	≤1 (mtd)			94
Euphorbia esula			25 (mtd)	0-8		65
Sanquinaria candensis	0.2-3.1		12			68
Sclerolaena dicantha (Australia)			77	4-77; 50-77 common		24
Trillium grandiflorum			10.0	<1-10.0		44
Trillium kamtschaticum (Japan)	0.6		3.3	0.2-3.3		61
Trillium ovatum			1.8 >30 (wasp)	0-1.8 >70% <0.6 >30 (wasp)		57 57 43
Trillium tschonoskii (Japan)	0.6		0.4	0.01-0.4		61
Viola odorata			50			77

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Viola pedata	0.4					23
Viola pensylvanica	0.6					23
Viola rostrata	0.6					23
Viola triloba	1.0					23
Other Fruits (n=3)						
Trees						
Pinus spp			22 km	12-22 km		86
Pinus edulis			22 km	7.5-22 km		88
Herbs						
Mimulus guttatus			1 km (deer)			90
WIND DISPERSED						
Trees (n=31)						
Abies alba	72		835 (mtd)			47 (39) 31
Acer griseum			29.2		124	51
Acer negundo			41.1		76 80 104	51 30 31
Acer platanoides	83		50.3		87 87	51 47 (30) 47 (39)
Acer pseudoplatanus	69		60.1		104 95	51 47 (30) 47 (39)
Acer rubrum			98.7 835 (mtd)		76	51 31
Acer saccharum			170		127 124	17 (32) 31

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Albizzia julibrissum			16.2		154	51
Betula papyrifera			835 (mtd)		55	37 (32) 31
Betula populifolia			64.1		39	51
Catalpa bignoides			16.8		186	51
Carpinus betulus	73					47 (39)
Carpinus caroliniana			19.4		129	51
Cedrus atlantica var. glauca			68.8		112	51
Fraxinus spp			>50	15% > 50	120-170	47 (29) 31
Fraxinus americana	19.3		70.1 131		104 142 131	51 30 17 (32) 22
Fraxinus excelsior	53		40.3		217	51 47 (39)
Larix decidua	29				119	47 (39) 32
Larix laricina			50	15-50	119	52 32
Liriodendron tulipifera	33.9		111.9		11	51 22
Picea glauca			300		61	52 32
Picea mariana			165 (mtd) 100			37 52
Pinus banksiana			40	34-40		52
Pinus contorta			rarely >61 244 60		61	52 52 30
Pinus rigida	15.1					22

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Pinus strobus	46		835 (mtd)			47 (39) 31
Platanus occidentalis			62.8		166	51
Pseudotsuga menziesii			122 (mtd)	61% 15-30 26% 61-76 13% 107-122		28 28 28
Thuja plicata			122 (mtd)	79% 15-30 17% 61-76		28 28
Thuja plicata			122 (mtd) 201	4% 107-122		28 52
Tilia americana	13.0		15.0		180	51 31 22
Tilia grandifolia	58					47 (39)
Tilia parviflora					133	47 (30)
Tsuga canadensis	19.7					22
Ulmus campestris	60					47 (39)
Shrubs (n=2)						
Alnus crispa			6.7		94	51
Halesia monticola			18.5		338	51
Vines (n=1)						
Clematis virginiana			3.2		129	51
Grasses (n=5)						
Agrostis hiemalis					96	69
Andropogon gerardi					154	69
Andropogon glomeratus					20.1	19
Andropogon virginicus					32.3	19

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Schizachyrium scoparium					91 101	69 19
Herbs (n=51)						
Apocynum cannabium			83.3		15	51
Asclepias syriaca	13.8		45 150 (mtd) 18.1	 4.2-25.3 2% >150	24.9 27	67 58 58 51
Asclepias syriaca (cont'd)	15.6-43.7					70
Apocynum sibiricum	25.7		75		9.9	67
Aster acuminatus			5.1		41	51
Aster prenanthoides			3.1		66	51
Carduus nutans			<3% >100 (mtd)	80% <40		78
Carduus pyconcephalus			45	3-45		63
Carduus tenuiflorus			2.1	0.7-2.1	78.6	75
Carlina vulgaris			1.5	0.5-1.5	58.5	75
Centauria scabiosa			1.6	0.5-1.6	219.8	75
Cirsium arvense			2 km (mtd) 11.4	 3.8-11.4	26 21.6	6 75
Cirsium palustre			6.8	2.3-6.8	34.4	75
Cirsium undulatum	18.4		35		30.0	67
Cirsium vulgare			11.6 32 (mtd) >>km	 50% <1 16% 1-2 10% >32	36	51 45 45 45
Cryptantha flava			31.3			21

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Erigeron acer			2.4	1.2-2.4	22.9	75
Erigeron annus			2.5	1-25 <1% >3		84
Eupatorium cannabinum			5.9 7.8	2.0-5.9	39.3 32	75 51
Eupatorium rugosum			7.1		45	51
Heterotheca latifolia	1.1-1.7		20 (mtd)			89
Hieracium aurantiacum			2.0 (mtd)	82-95% <1.0		83
Hieracium umbellatum			3.0		55	51
Hypochoeris glabra					45	5
Hypochoeris radicata			2.0	0.7-2.0	40.5	75
Leontodon autumnalis			1.1	0.6-1.1	51.2	75
Liatris aspera	2.5		9			49
Mimulus guttatus			4.8	44% <0.3 8% > 1		90
Physalis subglabrata			1.5		212	51
Rumex obtusifolia			2.5		126	51
Senecio jacobea disk achenes disk achenes	0.6-3.3		5.5 14	1.8-5.5 31% 1 58% 1-5	42.1	75 54 54
Senecio squalidus			1.8 2.5	0.6-1.8	45.7 33	75 51
Senecio viscosus			2.6	0.9-2.6	31.7	75
Senecio vulgaris			2.9	1.0-2.9	28.0	75
Solidago altissima			14.9 6-8 (mtd)	14.9	28	51 57
Solidago canadensis			30.9	16.8-30.9		96
Solidago gigantea			23.8			96

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Solidago graminifolia			21.1	12.0-21.1		96
Solidago missouriensis			29.4	16.2-29.4		96
Solidago nemoralis			39.0	27.9-39.0		96
Solidago rigida	4.9		15		33.9	67
Solidago speciosa			41.4	37.6-41.4		96
Sonchus arvensis			10.0	3.3-10.0	24.1	75
Sonchus oleraceus		0.1-0.9 (mode)	6.6	2.2-6.6	35.7	2 75
Taraxacum officinale			2.3 1.5	0.8-2.3	35.7 33.7 31 42	75 67 19 51
Tragopogon dubius		2 (mode)	>250			34 33 (62)
Tragopogon dubius					40.0	31
Tragopogon porrifolius			1.8 5.8 6.9	0.6-1.8	45.7 36 30	75 51 51
Trifolium arvense			0.8		125	51
Tusilago farfara			4 km (mtd) 4.4	1.5-4.4	15 19.2	6 75
Typha latifolia			46.9		13	51
BALLISTIC DISPERSED						
Shrubs (n=4)						
Ceanothus cuneatus			10 (mtd)	1% = 9		26
Ceanothus leucodermis			10 (mtd)	1% = 9		26
Dendromecon harfordii	3.6		5.1			9
Dendromecon rigida	1.3		4.8	2.9-4.8		9

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Herbs (n=42)						
Ballechores *s.l.*			45			8
Amphicarpa bracteata: chasmogamous seeds aerial cleistogamous seeds		 1.4 1.3	 4.3 3.8	 31% >2.0 25% >2.0		 87 87
Arceuthobium cryptopodum			14.6			35
Cardamine hirsuta			1.4			59 (50)
Cassia fasciculata	1.4-2.1		4.8	1.6% >4		48
Chamaecrista fasciculata	0.3-0.7					27
Chrysosplenium americanum			0.4			71
Cnidoscolus stimulosus	0.6		1.2			81
Crotalaria sp			4.3			49
Crotalaria rotundifolia	0.9		2.4			81
Erodium moschatum	0.6		0.9	0.0-0.9		79
Euphorbia marginata			4.0			60 (50)
Geranium carolinianum	3.3		4.2	1.8-4.2		80
Geranium columbinum			1.5			60 (50)
Geranium molle	1.8		2.8	1.0-2.8		80
Geranium maculatum	3.0		4.8	1.8-4.8		80
Impatiens capensis	0.2		1.6 2.0 2 2.1	0.1-1.6 1.5-2 most <0.2 15% >1.0		80 73 91 74 74
Impatiens pallida			2.0			73
Impatiens parviflora			3.4			60 (50)
Kalanchoe tubiflora			1.5			12
Lepidium campestre	0.3-0.8		2.0 (mtd)			85

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Lepidium vulgare			>1.9			99
Lupinus texensis	0.6		4			72
Mitella diphylla	0.3		0.8	0.1-0.8		71
Montia fontana			2.0			60 (50)
Oenothera biennis	1.8	<1	5 4		120	67 34
Oenothera rosea			1.0			12
Oxalis acetosella			2.3			60 (50)
Phlox drummondii	0.8		1.6	0.1-1.6		80
Phlox pilosa	1.2		3.6			49
Sagina decumbens			0.5			12
Salvia lyrata			2.0	0.5-2.0		13
Stillingia sylvatica	1.1		3.0			81
Verbascum thapsus		1	11			34
Viola blanda chasmogamous seeds cleistogamous seeds	 1.0 0.8		3.0 3.8 2.2	2.4-3.0		16 7 7
Viola cucullata	1.5		2.1			7
Viola eriocarpa	1.2		5.4			7
Viola fimbriatula						16
Viola lanceolata						16
Viola papilionacea chasmogamous seeds cleistogamous seeds	 2.1 1.0		 4.8 2.1			 7 7
Viola pedata	1.4		5.1			7
Viola rostrata	1.2		4.2			7

Appendix11. Representative seed dispersal distances of native and alien species in N. America.

Species	Seed Dispersal Distance					Ref.#
	Mean (m)	Median (m)	Maximum (m)	Range (m)	Terminal Velocity (cm/s)	
Viola striata chasmogamous seeds cleistogamous seeds	 1.5 1.1 0.8		 3.0 2.2 3.4	 0.1-3.4		 7 7 80
UNASSISTED						
Grasses (n=3)						
Anthoxanthum odoratum			2	95% <1		4
Vulpia ciliata	0.1					20
Vulpia fasciculata			0.4	79% <0.1		92
Herbs (n=11)						
Chamaelirium luteum	10.1		34			56
Chaenorrhinum minus			1.4	75% <0.1		3
Dipsacus sylvestris			1.5			95
Echeveria gibbiflora	1.1					64
Heterotheca latifolia ray achenes	 0.5-0.9		 12			 89
Lithospermum caroliniense			2.0 (mtd)	most <1		97
Mimulus gutttatus			4.8			90
Mirabilis hirsuta	 0.4		1.6 1.5		 217	66 67
Verbena stricta	1.0		3.5		166	67

APPENDIX12

PRINCIPAL FRUGIVORES OF EASTERN NORTH AMERICA

Appendix 12. Principal Frugivores of Eastern North America. Legend: * Major frugivore (≥ 10 stars, Martin *et al.* 1951, as calculated by Willson 1986); Sources: Birds: Willson 1986; Mammals: Hamilton 1941, Martin *et al.* 1951; Reptiles: Rust and Roth 1981, Willson 1986, Stiles 1992.

BIRDS (n=50)	
Eastern bluebird*	White-throated sparrow
Northern bobwhite	European starling*
Northern cardinal	Tree swallow
Gray catbird*	Summer tanager
Yellow-breasted chat	Brown thrasher*
American crow	Gray-cheeked thrush
Fish crow*	Hermit thrush
Purple finch	Swainson's thrush
Northern flicker	Wood thrush*
Great-crested flycatcher	Tufted titmouse
Evening grosbeak	Eastern towhee
Pine grosbeak	Wild turkey
Rose-breasted grosbeak	Veery
Ruffed-grouse*	Red-eyed vireo
Spruce grouse	Warbling vireo
Eastern kingbird	Bay-breasted warbler
Ruby-crowned kinglet	Chestnut-sided warbler
Northern mockingbird*	Tennessee warbler
Baltimore oriole	Yellow-rumped warbler
Orchard oriole	Bohemian waxwing
Ring-necked pheasant	Cedar waxwing*
American robin*	Downy woodpecker
Yellow-bellied sapsucker	Pileated woodpecker
Fox sparrow	Red-bellied woodpecker

Appendix 12. Principal Frugivores of Eastern North America (cont'd).

MAMMALS (n=14)	
Black bear*	Moose
Eastern chipmunk	Deer mouse
Common cottontail	White-footed mouse
New England cottontail	Raccoon
White-tailed deer*	Eastern fox squirrel
Eastern red fox	Eastern gray squirrel
Gray fox	Eastern red squirrel
REPTILES (n=1)	
Box Turtle	

APPENDIX 13

KNOWN MYRMECOCHORES IN THE U.S. NORTHEAST

Appendix 13. Known Myrmecochores in the U.S. Northeast. Sources: (1) Beattie and Lyons 1975, (2) Beattie *et al.* 1979, (3) Beattie and Culver 1978, (4) Beattie and Culver 1981, (5) Culver and Beattie 1978, (6) Culver and Beattie 1980, (7) Gaddy 1986, (8) Gates 1941, (9) Gates 1942, (10) Gunther and Lanza 1989, (11) Handel 1976, (12) Handel 1978b, (13) Heithaus 1981, (14) Pudlo *et al.* 1980, (15) Ruhren and Dudash 1996

Name	Reference	Nesting Preference
Aphaenogaster rudis	4,5,6,7,11,12,13,14,15	majority of *Aphaenogaster* spp. nest in the soil; usually start nest beneath some covering object; if a log, ants may construct part of nest in it but main part of nest is subterranean (Creighton 1950, p.139)
Aphaenogaster tennesseensis	12	usually nests on rotten stumps and fallen logs with few passages running into the soil (Creighton, 1950, p.139; Lynch *et al.* 1988)
Aphaenogaster texana	5	see *A. rudis*.
Camponotus nearcticus	14	most species of *Camponotus* nest in decaying wood, especially in soft and rotting parts; nests that occur in logs or trees rarely extend into the soil (Creighton 1950, p.365)
Camponotus pennsylvanicus	8,14	see *C. nearcticus*.
Crematogaster lineolata	7	nests in dead wood of standing or prostrate trunks (Wheeler 1960, p. 208)
Formica fusca	1	nests in soil beneath a covering object (Creighton 1950, p.528)
Formica integra	5,13	nests in stumps and in soil under cover of stones, logs, or branches (Wheeler 1960, pp. 204-206).
Formica neogagates	8,9	nests in soil beneath stones or other covering objects (Creighton 1950, p. 457)
Formica subsericea	1,2,5,8,13,14	nests in soil where it forms mounds up to 30 cm high (Wheeler 1960, pp. 203-204)

Appendix 13. Known Myrmecochores in the US Northeast (cont'd).

Name	Reference	Nesting Preference
Lasius alienus	1,5,8,9,13,14	remarkably flexible; most species prefer well drained soil that is not too dry; nest may be free in soil, under stones or other covering objects, or in and under rotten logs and stumps (Creighton 1950)
Leptothorax curvispinosus	5,13	genus nests by choice in preformed cavities; e.g., in crannies under rock chips, or under bark, in hollow twigs, dried grass stems, old galls, or empty nut shells (Creighton 1950, p. 255)
Leptothorax longispinosus	5,13	see *L. curvispinosus*.
Myrmecina americana	5	usually nests in moist shady areas, often under small stones (Creighton 1950, p.248)
Myrmica emeryana	9,14	most species in genus nest in soil under a covering object (Creighton 1950, p.91)
Myrmica fracticornis	8	see *M. emeryana*.
Myrmica punctiventris	1,2,3,10,13,14,	see *M. emeryana*.
Myrmica spatulata	1	see *M. emeryana*.
Phrenolepis imparis	13,14	often nests in damp soil in shady positions (Creighton 1950, p.135)
Stenamma schmitti	5,13	habits little known; nests in wooded areas in leaf mould, under stones or logs or beneath thick, loose moss (Creighton 1950, p.135)
Tapinoma sessile	1,5,13	not particular; in soil with or without a covering object, under bark, and in preformed cavities of various kinds (Creighton 1950, p.351)

APPENDIX 14

SPECIES PREVALENT IN THE HERB LAYER IN THE MAPLE-BASSWOOD FOREST REGION IN SOUTHERN WISCONSIN AND PRESENT IN SUGAR MAPLE DOMINATED STANDS IN THE VICINITY OF PETERBOROUGH, ONTARIO

Appendix 14. Species prevalent in the herb layer in the Maple-Basswood Forest Region in southern Wisconsin and present in sugar maple dominated stands in the vicinity of Peterborough, Ontario. "●" denotes that species achieves maximum presence in this forest type in Wisconsin. W=Wisconsin, P=Peterborough; Flowering phenology at Peterborough: E=early spring flowering (before June 1st); ML=mid to late season flowering (after June 1st). Source: Curtis 1959, p.521.

Species	W	P	Species	W	P
Actaea pachypoda		E	*Geum canadense*		E
Adiantum pedatum		?	*Hepatica acutiloba*	●	E
Allium tricoccum	●	E	*Hydrophyllum virginianum*	●	E
Amphicarpaea bracteata		ML	*Laportea canadensis*		ML
Arisaema triphyllum		E	*Maianthemum canadense*		E
Athyrium filix-femina		?	*Osmorhiza claytonii*		E
Botrychium virginianum		E	*Parthenocissus inserta*		ML
Brachyelytrum erectum		E	*Phryma leptostachya*		ML
Carex laxiflora		E	*Podophyllum peltatum*	●	E
Carex pensylvanica		E	*Polygonatum pubscens*		E
Caulophyllum thalictroides	●	E	*Prenanthes alba*		ML
Celastrus scandens		ML	*Ribes cynosbati*		ML
Circaea lutiana		ML	*Sanguinaria canadensis*	●	E
Claytonia caroliniana		E	*Solidago flexicaulis*		ML
Cryptotaenia canadensis		ML	*Thalictrum dioicum*		E
Erythronium americanum		E	*Trillium grandiflorum*	●	E
Galium aparine	●	E	*Uvularia grandiflora*		E
Galium triflorum		ML	*Viola cucullata*		E
Geranium maculatum		E	*Viola pubescens*	●	E

Notes:

Species prevalent in Wisconsin but absent from stands at Peterborough: *Erythronium albidum, Claytonia virginica, Galium concinnum, Sanicula gregaria, Smilax ecirrhata.*