PATTERNS AND PROCESSES OF SPECIES DIVERSITY
IN
FRAGMENTED NORTHERN HARDWOOD FORESTS

BY

WILLIAM BRUCE DRAPER

A THESIS SUBMITTED IN CONFORMITY WITH THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE
GRADUATE DEPARTMENT OF BOTANY, UNIVERSITY OF TORONTO

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PATTERNS AND PROCESSES OF SPECIES DIVERSITY
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William Bruce Draper, Department of Botany, University of Toronto

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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.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>ii</td>
</tr>
<tr>
<td>Acknowledgements</td>
<td>iii</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>v</td>
</tr>
<tr>
<td>Appendices</td>
<td>viii</td>
</tr>
<tr>
<td>List of Tables</td>
<td>ix</td>
</tr>
<tr>
<td>List of Figures</td>
<td>xi</td>
</tr>
<tr>
<td>1.0 INTRODUCTION</td>
<td></td>
</tr>
<tr>
<td>2.0 ENVIRONMENTAL PATTERNS</td>
<td></td>
</tr>
<tr>
<td>2.1 Introduction</td>
<td></td>
</tr>
<tr>
<td>2.2 Methods</td>
<td></td>
</tr>
<tr>
<td>2.2.1 Selection of Study Sites</td>
<td></td>
</tr>
<tr>
<td>2.2.2 Sampling Methods</td>
<td></td>
</tr>
<tr>
<td>2.2.3 Environmental Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.1 Soil Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.2 Forest Stand Structure Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.3 Vegetation Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.4 Plant Attribute Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.5 Microhabitat Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.6 Landscape Variables</td>
<td></td>
</tr>
<tr>
<td>2.2.3.7 Supplementary Data</td>
<td></td>
</tr>
<tr>
<td>2.2.4 Analytical Methods</td>
<td></td>
</tr>
<tr>
<td>2.2.4.1 Overview</td>
<td></td>
</tr>
<tr>
<td>2.2.4.2 Distribution of Species on Environmental Gradients</td>
<td></td>
</tr>
<tr>
<td>2.2.4.3 Distribution of Species in Forest Microhabitats</td>
<td></td>
</tr>
<tr>
<td>2.2.4.4 Distribution of Sugar Maple on a Moisture-Fertility Gradient</td>
<td></td>
</tr>
<tr>
<td>2.2.4.5 Distribution of Plant Attributes on Primary Gradients</td>
<td></td>
</tr>
<tr>
<td>2.3 Results</td>
<td></td>
</tr>
<tr>
<td>2.3.1 Vegetation Survey</td>
<td></td>
</tr>
<tr>
<td>2.3.2 Relationships Among Environmental Variables</td>
<td></td>
</tr>
<tr>
<td>2.3.3 Species Response to Environmental Gradients</td>
<td></td>
</tr>
<tr>
<td>2.3.4 Species Response to Forest Microhabitats</td>
<td></td>
</tr>
<tr>
<td>2.3.5 Response of Sugar Maple and Understory Herbs to Available Calcium</td>
<td></td>
</tr>
<tr>
<td>2.3.6 Plant Attributes</td>
<td></td>
</tr>
<tr>
<td>2.4 Discussion</td>
<td></td>
</tr>
<tr>
<td>2.5 Principal Findings</td>
<td></td>
</tr>
<tr>
<td>3.0 DISPERsal PATTERNS</td>
<td></td>
</tr>
<tr>
<td>3.1 Introduction</td>
<td></td>
</tr>
</tbody>
</table>
TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2 Methods</td>
<td>123</td>
</tr>
<tr>
<td>3.2.1 Classification of Dispersal Modes</td>
<td>123</td>
</tr>
<tr>
<td>3.2.1.1 Overview</td>
<td>123</td>
</tr>
<tr>
<td>3.2.1.2 Classification Criteria and Related Considerations</td>
<td>125</td>
</tr>
<tr>
<td>3.2.2 Classification of Other Plant Traits</td>
<td>131</td>
</tr>
<tr>
<td>3.2.3 Identification of Pattern</td>
<td>132</td>
</tr>
<tr>
<td>3.2.3.1 Pattern in Relation to Plant Attributes</td>
<td>132</td>
</tr>
<tr>
<td>3.2.3.2 Pattern in Relation to Environmental Variables</td>
<td>133</td>
</tr>
<tr>
<td>3.2.3.3 Pattern in Relation to Abundance Variables</td>
<td>135</td>
</tr>
<tr>
<td>3.2.3.4 Pattern in Relation to Spatial Scale</td>
<td>136</td>
</tr>
<tr>
<td>3.3 Results</td>
<td>136</td>
</tr>
<tr>
<td>3.3.1 Pattern in Relation to Plant Attributes</td>
<td>136</td>
</tr>
<tr>
<td>3.3.1.1 Life Form</td>
<td>137</td>
</tr>
<tr>
<td>3.3.1.2 Life History</td>
<td>139</td>
</tr>
<tr>
<td>3.3.1.3 Provenance</td>
<td>139</td>
</tr>
<tr>
<td>3.3.1.4 Modality</td>
<td>144</td>
</tr>
<tr>
<td>3.3.1.5 Fruit Type</td>
<td>144</td>
</tr>
<tr>
<td>3.3.1.6 Taxonomic Rank</td>
<td>149</td>
</tr>
<tr>
<td>3.3.2 Pattern in Relation to Environmental Variables</td>
<td>149</td>
</tr>
<tr>
<td>3.3.2.1 Habitat Affinity</td>
<td>149</td>
</tr>
<tr>
<td>3.3.2.2 Environmental Gradients</td>
<td>154</td>
</tr>
<tr>
<td>3.3.2.3 Microhabitats</td>
<td>169</td>
</tr>
<tr>
<td>3.3.3 Pattern in Relation to Abundance Variables</td>
<td>184</td>
</tr>
<tr>
<td>3.3.3.1 Frequency Class</td>
<td>184</td>
</tr>
<tr>
<td>3.3.3.2 Cover Class</td>
<td>184</td>
</tr>
<tr>
<td>3.3.3.3 Species Richness Class</td>
<td>187</td>
</tr>
<tr>
<td>3.3.4 Pattern in Relation to Spatial Scale</td>
<td>187</td>
</tr>
<tr>
<td>3.3.4.1 Patch Size</td>
<td>189</td>
</tr>
<tr>
<td>3.3.4.2 Patch Isolation</td>
<td>189</td>
</tr>
<tr>
<td>3.4 Discussion</td>
<td>192</td>
</tr>
<tr>
<td>3.5 Principal Findings</td>
<td>203</td>
</tr>
<tr>
<td>4.0 PATTERNS OF SPECIES RICHNESS</td>
<td>206</td>
</tr>
<tr>
<td>4.1 Introduction</td>
<td>206</td>
</tr>
<tr>
<td>4.2 Study Methods</td>
<td>213</td>
</tr>
<tr>
<td>4.2.1 Environmental Correlates of Richness</td>
<td>213</td>
</tr>
<tr>
<td>4.2.1.1 Generalized Linear Regression Models</td>
<td>214</td>
</tr>
<tr>
<td>4.2.1.2 Contribution of Forest Stand Structure</td>
<td>215</td>
</tr>
<tr>
<td>4.2.1.3 Contribution of Soil Fertility</td>
<td>216</td>
</tr>
<tr>
<td>4.2.1.4 Contribution of Patch Isolation and Patch Size</td>
<td>217</td>
</tr>
<tr>
<td>4.2.1.5 Contribution of Microhabitats</td>
<td>218</td>
</tr>
</tbody>
</table>
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.2.2</td>
<td>Plant Trait Correlates of Richness</td>
<td>218</td>
</tr>
<tr>
<td>4.2.3</td>
<td>Comparison of Alternative Models of Species Richness</td>
<td>219</td>
</tr>
<tr>
<td>4.2.4</td>
<td>Contribution of Phylogeny</td>
<td>220</td>
</tr>
<tr>
<td>4.3</td>
<td>Study Results</td>
<td>221</td>
</tr>
<tr>
<td>4.3.1.1</td>
<td>Environmental Correlates of Richness</td>
<td>221</td>
</tr>
<tr>
<td>4.3.1.2</td>
<td>Contribution of Forest Stand Structure</td>
<td>236</td>
</tr>
<tr>
<td>4.3.1.3</td>
<td>Contribution of Soil Fertility</td>
<td>239</td>
</tr>
<tr>
<td>4.3.1.4</td>
<td>Contribution of Patch Isolation and Patch Size</td>
<td>248</td>
</tr>
<tr>
<td>4.3.1.5</td>
<td>Contribution of Microhabitats</td>
<td>249</td>
</tr>
<tr>
<td>4.3.2</td>
<td>Plant Trait Correlates of Richness</td>
<td>257</td>
</tr>
<tr>
<td>4.3.3</td>
<td>Comparison of Alternative Models of Species Richness</td>
<td>270</td>
</tr>
<tr>
<td>4.3.4</td>
<td>Contribution of Phylogeny</td>
<td>279</td>
</tr>
<tr>
<td>4.4</td>
<td>Discussion</td>
<td>286</td>
</tr>
<tr>
<td>4.5</td>
<td>Principal Findings</td>
<td>301</td>
</tr>
<tr>
<td>5.0</td>
<td>GENERAL CONCLUSIONS</td>
<td>306</td>
</tr>
<tr>
<td>6.0</td>
<td>LITERATURE CITED</td>
<td>322</td>
</tr>
<tr>
<td>Appendix</td>
<td>Title</td>
<td>Page</td>
</tr>
<tr>
<td>----------</td>
<td>----------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>1</td>
<td>Location of study sites</td>
<td>369</td>
</tr>
<tr>
<td>2</td>
<td>Summary of plant attributes by species</td>
<td>372</td>
</tr>
<tr>
<td>3</td>
<td>Species codes</td>
<td>395</td>
</tr>
<tr>
<td>4</td>
<td>Distribution of species by soil parent material, soil order, soil moisture and canopy closure</td>
<td>407</td>
</tr>
<tr>
<td>5</td>
<td>Listing of species by microhabitat</td>
<td>424</td>
</tr>
<tr>
<td>6</td>
<td>Distribution of species by microhabitat: closed canopy</td>
<td>439</td>
</tr>
<tr>
<td>7</td>
<td>Distribution of species by microhabitat: open canopy</td>
<td>456</td>
</tr>
<tr>
<td>8</td>
<td>Environmental data summary by quadrat (I)</td>
<td>473</td>
</tr>
<tr>
<td>9</td>
<td>Environmental data summary by quadrat (II)</td>
<td>483</td>
</tr>
<tr>
<td>10</td>
<td>Environmental data summary by quadrat (III)</td>
<td>492</td>
</tr>
<tr>
<td>11</td>
<td>Representative seed dispersal distances of native and alien species in North America</td>
<td>501</td>
</tr>
<tr>
<td>12</td>
<td>Principal frugivores of eastern North America</td>
<td>514</td>
</tr>
<tr>
<td>13</td>
<td>Known myrmecochores in the U.S. Northeast</td>
<td>517</td>
</tr>
<tr>
<td>14</td>
<td>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</td>
<td>520</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table 1.1  Comparison of dispersal spectra in plant communities of broadly similar structure in eastern North America ................................................................. 4
Table 2.1  Size distribution of sampled forest patches .................................................. 13
Table 2.2  Summary of environmental variables .......................................................... 16
Table 2.3  Definition and areal extent of forest microhabitats ....................................... 27
Table 2.4  Summary of surveyed taxa by taxonomic rank, life form, life history and provenance ................................................................. 43
Table 2.5  Cover class of surveyed taxa in herb layer in 10m x 10m quadrats by life form, life history, provenance, and habitat affinity .................................................. 45
Table 2.6  Check list of surveyed taxa by family (alphabetical order) ............................... 46
Table 2.7  Distribution of selected environmental variables by soil parent material ......... 56
Table 2.8  Distribution of selected environmental variables by soil order ....................... 57
Table 2.9  Distribution of selected environmental variables by soil moisture class ........... 58
Table 2.10 Distribution of selected environmental variables by forest cover type .......... 59
Table 2.11 Attributes of forest stand structure by forest cover type ............................. 60
Table 2.12 Distribution of selected environmental variables by patch size ..................... 61
Table 2.13 Relative importance of environmental variables in species ordination (CCA) 68
Table 2.14 Number of species with a restricted and unrestricted spatial distribution in relation to soil parent material, soil order, soil moisture, forest cover type and canopy closure ................................................................. 70
Table 2.15 Number of microhabitats occupied by surveyed taxa .................................. 75
Table 2.16 Proportion of total inertia in the dispersion of species scores (CCA) explained by functional attributes of sampled plants .................................................. 88
Table 2.17 Shade tolerance of sampled flora by life form ............................................. 90
Table 2.18 Moisture tolerance of sampled flora by life form ........................................ 91
Table 2.19 Percentage of classified taxa in surveyed microhabitats by provenance, habitat affinity, and moisture affinity ................................................................. 92
Table 3.1  Dispersal modes of surveyed taxa by life form ............................................. 138
Table 3.2  Life history of surveyed taxa by dispersal mode and life form ......................... 140
Table 3.3  Provenance of surveyed taxa by dispersal mode and life form ......................... 142
Table 3.4  Modality of surveyed taxa by dispersal mode and life form ............................ 145
Table 3.5  Fruit type of surveyed herbs by dispersal mode ........................................... 147
Table 3.6  Distribution of dispersal modes by taxonomic rank I (genus) ......................... 150
Table 3.7  Distribution of dispersal modes by taxonomic rank II (family) ....................... 151
Table 3.8  Distribution of dispersal modes by taxonomic rank III (order) ....................... 152
Table 3.9  Dispersal modes of herbs by habitat affinity ............................................... 153
Table 3.10 Dispersal modes of herbs by moisture affinity ............................................ 155
Table 3.11 Dispersal modes of herbs by shade tolerance ............................................. 156
Table 3.12 Distribution of herbs in 10m x 10m quadrats by environmental attribute and dispersal mode .................................................................................. 158
Table 3.13 Number of observed and expected herbs in surveyed microhabitats by
LIST OF TABLES

Table 3.14 Difference in mean percent of herbs (n=234) by mode of dispersal in contrasting microhabitats within 10m x 10m quadrats: paired samples ........................................ 177
Table 3.15 Mean percent of herbs (n=234) by mode of dispersal in contrasting microhabitats within 10m x 10m quadrats: independent samples ........................................ 180
Table 3.16 Dispersal modes of herbs (n=252) by frequency class ........................................ 185
Table 3.17 Dispersal modes of herbs (n=252) by cover class ........................................ 186
Table 3.18 Dispersal modes of herbs (n=252) by species richness class ........................................ 188
Table 3.19 Dispersal modes of herbs (n=252) by patch size class ........................................ 190
Table 3.20 Dispersal modes of herbs (n=252) by patch isolation class ........................................ 191
Table 4.1 Environmental correlates of species richness in 10m x 10m quadrats ........................................ 222
Table 4.2 Species richness (10m x10m quadrats) of soil parent materials, soil orders, soil moisture classes, forest cover types and disturbance classes ........................................ 231
Table 4.3 Selected correlations involving # tree species, % stems sugar maple, and # tree stems 0-4 cm dbh ........................................ 237
Table 4.4 Contribution of microhabitats to species richness in 10m x 10m quadrats ........................................ 250
Table 4.5 Contribution of microhabitats to species richness in surveyed forest patches ........................................ 252
Table 4.6 Contribution of microhabitats to species richness at the landscape scale ........................................ 254
Table 4.7 Comparison of microhabitats by moisture and canopy closure class ........................................ 256
Table 4.8 Plant trait correlates of species richness in 10m x 10m quadrats ........................................ 258
Table 4.9 Comparison of selected GLM models of species richness ........................................ 271
Table 4.10 Summary of graphical evaluation of leading models of species richness ........................................ 275
Table 4.11 Explanatory variables included in leading models of species richness ........................................ 280
Table 4.12 Contribution of phylogeny to superior models of species richness ........................................ 282
Table 4.13 Proportion of taxa with selected plant attributes at progressively more inclusive taxonomic ranks ........................................ 285
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Distribution of forest patches (N=24) in relation to DCA axes 1 and 2</td>
<td>64</td>
</tr>
<tr>
<td>2.2</td>
<td>Species ordination (CCA) constrained by environmental variables</td>
<td>67</td>
</tr>
<tr>
<td>2.3</td>
<td>Partial decomposition of variance in CCA species ordination: local versus regional processes</td>
<td>72</td>
</tr>
<tr>
<td>2.4</td>
<td>Distribution of microhabitats in relation to DCA axes 1 and 2</td>
<td>74</td>
</tr>
<tr>
<td>2.5</td>
<td>DCA ordination of open, seasonally dry, canopy gaps</td>
<td>78</td>
</tr>
<tr>
<td>2.6</td>
<td>Distribution of species among microhabitats</td>
<td>80</td>
</tr>
<tr>
<td>2.7</td>
<td>Sugar maple abundance versus calcium in upper 15 cm of soil profile on Brunisolic and Luvisolic soils overlying calcareous till</td>
<td>82</td>
</tr>
<tr>
<td>2.8</td>
<td>Sugar maple abundance versus calcium in upper 15 cm of soil profile on Brunisolic soils overlying calcareous till</td>
<td>83</td>
</tr>
<tr>
<td>2.9</td>
<td>Herb response to increasing sugar maple abundance and available calcium on Brunisolic and Luvisolic soils overlying calcareous till</td>
<td>85</td>
</tr>
<tr>
<td>3.1</td>
<td>Mean calcium affinity and shade tolerance of understory plants in relation to flowering phenology</td>
<td>86</td>
</tr>
<tr>
<td>3.2</td>
<td>Distribution of herbs dispersed by animal ingestion and by animal adhesion in relation to DCA axes 1 and 2</td>
<td>162</td>
</tr>
<tr>
<td>3.3</td>
<td>Distribution of herbs dispersed by ants and wind in relation to DCA axes 1 and 2</td>
<td>163</td>
</tr>
<tr>
<td>3.4</td>
<td>Distribution of herbs dispersed by prolonged dormancy in the soil and by mechanical expulsion in relation to DCA axes 1 and 2</td>
<td>164</td>
</tr>
<tr>
<td>3.5</td>
<td>Distribution of herbs dispersed by unassisted means and by multiple modes in relation to DCA axes 1 and 2</td>
<td>165</td>
</tr>
<tr>
<td>3.6</td>
<td>Distribution of dispersal modes of herbs in relation to environmental variables</td>
<td>166</td>
</tr>
<tr>
<td>4.1</td>
<td>Scatter plots of selected correlates of species richness in 10m x 10m quadrats I</td>
<td>227</td>
</tr>
<tr>
<td>4.2</td>
<td>Scatter plots of selected correlates of species richness in 10m x 10m quadrats II</td>
<td>228</td>
</tr>
<tr>
<td>4.3</td>
<td>Scatter plots of selected correlates of species richness in 10m x 10m quadrats III</td>
<td>229</td>
</tr>
<tr>
<td>4.4</td>
<td>Scatter plots of selected correlates of species richness in 10m x 10m quadrats IV</td>
<td>230</td>
</tr>
<tr>
<td>4.5</td>
<td>Species richness, sugar maple abundance, and available calcium, in 10m x 10m quadrats on Brunisolic and Luvisolic soils overlying calcareous till</td>
<td>241</td>
</tr>
<tr>
<td>4.6</td>
<td>Species richness, sugar maple abundance, and available calcium, in 10m x 10m quadrats on Brunisolic soils overlying calcareous till</td>
<td>242</td>
</tr>
<tr>
<td>4.7</td>
<td>Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility I</td>
<td>244</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

| Figure 4.8 | Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility II. | 245 |
| Figure 4.9 | Comparison of mean plant response in 10m x 10m quadrats on soils of contrasting fertility III. | 246 |
| Figure 4.10 | Scatter plots of dispersal correlates of species richness in 10m x 10m quadrats I | 264 |
| Figure 4.11 | Scatter plots of dispersal correlates of species richness in 10m x 10m quadrats II. | 265 |
| Figure 4.12 | Representative results from graphical evaluation of leading GLM Models of species richness | 277 |
| Figure 4.13 | Graphical evaluation of superior GLM models of species richness. | 278 |
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 diaspor 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 (Schmid 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 Gurvies 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
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.

<table>
<thead>
<tr>
<th>Community</th>
<th>Mode of Dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AI</td>
</tr>
<tr>
<td>Deciduous Forests:</td>
<td></td>
</tr>
<tr>
<td>Illinois, Michigan, Tennessee(^4) (n=4)</td>
<td>29</td>
</tr>
<tr>
<td>Quebec: climax(^1) (n=3)</td>
<td>-</td>
</tr>
<tr>
<td>Quebec: disturbed(^1) (n=3)</td>
<td>-</td>
</tr>
<tr>
<td>Wisconsin: forest islands 1951(^2) (n=4)</td>
<td>23</td>
</tr>
<tr>
<td>Wisconsin: forest islands 1975(^2) (n=4)</td>
<td>26</td>
</tr>
<tr>
<td>This Study (n=24)</td>
<td>17</td>
</tr>
<tr>
<td>Conifer Forests:</td>
<td></td>
</tr>
<tr>
<td>Minnesota(^1) (n=1)</td>
<td>22</td>
</tr>
<tr>
<td>Quebec(^1) (n=1)</td>
<td>-</td>
</tr>
<tr>
<td>Island Flora:</td>
<td></td>
</tr>
<tr>
<td>Ontario(^3) (n=1)</td>
<td>42</td>
</tr>
</tbody>
</table>
Table 1.1 Comparison of dispersal spectra in plant communities of broadly similar structure in Eastern North America (cont’d).

<table>
<thead>
<tr>
<th>Community</th>
<th>Mode of Dispersal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AI</td>
</tr>
<tr>
<td>Old Field</td>
<td>-</td>
</tr>
<tr>
<td>Quebec¹ (n=1)</td>
<td>-</td>
</tr>
<tr>
<td>Bluegrass Meadow</td>
<td>-</td>
</tr>
<tr>
<td>Quebec¹ (n=1)</td>
<td>-</td>
</tr>
<tr>
<td>Alder Thicket</td>
<td>-</td>
</tr>
<tr>
<td>Fen</td>
<td>-</td>
</tr>
</tbody>
</table>
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 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),

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 (Horn 1971), 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 (Schmid 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).

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.

<table>
<thead>
<tr>
<th>Size Class (ha)</th>
<th>Landscape I (15% forest cover)</th>
<th></th>
<th>Landscape II (35% forest cover)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># Patches</td>
<td>% (N=12)</td>
<td># Patches</td>
</tr>
<tr>
<td>10-20</td>
<td>1</td>
<td>8.3</td>
<td>10-20</td>
</tr>
<tr>
<td>21-50</td>
<td>3</td>
<td>25.0</td>
<td>21-50</td>
</tr>
<tr>
<td>51-100</td>
<td>5</td>
<td>41.7</td>
<td>51-100</td>
</tr>
<tr>
<td>101-500</td>
<td>3</td>
<td>25.0</td>
<td>101-500</td>
</tr>
<tr>
<td>&gt;500</td>
<td>0</td>
<td>0</td>
<td>&gt;500</td>
</tr>
<tr>
<td>Total</td>
<td>12</td>
<td>100.0</td>
<td>Total</td>
</tr>
</tbody>
</table>

Notes:
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 09 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°C, with a mean daily temperature of -9.4°C in January and 20.0°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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Attribute</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>soil parent material</td>
<td>1. glacio-fluvial</td>
<td>Weber and Morwick (1946)</td>
</tr>
<tr>
<td></td>
<td>2. calcareous till</td>
<td>Gillespie and Acton (1981)</td>
</tr>
<tr>
<td></td>
<td>3. calcareous outwash</td>
<td>Hoffman and Acton (1974)</td>
</tr>
<tr>
<td></td>
<td>4. lacustrine</td>
<td></td>
</tr>
<tr>
<td>soil order</td>
<td>1. brunisol</td>
<td>Weber and Morwick (1946)</td>
</tr>
<tr>
<td></td>
<td>2. gleyed brunisol</td>
<td>Gillespie and Acton (1981)</td>
</tr>
<tr>
<td></td>
<td>3. luvisol</td>
<td>Hoffman and Acton (1974)</td>
</tr>
<tr>
<td></td>
<td>4. gleyed luvisol</td>
<td>field observation</td>
</tr>
<tr>
<td></td>
<td>5. gleysol</td>
<td></td>
</tr>
<tr>
<td>soil moisture class</td>
<td>1. seasonally wet depressions</td>
<td>field observation</td>
</tr>
<tr>
<td></td>
<td>2. seasonally moist depressions</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. seasonally dry depressions</td>
<td></td>
</tr>
<tr>
<td>soil organic matter</td>
<td>continuous variable</td>
<td>laboratory observation</td>
</tr>
<tr>
<td>soil pH</td>
<td>continuous variable</td>
<td>laboratory observation</td>
</tr>
<tr>
<td>base cations</td>
<td>1. available calcium</td>
<td>laboratory observation</td>
</tr>
<tr>
<td></td>
<td>2. calcium:magnesium ratio</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. potassium:magnesium ratio</td>
<td></td>
</tr>
<tr>
<td>tree diameter class. breast height</td>
<td>1. 0-30 cm: 2 cm increments</td>
<td>field observation</td>
</tr>
<tr>
<td></td>
<td>2. &gt; 30.0 cm: continuous values measured to nearest 0.1 cm</td>
<td></td>
</tr>
<tr>
<td>tree height class</td>
<td>1. &lt; 1 m</td>
<td>field observation</td>
</tr>
<tr>
<td></td>
<td>2. 1-3 m</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. 3-10 m</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4. 10-15 m</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5. 15-25 m</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6. &gt; 25 m</td>
<td></td>
</tr>
<tr>
<td>forest stratum</td>
<td>1. herb layer (&lt;1 m)</td>
<td>field observation</td>
</tr>
<tr>
<td></td>
<td>2. shrub layer (1-3 m)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. subcanopy (3-15m)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4. canopy (&gt;15 m)</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2  Summary of environmental variables (cont’d).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Attribute</th>
<th>Source</th>
</tr>
</thead>
</table>
| 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  
| 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).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Attribute</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>patch interior area class</td>
<td>1. 0-5 ha</td>
<td>M. Austen, <em>pers. com.</em></td>
</tr>
<tr>
<td></td>
<td>2. 6-10 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3. 11-20 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4. 21-50 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5. 51-100 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6. 101-200 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7. 201-500 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8. 501-1000 ha</td>
<td></td>
</tr>
<tr>
<td>patch area</td>
<td>continuous variable</td>
<td>Ontario Ministry of Natural Resources (1978, 1979, 1980)</td>
</tr>
<tr>
<td>patch isolation</td>
<td>continuous variable</td>
<td>NTS map sheets (1:50,000)</td>
</tr>
<tr>
<td>forest cover</td>
<td>continuous variable</td>
<td>NTS map sheets (1:50,000)</td>
</tr>
</tbody>
</table>
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 (Ponnampemuna 1972) and to lower rates of ammonification (Patrick and Mahaptera 1968, Ponnampemuna 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:

\[
\text{\% SOM} = \left( \frac{\text{"soil"} - \text{"ash"}}{\text{"soil"}} \right) \times 100
\]
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<sub>water</sub> 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 lanthanum chloride, with the aid
of a Nichiryo AutoDilutor. The following equation was used to calculate the concentration of base cations:

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

The concentration of cations was subsequently expressed in centimoles \((10^{-2} \text{ moles})\) per kg of soil \((\text{cmol/kg})\). 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 Straturn**: 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° 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 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 to 14 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 Ovaies. 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 (+); ii) 2-5 individuals (r); iii) < 1%; iv) 1-5%; v) 6-15%; vi) 16-25%; vii) 26-50%; viii) 51-75%; ix) 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 m²).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>% SA</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>seasonally dry forest floors-cc</td>
<td>54.3</td>
<td>forest floors, sensu stricto, that are seasonally dry and under a closed canopy</td>
</tr>
<tr>
<td>seasonally dry forest floors-oc</td>
<td>6.8</td>
<td>forest floors, sensu stricto, that are seasonally dry and under an open canopy</td>
</tr>
<tr>
<td>seasonally moist forest floors-cc</td>
<td>3.0</td>
<td>forest floors, sensu stricto, that are seasonally moist and under a closed canopy</td>
</tr>
<tr>
<td>seasonally moist forest floors-oc</td>
<td>3.0</td>
<td>forest floors, sensu stricto, that are seasonally moist and under an open canopy</td>
</tr>
<tr>
<td>seasonally moist forest depressions-cc</td>
<td>4.1</td>
<td>forest depressions (depression in forest floor &gt;20 cm deep) that are seasonally moist and under a closed canopy</td>
</tr>
<tr>
<td>seasonally moist forest depressions-oc</td>
<td>0.2</td>
<td>forest depressions (depression in forest floor &gt;20 cm deep) that are seasonally moist and under an open canopy</td>
</tr>
<tr>
<td>seasonally wet forest floors-cc</td>
<td>0.6</td>
<td>forest floors, sensu stricto, that are seasonally wet and under a closed canopy</td>
</tr>
<tr>
<td>seasonally wet forest depressions-cc</td>
<td>4.0</td>
<td>forest depressions (depression in forest floor &gt;20 cm deep) that are seasonally wet and under a closed canopy</td>
</tr>
<tr>
<td>seasonally wet forest depressions-oc</td>
<td>1.0</td>
<td>forest depressions (depression in forest floor &gt;20 cm deep) that are seasonally wet and under an open canopy</td>
</tr>
</tbody>
</table>
Table 2.3. Definition and areal extent of forest microhabitats (cont’d).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>% SA</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>seep-cc</td>
<td>0.9</td>
<td>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 &gt;30% by weight)</td>
</tr>
<tr>
<td>seep-oc</td>
<td>0.3</td>
<td>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 &gt;30% by weight)</td>
</tr>
<tr>
<td>seasonally dry gap-cc</td>
<td>2.2</td>
<td>forest floors, <em>sensu stricto</em>, that are seasonally dry, and under a closed canopy of trees, saplings or tall shrubs; canopy stratum (&gt;15 m) missing</td>
</tr>
<tr>
<td>seasonally dry gap-oc</td>
<td>6.8</td>
<td>forest floors, <em>sensu stricto</em>, that are seasonally dry, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (&gt;15 m) missing</td>
</tr>
<tr>
<td>seasonally moist gap-cc</td>
<td>0.5</td>
<td>forest floors, <em>sensu stricto</em>, that are seasonally moist, and under a closed canopy of trees, saplings or tall shrubs; canopy stratum (&gt;15 m) missing</td>
</tr>
<tr>
<td>seasonally moist gap-oc</td>
<td>3.0</td>
<td>forest floors, <em>sensu stricto</em>, that are seasonally moist, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (&gt;15 m) missing</td>
</tr>
<tr>
<td>seasonally wet gap-oc</td>
<td>1.0</td>
<td>forest floors, <em>sensu stricto</em>, that are seasonally wet, and under an open canopy; shrub (1-3m), subcanopy (3-15 m), and canopy stratum (&gt;15 m) missing</td>
</tr>
<tr>
<td>mound-cc</td>
<td>3.6</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying above the plane of the forest floor</td>
</tr>
<tr>
<td>Microhabitat</td>
<td>% SA</td>
<td>Description</td>
</tr>
<tr>
<td>-------------------</td>
<td>------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>mound-oc</td>
<td>0.4</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying above the plane of the forest floor</td>
</tr>
<tr>
<td>seasonally dry pit-cc</td>
<td>1.5</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying below the plane of the forest floor.</td>
</tr>
<tr>
<td>seasonally dry pit-oe</td>
<td>0.3</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying below the plane of the forest floor.</td>
</tr>
<tr>
<td>seasonally moist pit-cc</td>
<td>0.3</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying below the plane of the forest floor.</td>
</tr>
<tr>
<td>seasonally wet pit-cc</td>
<td>0.2</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying below the plane of the forest floor.</td>
</tr>
<tr>
<td>seasonally wet pit-oe</td>
<td>0.1</td>
<td>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; <em>sensu stricto</em>, the portion of a pit-mound complex lying below the plane of the forest floor.</td>
</tr>
<tr>
<td>log-cc</td>
<td>0.5</td>
<td>a tree hole (&gt; 4 cm dbh) that is in contact with the earth and under a closed canopy</td>
</tr>
<tr>
<td>log-oc</td>
<td>0.2</td>
<td>a tree hole (&gt; 4 cm dbh) that is in contact with the earth and under an open canopy</td>
</tr>
</tbody>
</table>
Table 2.3. Definition and areal extent of forest microhabitats (cont’d).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>% SA</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>stump-cc</td>
<td>0.2</td>
<td>the upright remnant of a cut or wind-thrown tree that is under a closed canopy</td>
</tr>
<tr>
<td>stump-oc</td>
<td>0.1</td>
<td>the upright remnant of a cut or wind-thrown tree that is under an open canopy</td>
</tr>
<tr>
<td>raised root mat-cc</td>
<td>1.3</td>
<td>the root mat of a partially wind-thrown tree, typically associated with seasonally moist or wet soils, and, a deep (&gt;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)</td>
</tr>
<tr>
<td>raised root mat-oc</td>
<td>0.6</td>
<td>the root mat of a partially wind-thrown tree, typically associated with seasonally moist or wet soils, and, a deep (&gt;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)</td>
</tr>
<tr>
<td>stone-cc</td>
<td>&lt;0.1</td>
<td>exposed, limestone, boulders, under a closed canopy</td>
</tr>
<tr>
<td>lane/road-cc</td>
<td>2.3</td>
<td>a farm lane, or forest access road, under a closed canopy</td>
</tr>
<tr>
<td>lane/road-oc</td>
<td>1.3</td>
<td>a farm lane, or forest access road, under an open canopy</td>
</tr>
<tr>
<td>ditch-cc</td>
<td>0.3</td>
<td>a ditch associated with a farm lane or forest access road, under a closed canopy</td>
</tr>
<tr>
<td>ditch-oc</td>
<td>&lt;0.1</td>
<td>a ditch associated with a farm lane or forest access road, under an open canopy</td>
</tr>
<tr>
<td>regenerating field-cc</td>
<td>1.3</td>
<td>a plowed, farm field that is undergoing forest succession and presently is under a closed canopy of saplings or tall shrubs</td>
</tr>
<tr>
<td>regenerating field-oc</td>
<td>1.3</td>
<td>a plowed, farm field that is undergoing forest succession and presently is in the &quot;old field&quot; stage, under an open canopy</td>
</tr>
</tbody>
</table>
Table 2.3. Definition and areal extent of forest microhabitats (cont’d).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>% SA</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>riparian meadow-oc</td>
<td>0.7</td>
<td>a seasonally flooded, riparian meadow, on mineral soil, under an open canopy that has been maintained by periodic cutting</td>
</tr>
<tr>
<td>riparian marsh-oc</td>
<td>0.4</td>
<td>a seasonally flooded, shallow marsh, on organic soil</td>
</tr>
<tr>
<td>riparian thicket-oc</td>
<td>0.1</td>
<td>a seasonally flooded thicket swamp, on mineral soil, under an open canopy that has been maintained by periodic cutting</td>
</tr>
</tbody>
</table>
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. comm.*). 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. comm.*). 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 $45^\circ$ 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, \textit{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 − 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 m², 11-20 m², 21-30 m², 31-40 m², 41-50 m², 51-60 m², 61-70 m², 71-80 m², 81-90 m², 91-100 m². 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 were 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 Appendix 2: 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.

<table>
<thead>
<tr>
<th>Plant Attribute</th>
<th># Taxa</th>
<th>% (n=413)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TAXONOMIC RANK</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>species</td>
<td>413</td>
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<tr>
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<tr>
<td>order</td>
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<tr>
<td><strong>LIFE FORM</strong></td>
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<td></td>
</tr>
<tr>
<td>tree</td>
<td>30</td>
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</tr>
<tr>
<td>shrub</td>
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<tr>
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</tr>
<tr>
<td><strong>LIFE HISTORY</strong></td>
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<tr>
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<td>3.1</td>
</tr>
<tr>
<td>biennial ( s.l. )</td>
<td>22</td>
<td>5.3</td>
</tr>
<tr>
<td>perennial ( s.l. )</td>
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<td>1.5</td>
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<td><strong>PROVENANCE</strong></td>
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<td>58</td>
<td>14.0</td>
</tr>
<tr>
<td>unknown</td>
<td>6</td>
<td>1.5</td>
</tr>
</tbody>
</table>
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 significantly 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 racemosum, 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 in 10m 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.

<table>
<thead>
<tr>
<th>Plant Attribute</th>
<th>Mean</th>
<th>Median</th>
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Table 2.6. Check list of surveyed taxa by family (alphabetical order).

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<td><em>Bidens frondosa</em> L.</td>
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<td><em>Carduus acanthoides</em> L.</td>
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<td><em>Carduus nutans</em> L.</td>
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<td><em>Chrysanthemum leucanthemum</em> L.</td>
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<td><em>Cirsium arvense</em> (L.) Scop.</td>
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<td><em>Cirsium vulgare</em> (Savi) Ten.</td>
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<td><em>Conyza canadensis</em> (L.) Cronq.</td>
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<td><em>Erigeron annuus</em> (L.) Pers.</td>
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<td><em>Erigeron philadelphicus</em> L. ssp. <em>philadelphicus</em></td>
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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 dentatum L.
Viburnum opulus L.
Viburnum trilobum Marshall

47
Table 2.6. Check list of surveyed taxa by family (alphabetical order).

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<th>FAMILY</th>
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<td><em>Stellaria longifolia</em> Muhlenb. ex Willd.</td>
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<td><em>Carex bebbii</em> (L. Bailey) Olney ex Fern.</td>
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<td><em>Carex crinita</em> Lam.</td>
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Table 2.6. Check list of surveyed species by family (alphabetical order).

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<td>Equisetum scirpooides Michaux</td>
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<td>Dicentra cucullaria (L.) Bernh.</td>
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<td>GERANIACEAE</td>
<td>Geranium maculatum L.</td>
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Table 2.6. Check list of surveyed species by family (alphabetical order).

<table>
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<th>Family</th>
<th>Species</th>
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<td><em>Ribes lacustre</em> (Pers.) Poiret</td>
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<td><em>Ribes rubrum</em> L.</td>
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<td><em>Ribes triste</em> Pall.</td>
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<td><em>Ribes specimen D827</em></td>
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<td><em>Iris species</em></td>
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<td>JUGLANDACEAE</td>
<td><em>Carya cordiformis</em> (Wangenh.) K. Koch</td>
</tr>
<tr>
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<td><em>Juncus tenuis</em> Willd.</td>
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<td><em>Galeopsis tetrahit</em> L.</td>
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<td><em>Leonurus cardiaca</em> L. ssp. cardiaca</td>
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<tr>
<td></td>
<td><em>Lycopus americanus</em> Muhlenb. ex Bartram</td>
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<tr>
<td></td>
<td><em>Lycopus uniflorus</em> Michaux</td>
</tr>
<tr>
<td></td>
<td><em>Mentha arvensis</em> L.</td>
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<td><em>Scutellaria lateriflora</em> L.</td>
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<td><em>Polygonatum pubescens</em> (Willd.) Pursh</td>
</tr>
<tr>
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<td><em>Spreptopus roseus</em> Michaux</td>
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<td><em>Trillium erectum</em> L.</td>
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<td><em>Trillium grandiflorum</em> (Michaux) Salisb.</td>
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<td></td>
<td><em>Uvularia grandiflora</em> Smith</td>
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<td>LYCOPODIACEAE</td>
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<td><em>Lycopodium dendroideum</em> Michaux</td>
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<td><em>Lycopodium obscurum</em> L. var. obscurum</td>
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<td><em>Lycopodium tristachyum</em> Pursh</td>
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<td>MENISPERMACEAE</td>
<td><em>Menispermum canadense</em> L.</td>
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<td>MONOTROPACEAE</td>
<td><em>Monotropa hypopithys</em> L.</td>
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<tr>
<td></td>
<td><em>Monotropa uniflora</em> L.</td>
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<td><em>Fraxinus americana</em> L.</td>
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<tr>
<td></td>
<td><em>Fraxinus nigra</em> Marshall</td>
</tr>
<tr>
<td></td>
<td><em>Fraxinus pennsylvanica</em> Marshall</td>
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<td>ONAGRACEAE</td>
<td><em>Circea alpina</em> L.</td>
</tr>
<tr>
<td></td>
<td><em>Circea lutetiana</em> L. ssp. canadensis (L.) Aschers. &amp; Magnus</td>
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<tr>
<td></td>
<td><em>Epilobium ciliatum</em> Raf.</td>
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50
Table 2.6. Check list of surveyed species by family (alphabetical order).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
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</thead>
<tbody>
<tr>
<td><strong>Epilobium coloratum</strong></td>
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<td><strong>Epilobium leptophyllum</strong></td>
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<td><strong>Epilobium parviflorum</strong></td>
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<td><strong>Botrychium matricariifolium</strong> A. Braun ex Koch</td>
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<td><strong>Botrychium multifidum</strong> (S. Gmelin) Rupr.</td>
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<td><strong>Botrychium virginianum</strong> (L.) Sw.</td>
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<td><strong>Orbanchaceae</strong></td>
<td><strong>Epifagus virginiana</strong> (L.) Barton</td>
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<td><strong>Cypripedium calceolus</strong> L.</td>
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<td></td>
<td><strong>Liparis loeselii</strong> (L.) Rich. ex Lindley</td>
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<td><strong>Osmunda regalis</strong> L.</td>
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<td><strong>Oxalis stricta</strong> L.</td>
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<td><strong>Sanguinaria canadensis</strong> L.</td>
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<td><strong>Pinaceae</strong></td>
<td><strong>Abies balsamea</strong> (L.) Miller</td>
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<tr>
<td></td>
<td><strong>Picea glauca</strong> (Moench) Voss</td>
</tr>
<tr>
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<td><strong>Pinus strobus</strong> L.</td>
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<td></td>
<td><strong>Tsuga canadensis</strong> (L.) Carriere</td>
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<tr>
<td><strong>Plantaginaceae</strong></td>
<td><strong>Plantago lanceolata</strong> L.</td>
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<td></td>
<td><strong>Plantago major</strong> L.</td>
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<td></td>
<td><strong>Plantago rugelii</strong> Decne.</td>
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<tr>
<td><strong>Poaceae</strong></td>
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<tr>
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<td><strong>Agrostis stolonifera</strong> L.</td>
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<td><strong>Brachyelytrum erectum</strong> (Schreber in Roth ex Sprengel) P. Beauv.</td>
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<td><strong>Bromus inermis</strong> Leysser</td>
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<td><strong>Cinna latifolia</strong> (Trevir.ex Goeppinger) Griseb. in Ledeb.</td>
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<td><strong>Dactylis glomerata</strong> L.</td>
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<td></td>
<td><strong>Dianthus spicata</strong> (L.) P. Beauv. ex Roemer &amp; Schultes</td>
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<td><strong>Elymus repens</strong> (L.) Gould</td>
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<td><strong>Elymus virginicus</strong> L.</td>
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<td><strong>Festuca arundinacea</strong> Schreber</td>
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<td><strong>Festuca pratensis</strong> Hudson</td>
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<td></td>
<td><strong>Festuca rubra</strong> L.</td>
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<td><strong>Festuca subverticillata</strong> (Pers.) E. Alexeev.</td>
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<td><strong>Glyceria striata</strong> (Lam.) A. Hitch.</td>
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<td></td>
<td><strong>Hystrix patula</strong> Moench</td>
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<tr>
<td></td>
<td><strong>Leersia oryzoides</strong> (L.) Sw.</td>
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<tr>
<td></td>
<td><strong>Leersia virginica</strong> Willd.</td>
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<tr>
<td></td>
<td><strong>Milium effusum</strong> L.</td>
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<tr>
<td></td>
<td><strong>Muhlenbergia frondosa</strong> (Poiret in Lam.) Fern.</td>
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<tr>
<td></td>
<td><strong>Muhlenbergia mexicana</strong> (L.) Trin.</td>
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<tr>
<td></td>
<td><strong>Oryzopsis asperifolia</strong> Michaux</td>
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<tr>
<td></td>
<td><strong>Panicum acuminatum</strong> Sw.</td>
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<tr>
<td></td>
<td><strong>Panicum capillare</strong> L.</td>
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<td></td>
<td><strong>Phalaris arundinacea</strong> L.</td>
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<tr>
<td></td>
<td><strong>Phleum pratense</strong> L.</td>
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<tr>
<td></td>
<td><strong>Poa alsodes</strong> A. Gray</td>
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51
Table 2.6. Check list of surveyed species by family (alphabetical order).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
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</thead>
<tbody>
<tr>
<td>Poa compressa L.</td>
<td>Anemone quinquefolia L.</td>
</tr>
<tr>
<td>Poa palustris L.</td>
<td>Anemone virginiana L.</td>
</tr>
<tr>
<td>Poa pratensis L. ssp. pratensis</td>
<td>Aquilegia canadensis L.</td>
</tr>
<tr>
<td>Poa saltuensis Fern. &amp; Wieg.</td>
<td>Calthus palustris L. ssp. palustris</td>
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<tr>
<td>Poa species</td>
<td>Clematis virginiana L.</td>
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<td>Ranunculus acris L.</td>
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<tr>
<td>Phlox species</td>
<td>Ranunculus hispidus Michaux</td>
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<td>POLYGALACEAE</td>
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<td>Polygonum persicaria L.</td>
<td>Thalictrum dioicum L.</td>
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<td>Rumex orbiculatus A. Gray</td>
<td>Thalictrum pubescens Pursh</td>
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<td>PORTULACACEAE</td>
<td>Rhamnus cathartica L.</td>
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<td>Claytonia caroliniana Michaux</td>
<td>RHAMNACEAE</td>
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<td>Ceanothus americanus L.</td>
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<td>Lysimachia ciliata L.</td>
<td>Rhamnus alnifolia L'Her.</td>
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<td>Lysimachia nummularia L.</td>
<td>Rhamnus cathartica L.</td>
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<td>Lysimachia terrestris (L.) Britton, Sterns &amp; Pogg.</td>
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<td>Tridentalis borealis Raf. ssp. borealis</td>
<td>Agrimonia gryposepala Wallr.</td>
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<td>Amelanchier interior Nielson</td>
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<td>Amelanchier species</td>
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<td>Crataegus species #2</td>
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<td>RANUNCLULACEAE</td>
<td>Crataegus species #3</td>
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<td>Anemone canadensis L.</td>
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<td>Fragaria vesca L. ssp. americana (Porter) Staudt</td>
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<td>Fragaria virginiana Miller</td>
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<td></td>
<td>Geum allepicum Jacq.</td>
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<td>Geum laciniatum Murray</td>
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</table>
Table 2.6. Check list of surveyed species by family (alphabetical order).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
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<tbody>
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<td>Geum urbanum L.</td>
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<td>Geum species</td>
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<td>Potentilla norvegica L.</td>
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<td>Potentilla recta L.</td>
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<td></td>
<td>Prunus serotina Ehrh.</td>
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<tr>
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<td>Prunus virginiana L. spp. virginiana</td>
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<td></td>
<td>Rosa blanda Aiton</td>
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<td></td>
<td>Rosa palustris Marshall</td>
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<td></td>
<td>Rubus allegheniensis Porter</td>
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<td></td>
<td>Rubus idaeus L.</td>
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<td>Rubus occidentalis L.</td>
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<td>Rubus odoratus L.</td>
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<tr>
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<td>Rubus pubescens Raf.</td>
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<td>Rubus specimen D840</td>
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<td>Salix bebbiana Sarg.</td>
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<td>Salix discolor Muhlenb.</td>
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<td>Salix eriocephala Michaux</td>
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<td></td>
<td>Salix petiolaris Smith</td>
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<tr>
<td>SAXIFRAGACEAE</td>
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<td>Mitella diphylla L.</td>
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<td>Tiarella cordifolia L.</td>
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<td>SCROPHULARIACEAE</td>
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<td>Veronica officinalis L.</td>
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<td>Veronica serpyllifolia L.</td>
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<td>Smilax herbacea L.</td>
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<td>Smilax hispida Muhlenb.</td>
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<td>SOLANACEAE</td>
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<td></td>
<td>Solanum dulcamara L.</td>
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<td>TAXACEAE</td>
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<td>THELYPTERIDACEAE</td>
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<td>Phegopteris connectilis (Michaux) Watt</td>
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<td>Thelypteris noveboracensis (L.) Nieuwl.</td>
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<td>Thelypteris palustris (Salisb.) Schott</td>
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<td>THYMELAEACEAE</td>
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<td>Dirca palustris L.</td>
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<td>TYPHACEAE</td>
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<td>Typha latifolia L.</td>
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<td>Tilia americana L.</td>
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<td>ULMACEAE</td>
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53
Table 2.6. Check list of surveyed species by family (alphabetical order).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urticaceae</td>
<td><em>Ulmus americana</em> L.</td>
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<td><em>Boehmeria cylindrica</em> (L.) Sw.</td>
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<td></td>
<td><em>Laportea canadensis</em> (L.) Wedd.</td>
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<tr>
<td></td>
<td><em>Pilea pumila</em> (L.) A. Gray</td>
</tr>
<tr>
<td></td>
<td><em>Urtica dioica</em> L. ssp. <em>gracilis</em></td>
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<tr>
<td></td>
<td><em>Urtica dioica</em> L. ssp. <em>dioica</em></td>
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<td>Verbenaeeae</td>
<td><em>Phryma leptostachya</em> L.</td>
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<td><em>Verbena hastata</em> L.</td>
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<td></td>
<td><em>Verbena urticifolia</em> L.</td>
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<td>Violaceae</td>
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<td><em>Viola labradorica</em> Schrank</td>
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<td><em>Viola pubescens</em> Aiton</td>
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<td><em>Viola rostrata</em> Pursh</td>
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<td><em>Viola sororia</em> Willd</td>
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<td>Vitaceae</td>
<td><em>Parthenocissus inserta</em> (A. Kerner) Fritsch</td>
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<td></td>
<td><em>Vita riparia</em> Michaux</td>
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</tbody>
</table>
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.

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<td>GF (n=40)</td>
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<td>obs.</td>
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<td><strong>SOIL ATTRIBUTES</strong></td>
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<tr>
<td>seasonally dry depressions</td>
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</tr>
<tr>
<td>seasonally moist depressions</td>
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<tr>
<td>seasonally wet depressions</td>
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<tr>
<td>soil pH</td>
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<tr>
<td>available calcium (cmol/kg)</td>
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</tr>
<tr>
<td>% soil organic matter</td>
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<tr>
<td><strong>SOIL ORDER</strong></td>
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<tr>
<td>brunisol</td>
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</tr>
<tr>
<td>luvisol</td>
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</tr>
<tr>
<td>gleyed luvisol</td>
<td>0</td>
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<td>gleyso1</td>
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</tr>
<tr>
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</tr>
<tr>
<td>oak + sugar maple</td>
<td>30</td>
</tr>
<tr>
<td>sugar maple</td>
<td>10</td>
</tr>
<tr>
<td>sugar maple + wet mesic/wet</td>
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</tr>
<tr>
<td>wet mesic/wet</td>
<td>0</td>
</tr>
<tr>
<td><strong>STAND STRUCTURE</strong></td>
<td></td>
</tr>
<tr>
<td>% canopy closure</td>
<td>87.7</td>
</tr>
<tr>
<td># live stems 0-4cm dbh</td>
<td>28.8</td>
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</table>
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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>B (n=70)</th>
<th>gB (n=26)</th>
<th>L (n=57)</th>
<th>gL (n=31)</th>
<th>G (n=8)</th>
</tr>
</thead>
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<tr>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>seasonally dry depressions</td>
<td>67 43.0</td>
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<td>50 35.0</td>
<td>0 19.1</td>
<td>0 4.9</td>
</tr>
<tr>
<td>seasonally moist depressions</td>
<td>0 15.3</td>
<td>19 5.7</td>
<td>1 12.5</td>
<td>18 6.8</td>
<td>4 1.8</td>
</tr>
<tr>
<td>seasonally wet depressions</td>
<td>3 11.7</td>
<td>6 4.3</td>
<td>6 9.5</td>
<td>13 5.2</td>
<td>4 1.3</td>
</tr>
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<td>7.6</td>
<td>6.4</td>
<td>6.7</td>
<td>7.2</td>
</tr>
<tr>
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<td>6.5</td>
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<td>37.4</td>
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<td>41.0</td>
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<td></td>
<td></td>
<td></td>
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<td>0 11.9</td>
<td>0 6.5</td>
<td>0 1.7</td>
</tr>
<tr>
<td>calcareous till</td>
<td>26 37.9</td>
<td>22 14.1</td>
<td>32 30.9</td>
<td>16 16.8</td>
<td>8 4.3</td>
</tr>
<tr>
<td>lacustrine</td>
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<td>0 1.1</td>
<td>0 2.4</td>
<td>8 1.3</td>
<td>0 0.3</td>
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<tr>
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<td>4 5.4</td>
<td>25 11.9</td>
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<td>0 1.7</td>
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</tr>
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<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>oak + sugar maple</td>
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<td>0 7.4</td>
<td>9 15.8</td>
<td>0 8.8</td>
<td>0 2.3</td>
</tr>
<tr>
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<td>4 10.1</td>
<td>43 21.7</td>
<td>8 12.0</td>
<td>0 3.1</td>
</tr>
<tr>
<td>sugar maple + wet mesic/wet</td>
<td>2 18.3</td>
<td>18 6.8</td>
<td>4 14.7</td>
<td>22 8.1</td>
<td>4 2.1</td>
</tr>
<tr>
<td>wet mesic /wet</td>
<td>4 4.8</td>
<td>4 1.8</td>
<td>0 3.8</td>
<td>1 2.1</td>
<td>4 0.5</td>
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<td></td>
<td></td>
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57
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.

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<td>obs.</td>
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</tr>
<tr>
<td>soil pH</td>
<td>6.4</td>
</tr>
<tr>
<td>available calcium (cmol/kg)</td>
<td>6.6</td>
</tr>
<tr>
<td>% soil organic matter</td>
<td>7.3</td>
</tr>
<tr>
<td><strong>SOIL PARENT MATERIAL</strong></td>
<td></td>
</tr>
<tr>
<td>glacial-fluvial</td>
<td>40</td>
</tr>
<tr>
<td>calcareous till</td>
<td>57</td>
</tr>
<tr>
<td>lacustrine</td>
<td>0</td>
</tr>
<tr>
<td>calcareous outwash</td>
<td>21</td>
</tr>
<tr>
<td><strong>SOIL ORDER</strong></td>
<td></td>
</tr>
<tr>
<td>brunsisol</td>
<td>67</td>
</tr>
<tr>
<td>gleyed brunsisol</td>
<td>1</td>
</tr>
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<td>luvisol</td>
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<td>gleyed luvisol</td>
<td>0</td>
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<td>gleyisol</td>
<td>0</td>
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</tr>
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<td>oak</td>
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</tr>
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<td>oak + sugar maple</td>
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<tr>
<td>sugar maple</td>
<td>59</td>
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<tr>
<td>sugar maple + wet mesic/wet</td>
<td>3</td>
</tr>
<tr>
<td>wet mesic /wet</td>
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</tr>
<tr>
<td><strong>CANOPY CLOSURE</strong></td>
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<tr>
<td>% canopy closure</td>
<td>87.7</td>
</tr>
<tr>
<td># live stems 0-4cm dbh</td>
<td>39.9</td>
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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.

<table>
<thead>
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<th>Variable</th>
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<td>4 (n=49)</td>
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<td>obs.</td>
<td>exp.</td>
<td>obs.</td>
<td>exp.</td>
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<td>10</td>
<td>16.3</td>
<td>29</td>
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<td>0</td>
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<td>5</td>
<td>12.4</td>
<td>18</td>
</tr>
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<td>6.6</td>
<td>6.9</td>
<td>7.4</td>
<td></td>
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<td>23.0</td>
<td>29.8</td>
<td></td>
</tr>
<tr>
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<td>11.1</td>
<td>22.9</td>
<td>29.9</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>10</td>
<td>15.5</td>
<td>0</td>
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<td>35</td>
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<td>1</td>
<td>3.1</td>
<td>6</td>
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<td>19</td>
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<td>9</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>brunisol</td>
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<td>19.8</td>
<td>19</td>
<td>27.1</td>
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<td>4</td>
<td>10.1</td>
<td>18</td>
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<td>21.7</td>
<td>14.6</td>
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<td>0</td>
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<td>8</td>
<td>12.0</td>
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<td>0</td>
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59
Table 2.1. Attributes of forest stand structure by forest cover type. Cell values: mean percent of taxa in 10m 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.

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<tr>
<td>mean number</td>
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</tr>
<tr>
<td>median number</td>
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<tr>
<td>range</td>
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<tr>
<td>DBH SIZE CLASS</td>
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<td>% stems 0-4 cm</td>
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</tr>
<tr>
<td>% stems 4-10 cm</td>
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<tr>
<td>% stems 10-30 cm</td>
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</tr>
<tr>
<td>% stems &gt;30 cm</td>
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<tr>
<td>maximum DBH</td>
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<td>mean # species</td>
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<tr>
<td>median # species</td>
<td>-</td>
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<td>range</td>
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<tr>
<td>% CANOPY CLOSURE</td>
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<td>median % closure</td>
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<td>range</td>
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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=43–121 ha, Small=<42 ha. n = number of quadrats in category. Note: oak cover type excluded from analysis.

<table>
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<td>65</td>
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<td>21</td>
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<td>10.5</td>
<td>15</td>
<td>19.3</td>
<td>11</td>
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<tr>
<td>seasonally wet depressions</td>
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</tr>
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<td>glacial-fluvial</td>
<td>16</td>
<td>10.0</td>
<td>24</td>
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<td>0</td>
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<td>0</td>
<td>3.7</td>
<td>0</td>
</tr>
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<td>10.0</td>
<td>8</td>
<td>18.3</td>
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<td>16</td>
<td>11.9</td>
<td>10</td>
</tr>
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<td>luvisol</td>
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<td>26.1</td>
<td>25</td>
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<tr>
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<td>8</td>
<td>3.7</td>
<td>0</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>oak</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>oak + sugar maple</td>
<td>24</td>
<td>13.3</td>
<td>30</td>
<td>24.9</td>
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<tr>
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<td>38</td>
<td>34.1</td>
<td>23</td>
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<td>12.3</td>
<td>16</td>
<td>23.0</td>
<td>25</td>
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<tr>
<td>wet mesic/wet</td>
<td>1</td>
<td>3.2</td>
<td>4</td>
<td>5.0</td>
<td>8</td>
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</tbody>
</table>
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
calcareaous 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 25, 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 1 and 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, forest 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 4-10 cm dbh, # microhabitats, and disturbed
Legend Figure 2.2

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

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 ÷ 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 1) = 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. ASTE-CORD, CARDDPH, CARERCT, CAREDEWE, CARELAXI, CAREROSE, CARPCARO, CLAYCARO, CLINBIOR, EQUISCIR, HYDRVIRG, LACT-CANA, PANAQUIN, RANUABOR, RIEBCYNO, SANGCANA, TILEAME, THUCC, VIOLPUR, 2. ABIBALS, ACERNEGU, ALITRIFIC, CAREPLAN, CAULETHAL, CIRC-LUTE, DRYOCART, DRYOINTE, FRAGVESC, MILIEFFU, POLYACRO, RUBHUDOR, VERBHAP, 3. AMBRARTE, ARCTMINU, CARERADI, CARE, 868, EQUARVE, FESTPRAT, FRAXPENN, JUNCTENU, LODE, SP, POA, ALSO, POTENORV, RUMEORBI, SOLICANA, SOLIRUGO, TARAOFF, VERBHAAS.
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 - Σ unconstrained 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.

<table>
<thead>
<tr>
<th>Environmental Variable</th>
<th>% Variance in Species Composition Explained</th>
<th>% Total Variance</th>
<th>% Unique</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree species</td>
<td>4.7</td>
<td>6.4</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>1.64</td>
<td>1.1</td>
<td>1.8</td>
<td>0.001</td>
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<tr>
<td>Cover type</td>
<td>0.248</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil type</td>
<td>0.61</td>
<td>0.9</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>% Canopy closure</td>
<td>-0.457</td>
<td>-0.464</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Open microhabitats</td>
<td>0.263</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil order</td>
<td>0.248</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Trees 0-30 cm dbh</td>
<td>-0.389</td>
<td>-0.438</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>% Soil organic matter</td>
<td>0.263</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Disturbed microhabitats</td>
<td>0.284</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
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<tr>
<td>Patch isolation</td>
<td>-0.370</td>
<td>-0.438</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Trees 0-4 cm dbh</td>
<td>-0.389</td>
<td>-0.438</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Soil pH</td>
<td>0.263</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td># Live tree species</td>
<td>0.248</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
</tr>
<tr>
<td>Trees 4-10 cm dbh</td>
<td>0.263</td>
<td>0.31</td>
<td>1.8</td>
<td>0.001</td>
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</table>

68
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.

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

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

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

**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 (>>100m²) 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 10m² 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.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Σ Constrained Eigenvalues</th>
<th>Σ Unconstrained Eigenvalues</th>
<th>% Total Inertia Explained</th>
<th>F statistic</th>
<th>p&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Affinity¹</td>
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<td>7.100</td>
<td>10.5</td>
<td>7.35</td>
<td>0.001</td>
</tr>
<tr>
<td>Life Form²</td>
<td>0.689</td>
<td>7.100</td>
<td>9.7</td>
<td>3.31</td>
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</tr>
<tr>
<td>Provenance³</td>
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<td>10.25</td>
<td>0.001</td>
</tr>
<tr>
<td>Life History⁴</td>
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<td>7.100</td>
<td>2.4</td>
<td>2.30</td>
<td>0.001</td>
</tr>
<tr>
<td>Habitat Affinity + Life Form⁵</td>
<td>1.225</td>
<td>7.100</td>
<td>17.3</td>
<td>4.22</td>
<td>0.001</td>
</tr>
</tbody>
</table>

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 ($\chi^2$=66.44, p<0.0001, Likelihood ratio test). Shade tolerance classification derived from Nimerfro and Brand (1993) and Ellenberg (1988).

<table>
<thead>
<tr>
<th>Life Form</th>
<th>Shade Tolerance Class (% Classified Taxa)</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Tree</td>
<td>26.9</td>
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<tr>
<td>Shrub</td>
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<td>17.0</td>
</tr>
<tr>
<td>Vine</td>
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<td>11.1</td>
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<tr>
<td>Fern</td>
<td>47.4</td>
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</tr>
<tr>
<td>Fern Ally</td>
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<td>40.0</td>
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<tr>
<td>Grass</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Herb</td>
<td>18.2</td>
<td>11.9</td>
</tr>
</tbody>
</table>
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 ($\chi^2=57.11$, p<0.0002, Likelihood ratio test). Moisture tolerance classification derived from Oldham et al. (1995).

<table>
<thead>
<tr>
<th>Life Form</th>
<th>Moisture Tolerance Class (% Classified Taxa)</th>
<th>Summary</th>
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<tr>
<td>Fern</td>
<td>13.0</td>
<td>26.1</td>
</tr>
<tr>
<td>Fern Ally</td>
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<td>12.5</td>
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<tr>
<td>Grass</td>
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<tr>
<td>Herb</td>
<td>28.3</td>
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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).

<table>
<thead>
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<th>% SA</th>
<th># Taxa</th>
<th>Provenance</th>
<th>Habitat Affinity</th>
<th>Moisture Affinity</th>
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<td>88.8</td>
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<td>84.3</td>
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Table 4. Percentage of classified taxa (all life forms) in surveyed microhabitats by provenance, habitat affinity, and moisture affinity.
Table 4. Percentage of classified taxa (all life forms) in surveyed microhabitats by provenance, habitat affinity and moisture affinity.

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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 m²). 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 m² 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 suggest 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, Trillium 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
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 ($F=11.5, r^2_{adj.} = 0.052$, 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
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. 

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 as 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 DISPERAL 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 (Ridley 1930, Berg 1983, Little and Jones 1980). 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 diaspor will land in a site suitable for germination (Harper 1977, Sorensen 1978, Venable and Levin 1985), 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 Augspurger 1996), 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 diasporas 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 diasporas travel in space or time, the nature of the dispersing agent, and the character of the receiving environment. The distance diasporas 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, diasporas with facilitating features travel farther than those without special devices (Willson 1993), smaller and lighter diasporas travel farther than larger and heavier diasporas of similar mode (Hoppes 1988, Matlack 1989), diasporas 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 diaspires 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 diaspor lands is governed by its mode of dispersal: iv) dispersal is primarily a deterministic process for diaspires 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 Levin 1987, 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 diasporas 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.
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 diasporas 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 diasporas 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 diasporas, 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 diasporas 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 (myrmecochochory).

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 erectum* 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 diaspores 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 diaspare 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 overripe and adhere to the hair and bristles of animals.

The criterion for dispersal by adhesion also excludes diasproes 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 diasproes 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 diasproes 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). Diasproes 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 elaioosome (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" (Semander 1906) and "vespichory" (Jules 1996), respectively. In this study, the elaioosome may be attached to the seed (typically), schizocarp (Galium), base of the style (Carduus, Cirsium), or comprise the basal portion of the perigynium (Carex) (Semander 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 (Semander 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 (Semander 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 intumescentis*, *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 chronooches 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 siliqua). 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:

\[
\text{Expected value} = \frac{\text{the number of herbs dispersed by mode in sampled patches} - \text{the total number of herbs in the data set}}{\text{the total number of herbs in sampled patches}} \times \text{the number of herbs with the trait of interest}.
\]

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" (≥25 quadrats), "intermediate" (3-24 quadrats), and "low" (≤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° 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 one 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.

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<th>Life Form</th>
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<th>AA</th>
<th>AC</th>
<th>Total</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
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<td>78</td>
<td>39</td>
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<td>53</td>
<td>40</td>
<td>159</td>
<td>126</td>
<td>64</td>
<td>19</td>
<td>91</td>
<td>51</td>
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<td>12.8</td>
<td>9.7</td>
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<td>30.5</td>
<td>15.5</td>
<td>4.6</td>
<td>22.0</td>
<td>12.3</td>
<td>35.8</td>
</tr>
</tbody>
</table>

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. Superscript¹: total includes taxa with unknown life history. Superscript²: includes taxa dispersed by more than one mode.

<table>
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<tr>
<th>Dispersal Mode</th>
<th>Mode by Life Form</th>
<th>Taxa #</th>
<th>Annual #</th>
<th>Annual %</th>
<th>Biennial #</th>
<th>Biennial %</th>
<th>Perennial #</th>
<th>Perennial %</th>
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<td>22²</td>
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<td>372²</td>
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<td>9</td>
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Table 3.2. Life history of surveyed taxa by dispersal mode and life history (cont’d).

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<th>Annual %</th>
<th>Biennial #</th>
<th>Biennial %</th>
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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.

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

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</table>
Table 3.5. Fruit type of surveyed herbs (N=251) by dispersal mode. Legend: Al = 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.

<table>
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<th>Fruit Type</th>
<th># Taxa</th>
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<th>Dispersal Mode</th>
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<td>silique</td>
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<td>Total</td>
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<td>100</td>
<td>17</td>
<td>34</td>
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</table>
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.

<table>
<thead>
<tr>
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<th>AC n=20</th>
<th>W n=65</th>
<th>PD n=59</th>
<th>ME n=14</th>
<th>U n=44</th>
<th>MM n=6</th>
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<td></td>
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<td>3</td>
<td>5</td>
<td>-</td>
<td>3</td>
<td>6'</td>
</tr>
</tbody>
</table>

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.

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<th>AC ( n=14 )</th>
<th>W ( n=27 )</th>
<th>PD ( n=27 )</th>
<th>ME ( n=11 )</th>
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</tr>
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<td>7</td>
<td>14</td>
<td>4</td>
<td>13</td>
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</table>

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.

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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
   - Lamiinales: 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).

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<td>(n=54) Obs.</td>
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</tr>
<tr>
<td>splash-cup</td>
<td>2</td>
<td>2*</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>wind-push</td>
<td>5</td>
<td>0</td>
<td>1.2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Unassisted</td>
<td>69</td>
<td>19</td>
<td>16.2</td>
<td>18</td>
<td>27</td>
</tr>
<tr>
<td>Multimodal</td>
<td>39</td>
<td>3*</td>
<td>9.2</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Vegetative Expansion</td>
<td>92</td>
<td>22</td>
<td>21.6</td>
<td>23</td>
<td>37</td>
</tr>
</tbody>
</table>

153
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).

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th># Taxa (n=233)</th>
<th>Moisture Affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upland (n=116)</td>
<td>Intermediate (n=42)</td>
</tr>
<tr>
<td>Animal*</td>
<td>75</td>
<td>48</td>
</tr>
<tr>
<td>ingestion</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>adhesion</td>
<td>31</td>
<td>19</td>
</tr>
<tr>
<td>ant</td>
<td>31</td>
<td>20</td>
</tr>
<tr>
<td>Wind</td>
<td>60</td>
<td>33</td>
</tr>
<tr>
<td>Prolonged Dormancy</td>
<td>49</td>
<td>27</td>
</tr>
<tr>
<td>Mechanical Expulsion</td>
<td>18</td>
<td>11</td>
</tr>
<tr>
<td>explosive</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td>splash-cup</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>wind-push</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Unassisted*</td>
<td>69</td>
<td>23</td>
</tr>
<tr>
<td>Multimodal</td>
<td>38</td>
<td>25</td>
</tr>
<tr>
<td>Vegetative Expansion</td>
<td>91</td>
<td>45</td>
</tr>
</tbody>
</table>
Table 3.1. Dispersal modes of herbs by shade tolerance. N = 143 herbs. Shade tolerance classification based on Nimerfro and Brand (1993) and Ellenbeq (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. chisquare tests of homogeneity by row. df2, and cell. df1: dispersal mode in bold when differences among classes significant after Bonferroni correction for the total number of tests (13 tests by row).

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

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th>Canopy Closure¹</th>
<th>Moisture Class²</th>
<th>% SOM³</th>
<th>Cover Type⁴</th>
<th>Disturbance⁵</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low  Med  High</td>
<td>Dry  Moist  Wet</td>
<td>Low  Med  High</td>
<td>1  2  3  4  5</td>
<td>Yes  No</td>
</tr>
<tr>
<td>ANIMAL</td>
<td>22.4  28.7  27.5</td>
<td>29.2  22.7  23.6</td>
<td>24.3  29.3  23.9</td>
<td>10.5  25.5  32.2  23.8  13.9</td>
<td>24.5  27.9</td>
</tr>
<tr>
<td>ingestion</td>
<td>6.9  10.9  11.4</td>
<td>12.0  7.8  5.7</td>
<td>11.7  10.6  7.1</td>
<td>3.5  13.0  10.7  7.7  2.8</td>
<td>7.9  10.9</td>
</tr>
<tr>
<td>adhesion</td>
<td>7.2  5.7  4.3</td>
<td>4.5  7.1  8.4</td>
<td>3.3  5.5  8.6</td>
<td>3.5  2.9  6.6  6.9  8.7</td>
<td>7.1  5.1</td>
</tr>
<tr>
<td>ant</td>
<td>8.4  12.4  12.0</td>
<td>13.0  7.8  9.5</td>
<td>9.4  13.5  8.2</td>
<td>5.3  9.7  15.3  9.3  2.4</td>
<td>9.6  12.0</td>
</tr>
<tr>
<td>WIND</td>
<td>14.6  8.8  8.4</td>
<td>8.3  12.2  14.3</td>
<td>7.9  10.1  12.4</td>
<td>21.1  7.1  8.7  12.2  22.9</td>
<td>13.7  8.6</td>
</tr>
<tr>
<td>PROLONGED</td>
<td>9.0  4.3  3.3</td>
<td>3.5  8.0  7.8</td>
<td>3.5  4.8  7.9</td>
<td>12.3  1.7  4.9  7.2  13.8</td>
<td>8.1  4.0</td>
</tr>
<tr>
<td>DORMANCY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MECHANICAL</td>
<td>3.8  3.0  2.9</td>
<td>1.8  5.0  6.0</td>
<td>2.0  2.2  6.4</td>
<td>7.0  1.4  3.1  5.1  4.0</td>
<td>3.7  3.0</td>
</tr>
<tr>
<td>EXPULSION</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.12. Distribution of herbs in 10m x 10m quadrats by environmental attribute and dispersal mode (mean %) (cont’d).

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th>Canopy Closure&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Moisture Class&lt;sup&gt;2&lt;/sup&gt;</th>
<th>% SOM&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Cover Type&lt;sup&gt;4&lt;/sup&gt;</th>
<th>Disturbance&lt;sup&gt;5&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low Med High</td>
<td>Dry Moist Wet</td>
<td>Low Med High</td>
<td>1 2 3 4 5</td>
<td>Yes No</td>
</tr>
<tr>
<td>UNASSISTED</td>
<td>12.4 10.7 8.7</td>
<td>8.5 12.5 15.9</td>
<td>7.9 10.6 13.3</td>
<td>3.5 6.5 10.8 13.1 18.1</td>
<td>11.9 10.0</td>
</tr>
<tr>
<td>MULTIMODAL</td>
<td>7.6 4.7 3.4</td>
<td>3.5 6.9 8.3</td>
<td>2.8 4.6 8.3</td>
<td>12.3 1.6 5.2 7.0 11.4</td>
<td>7.3 4.1</td>
</tr>
<tr>
<td>VEGETATIVE EXPANSION</td>
<td>25.9 27.1 26.9</td>
<td>27.5 25.4 26.0</td>
<td>27.5 27.1 25.4</td>
<td>21.1 27.5 27.6 26.0 21.8</td>
<td>26.3 27.0</td>
</tr>
</tbody>
</table>
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 ≥ 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 $\geq 75\%$ 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 m²). # Herbs = number classified herbs in microhabitat. Closed microhabitats (-cc); open microhabitats (-oc). N=234 herbs.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>Variable</th>
<th>% SA</th>
<th># Herbs</th>
<th>AI</th>
<th>AA</th>
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170
| Microhabitat                        | Dispersal Mode | % | # | SA | A1 | AA | AC | W | PD | ME | VE |
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| seasonally moist forest depressions-oce |                | 0.2 | 20 | 1  | -0.4 | +3.5 | -1.5 | +0.1 | +1.6 | +1.5 | -1.5 | +0.9 | -2.3 |
| seasonally wet forest floors/rises-cc |                | 0.6 | 50 | 1  | -2.4 | -2.4 | +5.2 | +0.4 | 0.0 | +1.4 | -1.4 | +12.3 | -2.8 | -1.3 |
| seasonally wet forest depressions-cc |                | 4.0 | 66 | 1  | -1.2 | -1.2 | +3.7 | +5.1 | -5.1 | +1.5 | +1.5 | -1.3 | +3.9 | +5.8 |
| seasonally wet forest depressions-cc |                | 1.0 | 24 | 1  | -0.6 | +1.0 | +0.5 | -0.5 | -2.0 | +1.1 | +1.1 | +0.2 | +1.4 | +3.4 | +3.3 | -1.8 |
| seasonally dry gap-cc               |                | 0.9 | 19 | 0  | -1.3 | -0.3 | -0.7 | +0.7 | +0.7 | +0.7 | +0.7 | +0.7 | +3.2 | -2.0 | +8.4 |
| seasonally moist gap-cc             |                | 2.2 | 59 | 1  | -1.3 | -1.3 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | -1.3 |
| seasonally dry gap-cc               |                | 6.9 | 125| 1  | +3.5 | +3.5 | +5.6 | +4.9 | +4.9 | +4.9 | +4.9 | +4.9 | +4.9 | +4.9 | +4.9 | +4.9 |
| seasonally moist gap-cc             |                | 0.5 | 38 | 1  | +2.4 | +2.4 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | +1.7 | -1.3 |

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

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172
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Table 3.13. Number of observed and expected herbs (n=234) in surveyed microhabitats by dispersal mode (cont’d).

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<td>-5.6</td>
<td>+11.8</td>
<td>+6.9</td>
<td>+2.2</td>
<td>+0.4</td>
<td>+3.6</td>
<td>+0.5</td>
<td></td>
</tr>
<tr>
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<td>42</td>
<td>1</td>
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<td>14</td>
<td>9</td>
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<td>-0.2</td>
<td>-2.2</td>
<td>+3.6</td>
<td>+0.6</td>
<td>+0.2</td>
<td>+3.5</td>
<td>-0.5</td>
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</tr>
<tr>
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<td>9</td>
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<td></td>
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<td></td>
<td>-1.7</td>
<td>+2.8</td>
<td>-2.2</td>
<td>+3.6</td>
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</tr>
<tr>
<td>riparian thicket-oc</td>
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<td>6</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>-1.6</td>
<td>+4.2</td>
<td>-1.8</td>
<td>+2.3</td>
<td>-1.6</td>
<td>-1.6</td>
<td>-0.3</td>
<td>-1.6</td>
<td>-4.4</td>
<td></td>
</tr>
</tbody>
</table>
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. Al = 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: * 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.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>(n=)</th>
<th>Al</th>
<th>AA</th>
<th>A</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
</tr>
</thead>
<tbody>
<tr>
<td>DRY FOREST FLOOR/RISE-CC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dry forest floor/RISE-oc</td>
<td>13</td>
<td>+2.8</td>
<td>+1.4</td>
<td>-5.9</td>
<td>+2.6</td>
<td>+5.5</td>
<td>+1.4</td>
<td>-0.9</td>
<td>+5.7</td>
<td>-2.8</td>
</tr>
<tr>
<td>natural disturbance-cc</td>
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<td>-3.1*</td>
<td>-4.5*</td>
<td>+2.7</td>
<td>+1.6</td>
<td>+6.3*</td>
<td>-5.6**</td>
<td>+1.4</td>
<td>+5.7*</td>
</tr>
<tr>
<td>pit/mound-cc</td>
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<td>-1.5</td>
<td>+4.3</td>
<td>+2.8</td>
<td>-0.4</td>
<td>-4.6*</td>
<td>+2.7</td>
<td>+2.4</td>
</tr>
<tr>
<td>log/stump-cc</td>
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<td>+3.9</td>
<td>+24.1***</td>
<td>-10.9***</td>
<td>+3.7</td>
<td>+17.0***</td>
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<tr>
<td>log/stump/root mat-cc</td>
<td>42</td>
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<td>-13.7***</td>
<td>+2.0</td>
<td>+4.2</td>
<td>+16.3***</td>
<td>-9.4***</td>
<td>+4.6</td>
<td>+13.0***</td>
</tr>
<tr>
<td>human disturbance-cc</td>
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<td>-3.7</td>
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<td>+1.8</td>
<td>-10.4</td>
<td>+14.2</td>
<td>+2.4</td>
<td>-3.7</td>
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<tr>
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<td></td>
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</tr>
<tr>
<td>all forest F/R/D-oc</td>
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<td>+1.9</td>
<td>+1.3</td>
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<td>-3.6*</td>
<td>+0.9</td>
<td>+2.4</td>
<td>+6.2*</td>
<td>-5.8***</td>
<td>+1.2</td>
<td>+5.8***</td>
</tr>
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<td>natural disturbance-oc</td>
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<td>-3.7</td>
<td>-0.1</td>
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<td>-2.4</td>
<td>+19.1*</td>
<td>-2.2</td>
<td>+1.7</td>
<td>-2.6</td>
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</table>
Table 3.14. Difference in mean percent of herbs (n=234) dispersed by various modes in contrasting microhabitats (cont’d).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>(n=)</th>
<th>AI</th>
<th>AA</th>
<th>A</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
</tr>
</thead>
<tbody>
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<td><strong>DRY FOREST FLOOR/RISE-CC</strong></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>moist forest depressions-cc</td>
<td>18</td>
<td>-3.8</td>
<td>+5.7</td>
<td>-10.2**</td>
<td>+4.8</td>
<td>-2.4</td>
<td>-2.8</td>
<td>+4.2</td>
<td>-3.5</td>
<td>-4.3</td>
</tr>
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<td>-1.5</td>
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<td>+6.7</td>
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<td>-0.4</td>
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<td>-11.7*</td>
</tr>
<tr>
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<td>natural disturbance-oc</td>
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<td>+1.5</td>
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<td>+3.9</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>log/stump/raised root mat-cc</td>
<td>16</td>
<td>+8.6</td>
<td>-9.5*</td>
<td>-11.3*</td>
<td>+4.9</td>
<td>+10.3</td>
<td>+13.6</td>
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<td><strong>LOG/STUMP-CC</strong></td>
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<td>-15.3*</td>
<td>+6.0</td>
<td>-1.4</td>
<td>-10.4*</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>(n=)</th>
<th>AI</th>
<th>AA</th>
<th>A</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
</tr>
</thead>
<tbody>
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<td>9.2</td>
<td>19.7</td>
<td>10.8</td>
<td>60.4*</td>
</tr>
<tr>
<td>dry forest floor/rise-oc</td>
<td>12</td>
<td>13.4</td>
<td>16.9*</td>
<td>22.0</td>
<td>25.1*</td>
<td>20.6**</td>
<td>9.5</td>
<td>18.4</td>
<td>20.5**</td>
<td>49.2</td>
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<td>11.0</td>
<td>9.3</td>
<td>19.7</td>
<td>10.7</td>
<td>60.4***</td>
</tr>
<tr>
<td>moist forest floor/rise-cc</td>
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<td>15.7</td>
<td>15.2</td>
<td>11.2</td>
<td>25.4**</td>
<td>14.8</td>
<td>13.5</td>
<td>21.6</td>
<td>13.5*</td>
<td>47.6</td>
</tr>
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<td>all forest floors/rises/depressions-oc</td>
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<td>18.4*</td>
<td>10.7</td>
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<td>19.2**</td>
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Table 3.15. Mean per cent of herbs dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats (cont’d).

<table>
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<th>Microhabitat</th>
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<th>AA</th>
<th>A</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
</tr>
</thead>
<tbody>
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<td>58.6</td>
</tr>
<tr>
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<td>6.8</td>
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<td>15</td>
<td>20.3</td>
<td>26.7**</td>
<td>23.4</td>
<td>31.7</td>
<td>20.7</td>
<td>25.0</td>
<td>19.3</td>
<td>23.2</td>
<td>62.5</td>
</tr>
<tr>
<td>pit/mound-cc</td>
<td>59</td>
<td>32.2</td>
<td>15.7</td>
<td>33.5</td>
<td>26.9</td>
<td>15.6</td>
<td>12.8</td>
<td>19.5</td>
<td>16.5</td>
<td>66.5</td>
</tr>
<tr>
<td>pit/mound-oc</td>
<td>5</td>
<td>32.0</td>
<td>18.4</td>
<td>29.1</td>
<td>25.6</td>
<td>22.6</td>
<td>14.3</td>
<td>20.1</td>
<td>20.8</td>
<td>70.1</td>
</tr>
<tr>
<td>pit/mound-cc</td>
<td>50</td>
<td>30.6</td>
<td>15.1</td>
<td>34.6*</td>
<td>26.9</td>
<td>14.5</td>
<td>13.1</td>
<td>20.0</td>
<td>15.6</td>
<td>66.1</td>
</tr>
<tr>
<td>log/stump-cc</td>
<td>37</td>
<td>42.9</td>
<td>21.4*</td>
<td>21.5</td>
<td>30.5</td>
<td>22.3**</td>
<td>35.3***</td>
<td>29.2*</td>
<td>25.5***</td>
<td>66.8</td>
</tr>
</tbody>
</table>
Table 3.15. Mean per cent of herbs dispersed by various modes in contrasting microhabitats within 10m x 10m quadrats (cont’d).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>(n=)</th>
<th>AI</th>
<th>AA</th>
<th>A</th>
<th>W</th>
<th>PD</th>
<th>ME</th>
<th>U</th>
<th>MM</th>
<th>VE</th>
</tr>
</thead>
<tbody>
<tr>
<td>pit/mound-cc</td>
<td>53</td>
<td>32.4</td>
<td>15.2</td>
<td>34.5***</td>
<td>27.9</td>
<td>16.0</td>
<td>13.4</td>
<td>19.1</td>
<td>16.8</td>
<td>66.9**</td>
</tr>
<tr>
<td>raised root mat-cc</td>
<td>19</td>
<td>27.1</td>
<td>19.8</td>
<td>16.9</td>
<td>25.5</td>
<td>19.4</td>
<td>16.5</td>
<td>23.2</td>
<td>19.7</td>
<td>652.6</td>
</tr>
</tbody>
</table>

| 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 |

182
Herbs dispersed by animal ingestion were most strongly associated with closed, dry forest floors: logs and stumps under closed canopies; and with natural rather than 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
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 (≥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 (df2) and cell (df1), 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.

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th>Mode</th>
<th># Herbs</th>
<th>High ≥25 quadrats</th>
<th>Intermediate 3-24 quadrats</th>
<th>Low 1-2 quadrats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Obs.</td>
<td>Exp.</td>
<td>Obs.</td>
</tr>
<tr>
<td>Animal</td>
<td>81</td>
<td>23</td>
<td>15.8</td>
<td>38</td>
<td>40.8</td>
</tr>
<tr>
<td>Ingestion</td>
<td>17</td>
<td>10***</td>
<td>3.3</td>
<td>4</td>
<td>8.6</td>
</tr>
<tr>
<td>Adhesion</td>
<td>34</td>
<td>5</td>
<td>6.6</td>
<td>20</td>
<td>17.1</td>
</tr>
<tr>
<td>Conveyance (ant)</td>
<td>33</td>
<td>8</td>
<td>6.4</td>
<td>16</td>
<td>16.6</td>
</tr>
<tr>
<td>Wind</td>
<td>64</td>
<td>11</td>
<td>12.4</td>
<td>35</td>
<td>32.3</td>
</tr>
<tr>
<td>Prolonged Dormancy</td>
<td>50</td>
<td>5</td>
<td>9.7</td>
<td>31</td>
<td>25.2</td>
</tr>
<tr>
<td>Mechanical Expulsion</td>
<td>18</td>
<td>3</td>
<td>3.5</td>
<td>8</td>
<td>9.1</td>
</tr>
<tr>
<td>Unassisted</td>
<td>78</td>
<td>12</td>
<td>15.2</td>
<td>39</td>
<td>39.3</td>
</tr>
<tr>
<td>Multiple Modes</td>
<td>39</td>
<td>5</td>
<td>7.6</td>
<td>24</td>
<td>19.7</td>
</tr>
<tr>
<td>Vegetative Expansion</td>
<td>95</td>
<td>23</td>
<td>18.5</td>
<td>49</td>
<td>47.9</td>
</tr>
</tbody>
</table>

N=192 10m x10 quadrats.
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.

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

186
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.

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

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th>Patch Size Class</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Large 122 ha n=48 quadrats</td>
<td>Intermediate 43-121 ha n=88 quadrats</td>
<td>Small ≤ 42 ha n=56 quadrats</td>
<td></td>
</tr>
<tr>
<td>Animal**</td>
<td>22.8</td>
<td>29.4**</td>
<td>26.9</td>
<td></td>
</tr>
<tr>
<td>Ingestion</td>
<td>10.2</td>
<td>10.5</td>
<td>9.1</td>
<td></td>
</tr>
<tr>
<td>Adhesion</td>
<td>5.7</td>
<td>5.7</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>Conveyance (ant)</td>
<td>7.0</td>
<td>13.2****</td>
<td>11.9</td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>8.5</td>
<td>10.8</td>
<td>11.1</td>
<td></td>
</tr>
<tr>
<td>Prolonged Dormancy*</td>
<td>3.4</td>
<td>5.9*</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>Mechanical Expulsion</td>
<td>3.4</td>
<td>2.4</td>
<td>4.4***</td>
<td></td>
</tr>
<tr>
<td>Unassisted</td>
<td>8.3</td>
<td>10.4</td>
<td>13.0****</td>
<td></td>
</tr>
<tr>
<td>Multiple Modes*</td>
<td>3.4</td>
<td>5.8*</td>
<td>5.5</td>
<td></td>
</tr>
<tr>
<td>Vegetative Expansion*</td>
<td>24.6</td>
<td>27.3</td>
<td>27.7*</td>
<td></td>
</tr>
</tbody>
</table>
Table 3.20. Dispersal modes of herbs (n=252) by isolation class. High: mean distance to nearest 8 woodlots in 45° sectors ≥ 477 m; 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.

<table>
<thead>
<tr>
<th>Dispersal Mode</th>
<th>Isolation Class</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>High ≥477 m</td>
</tr>
<tr>
<td></td>
<td>n=48quadrats</td>
</tr>
<tr>
<td>Animal</td>
<td>56.1</td>
</tr>
<tr>
<td>Ingestion</td>
<td>20.7</td>
</tr>
<tr>
<td>Adhesion</td>
<td>12.0</td>
</tr>
<tr>
<td>Conveyance (ant)</td>
<td>23.4</td>
</tr>
<tr>
<td>Wind</td>
<td>18.9</td>
</tr>
<tr>
<td>Prolonged Dormancy</td>
<td>11.4</td>
</tr>
<tr>
<td>Mechanical Expulsion</td>
<td>7.0</td>
</tr>
<tr>
<td>Unassisted*</td>
<td>18.6</td>
</tr>
<tr>
<td>Multiple Modes</td>
<td>11.5</td>
</tr>
<tr>
<td>Vegetative Expansion*</td>
<td>48.0</td>
</tr>
</tbody>
</table>
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, Ehrler and Erikssson 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 diasporas 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-fruiting 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-fruiting 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-fruiting 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) (Appendix 13). 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 (x̄ = 18.0 quadrats, n=6 herbs) than for herbs with affinity for "open" habitats (x̄ = 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 (x̄ =43.2 quadrats, n=6 herbs with affinity for "forest + open habitats": x̄=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 limitation 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 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.


**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 Lawton 1992, 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

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.

4.2.1.1 Generalized 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 (r² 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 pennsylvanicu*, *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 pseudoacacdia*); 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 x 10m 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, and % soil organic matter. Indicators of potential differences in available light were: % canopy closure: % taxa shade tolerant herbs (Nimertfro 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 minimum 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 (r² 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, r² adjusted 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 PRESSp 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 \( p \leq W \) value and a high mean square error. Superior models with a higher \( r^2 \) adjusted value were considered to be more informative than superior models with a lower \( r^2 \) adjusted 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
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=gleysed brunisol; gl=gleysed 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=mesic or wet species, no sugar maple, no red or white oak; ln p/q = ln [(proportion)/(1-proportion)].

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
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<td>1. EDAPHIC VARIABLES</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>soil parent material³,5,8,10,16,24,26,31,35</td>
<td>sqrt # spp</td>
<td>18.99</td>
<td>0.0001</td>
<td>0.2203</td>
<td>0.29</td>
<td>co&gt;lac&gt;ct&gt;gf</td>
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<tr>
<td>soil order²,4,10,15,16,33,34,35</td>
<td>ln sqrt # spp</td>
<td>17.13</td>
<td>0.0001</td>
<td>0.2525</td>
<td>0.18</td>
<td>gb&gt;gl&gt;b&gt;l&gt;g</td>
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<tr>
<td>soil moisture³,5,15,21,24,27,28,35</td>
<td>sqrt # spp</td>
<td>32.32</td>
<td>0.0001</td>
<td>0.2469</td>
<td>0.58</td>
<td>wet&gt;dry</td>
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<td>ln % soil organic matter²,3,10,11,16,18,19,20,29</td>
<td>ln # spp</td>
<td>11.52</td>
<td>0.0008</td>
<td>0.0522</td>
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<td>soil pH²,3,10,11,12,14,16,18,19,20,21</td>
<td>sqrt # spp</td>
<td>28.91</td>
<td>0.0001</td>
<td>0.1403</td>
<td>0.06</td>
<td>positive</td>
</tr>
<tr>
<td>available calcium²,10,14,18,19,24,27</td>
<td>sqrt # spp</td>
<td>5.52</td>
<td>0.0194</td>
<td>0.0260</td>
<td>0.15</td>
<td>positive</td>
</tr>
<tr>
<td>Best Model: soil moisture + soil parent material⁹</td>
<td>sqrt # spp</td>
<td>29.36</td>
<td>0.0001</td>
<td>0.3557</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>2. FOREST STAND STRUCTURE</td>
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<td>0.99</td>
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</tr>
<tr>
<td>% canopy closure (ln p/q)³,8,16,21,35</td>
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<td>0.1503</td>
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</tr>
<tr>
<td>ln # tree species (&gt;1m)⁸,14,15,27,35</td>
<td>ln sqrt # spp</td>
<td>71.00</td>
<td>0.0001</td>
<td>0.2682</td>
<td>0.65</td>
<td>positive</td>
</tr>
<tr>
<td>ln # wet-mesic or wet tree species³,5,8,10,16,17,25</td>
<td>sqrt # spp</td>
<td>30.07</td>
<td>0.0001</td>
<td>0.2235</td>
<td>0.50</td>
<td>positive</td>
</tr>
</tbody>
</table>

222
Table 4.1. Environmental correlates of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>sqrt # live tree stems 0-4 cm dbh¹,10,12,15,18,24,27,29,33</td>
<td>sqrt # spp</td>
<td>47.65</td>
<td>0.0001</td>
<td>0.1963</td>
<td>0.28</td>
<td>positive</td>
</tr>
<tr>
<td>sqrt # live tree stems 4-10 cm dbh¹,4,8,10,12,14,18,24,31,34</td>
<td>sqrt # spp</td>
<td>1.49</td>
<td>0.2237</td>
<td>0.0026</td>
<td>0.07</td>
<td>positive</td>
</tr>
<tr>
<td>ln # live tree stems 10-30 cm dbh²,3,5,11,13,20,29</td>
<td>ln sqrt # spp</td>
<td>0.28</td>
<td>0.5990</td>
<td>0.0042</td>
<td>0.04</td>
<td>-</td>
</tr>
<tr>
<td># live tree stems &gt;30 cm dbh¹,33</td>
<td>sqrt # spp</td>
<td>7.37</td>
<td>0.0072</td>
<td>0.0323</td>
<td>0.07</td>
<td>negative</td>
</tr>
<tr>
<td>sqrt % stems sugar maple ⁵,8,14,15,27,31,35</td>
<td>sqrt # spp</td>
<td>66.55</td>
<td>0.0001</td>
<td>0.2555</td>
<td>0.28</td>
<td>negative</td>
</tr>
<tr>
<td>sqrt % stems sugar maple 0-4 cm dbh⁵,8,20,24,27,29,33,35</td>
<td>sqrt # spp</td>
<td>66.01</td>
<td>0.0001</td>
<td>0.2539</td>
<td>0.74</td>
<td>negative</td>
</tr>
<tr>
<td>sqrt % stems sugar maple 4-10 cm dbh⁴,15,16,20,24,29,35</td>
<td>sqrt # spp</td>
<td>20.38</td>
<td>0.0001</td>
<td>0.0991</td>
<td>0.11</td>
<td>negative</td>
</tr>
<tr>
<td>% stems sugar maple 10-30 cm dbh⁴,11,16,35</td>
<td>sqrt # spp</td>
<td>19.14</td>
<td>0.0001</td>
<td>0.0959</td>
<td>0.07</td>
<td>negative</td>
</tr>
<tr>
<td>Best Model 1: ln # tree species (&gt;1m) + canopy closure (ln p/q) + forest cover type¹²</td>
<td>sqrt # spp</td>
<td>39.67</td>
<td>0.0001</td>
<td>0.5485</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td>Best Model 2: sqrt # stems 0-4 cm dbh + canopy closure (ln p/q) + forest cover type¹³</td>
<td>sqrt # spp</td>
<td>32.52</td>
<td>0.0001</td>
<td>0.4975</td>
<td>0.92</td>
<td></td>
</tr>
</tbody>
</table>

3. HUMAN DISTURBANCE

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>open trail²,10,13,15,26,25,27,29,33</td>
<td>sqrt # spp</td>
<td>19.57</td>
<td>0.0001</td>
<td>0.0886</td>
<td>0.28</td>
<td>present &gt; absent</td>
</tr>
<tr>
<td>closed trail¹,13,24,26,29</td>
<td>sqrt # spp</td>
<td>9.59</td>
<td>0.0022</td>
<td>0.0431</td>
<td>0.06</td>
<td>present &gt; absent</td>
</tr>
<tr>
<td>open regenerating field²,10,25,27,29</td>
<td>sqrt # spp</td>
<td>17.41</td>
<td>0.0001</td>
<td>0.0791</td>
<td>0.03</td>
<td>present &gt; absent</td>
</tr>
<tr>
<td>open canopy gap⁴,12,14,18,19,24,26,31</td>
<td>sqrt # spp</td>
<td>9.21</td>
<td>0.0027</td>
<td>0.0412</td>
<td>0.04</td>
<td>present &gt; absent</td>
</tr>
</tbody>
</table>
Table 4.1. Environmental correlates of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt; W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>closed canopy gap³,²⁹</td>
<td>sqrt # spp</td>
<td>0.04</td>
<td>0.8371</td>
<td>0.0050</td>
<td>0.02</td>
<td>present &gt; absent</td>
</tr>
<tr>
<td>disturbed microhabitats⁵,¹⁴, 16, 20, 24, 25, 26, 28, 31, 34</td>
<td>sqrt # spp</td>
<td>19.67</td>
<td>0.0001</td>
<td>0.0890</td>
<td>0.04</td>
<td>present &gt; absent</td>
</tr>
<tr>
<td>Best Model: open trail + open regenerating field¹⁰</td>
<td>sqrt # spp</td>
<td>15.03</td>
<td>0.0001</td>
<td>0.1280</td>
<td>0.20</td>
<td></td>
</tr>
</tbody>
</table>

4. ENVIRONMENTAL HETEROGENEITY

| # microhabitats², 10, 15, 16, 19, 27, 29 | ln sqrt # spp     | 11.84| 0.0007  | 0.0537  | 0.05  | positive              |

5. LANDSCAPE VARIABLES³²

| % forest cover (within 5km x 5km square centered on study site)¹, 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)¹, 10, 15, 29, 31, 35                | ln sqrt # spp     | 1.01 | 0.3169  | 0.0000  | 0.01  | negative              |
| sqrt patch area², 3, 4, 10, 11, 12, 14, 16, 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 microhabitats³⁶ | 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 material³⁷   | sqrt # spp        | 34.10| 0.0001  | 0.5495  | 0.69  |                      |

Notes:
1. Shapiro-Wilk W test for normality of residuals (residuals normal when p > 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.
7. 2^ 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 0-1 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 45º 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 = gleysoil. 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.

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

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

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 x 10m quadrats were forest cover type ($r^2_{adj.}=0.277$), # tree species ($r^2_{adj.}=0.268$), % stems sugar maple ($r^2_{adj.}=0.256$), % stems sugar maple 0-4 cm dbh ($r^2_{adj.}=0.254$), # wet-mesic. wet. tree species ($r^2_{adj.}=0.224$), and, # live tree stems 0-4 cm dbh ($r^2_{adj.}=0.196$) (Table 4.1. variables variously transformed). Significant, but less informative, stand structure variables were % canopy closure ($r^2_{adj.}=0.150$), % stems sugar maple 4-10 cm dbh ($r^2_{adj.}=0.099$), % stems sugar maple 10-30 cm dbh ($r^2_{adj.}=0.096$), and, # live tree stems >30 cm dbh ($r^2_{adj.}=0.032$) (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 ($> 1$ m), 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) ($r^2$adj. = 0.089), open trails ($r^2$adj. = 0.089), and open regenerating fields ($r^2$adj. = 0.079). Significant, but less informative, variables were closed trails ($r^2$adj. = 0.043) and open canopy gaps ($r^2$adj. = 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 x 10m 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 ($r^2$adj.$=0.066$). and. patch area ($r^2$adj.$=0.019$) (Table 4.1). The mean distance to the nearest forest patch (in 45° 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° arcs). and. negatively correlated with the percent forest cover in the surrounding landscape. and. with patch area.


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) ($r^2$adj.$=0.582$) (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 ($r^2$adj.$=0.5495$).
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.

<table>
<thead>
<tr>
<th>X</th>
<th>Y</th>
<th>Spearman Rho</th>
<th>Prob &gt;</th>
<th>Rho</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td># tree species</td>
<td># species (all life forms)</td>
<td>0.5191</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>% stems sugar maple</td>
<td>-0.5937</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>% stems wet-mesic, wet, tree species</td>
<td>0.4430</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>% stems shade intolerant, very shade intolerant, tree species</td>
<td>0.3220</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>moisture class (1=dry, 2=moist,wet)</td>
<td>0.1382</td>
<td>0.0562</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>% canopy closure</td>
<td>-0.0804</td>
<td>0.2677</td>
<td></td>
<td></td>
</tr>
<tr>
<td># tree species</td>
<td>human disturbance (1=no, 2=yes)</td>
<td>-0.0044</td>
<td>0.9521</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>% species (all life forms)</td>
<td>-0.4857</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td># tree species</td>
<td>-0.6184</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>% stems wet-mesic, wet tree species</td>
<td>-0.4521</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>% stems shade intolerant, very shade intolerant, tree species</td>
<td>-0.3709</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>moisture class (1=dry, 2=moist,wet)</td>
<td>-0.3512</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>% canopy closure</td>
<td>0.2142</td>
<td>0.0029</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>calcium (cmol/kg)</td>
<td>-0.2137</td>
<td>0.0049</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3. Selected correlations involving # tree species, % stems sugar maple, and, # tree stems 0-4 cm dbh (cont’d).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>human disturbance (1=no, 2=yes)</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td># species (all life forms)</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td># tree species</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>% stems sugar maple</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>% stems wet mesic, wet, tree species</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>% stems shade intolerant, very shade intolerant</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>moisture class (1=dry, 2=moist,wet)</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>human disturbance (1=no, 2=yes)</td>
</tr>
<tr>
<td># tree stems 0-4 cm dbh</td>
<td>% canopy closure</td>
</tr>
</tbody>
</table>
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 x 10m 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.
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 $\text{pH}_{\text{water}}$ 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 Brunisolic 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 ($r^2_{\text{adj.}}=0.45$ when the analysis includes Brunisolic and Luvisolic soils; $r^2_{\text{adj.}}=0.68$ 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° 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 species
Table 4.4. Contribution of microhabitats to species richness in 10m x 10m quadrats. Legend: %SA = % of sampled area (19,200 m²). # 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                |

250
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 m²). # 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  | 3         | 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   |

253
Table 4.6. Contribution of microhabitats to species richness at the landscape scale. Legend: % SA = percent total surveyed area (19,200 m²)

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>% SA</th>
<th># Species Restricted to Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>seasonally dry forest floors-cc¹</td>
<td>54.3</td>
<td>16</td>
</tr>
<tr>
<td>seasonally dry forest floors-oc²</td>
<td>6.8</td>
<td>6</td>
</tr>
<tr>
<td>seasonally moist forest floors-cc³</td>
<td>3.0</td>
<td>5</td>
</tr>
<tr>
<td>seasonally wet forest floors-cc⁴</td>
<td>0.6</td>
<td>1</td>
</tr>
<tr>
<td>seasonally wet forest depressions-cc⁵</td>
<td>4.0</td>
<td>3</td>
</tr>
<tr>
<td>seep-oc⁶</td>
<td>0.3</td>
<td>1</td>
</tr>
<tr>
<td>mound-cc⁷</td>
<td>3.6</td>
<td>1</td>
</tr>
<tr>
<td>log-cc⁸</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>raised root mat-oc⁹</td>
<td>1.3</td>
<td>1</td>
</tr>
<tr>
<td>lane/road-oc¹⁰</td>
<td>1.3</td>
<td>6</td>
</tr>
<tr>
<td>regenerating field-cc¹¹</td>
<td>1.3</td>
<td>1</td>
</tr>
<tr>
<td>regenerating field-oc¹²</td>
<td>1.3</td>
<td>8</td>
</tr>
<tr>
<td>riparian marsh-oc¹³</td>
<td>0.4</td>
<td>1</td>
</tr>
</tbody>
</table>

Notes:
4. Astreum umbellatus.
6. Carex crinita.
7. Monarda fistulosa.
8. Echinocystis lobata.
11. Rudbeckia hirta.
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 m²).

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th># Quadrats Present</th>
<th>Mean Area (m²) per Quadrat When Present</th>
<th>Total Area</th>
<th>m²</th>
<th>% SA</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. MOISTURE STATUS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry Habitats</td>
<td>188</td>
<td>80.3</td>
<td>15.105</td>
<td>78.7</td>
<td></td>
</tr>
<tr>
<td>closed canopy</td>
<td>170</td>
<td>76.8</td>
<td>13.051</td>
<td>68.0</td>
<td></td>
</tr>
<tr>
<td>open canopy</td>
<td>43</td>
<td>47.8</td>
<td>2.054</td>
<td>10.7</td>
<td></td>
</tr>
<tr>
<td>Moist/Wet Habitats</td>
<td>71</td>
<td>57.7</td>
<td>4.095</td>
<td>21.3</td>
<td></td>
</tr>
<tr>
<td>closed canopy</td>
<td>58</td>
<td>51.5</td>
<td>2.986</td>
<td>15.6</td>
<td></td>
</tr>
<tr>
<td>open canopy</td>
<td>19</td>
<td>58.4</td>
<td>1.109</td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td>II. LIGHT STATUS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Closed Habitats</td>
<td>174</td>
<td>92.2</td>
<td>16.037</td>
<td>83.5</td>
<td></td>
</tr>
<tr>
<td>dry habitats</td>
<td>170</td>
<td>76.8</td>
<td>13.051</td>
<td>68.0</td>
<td></td>
</tr>
<tr>
<td>moist/wet habitats</td>
<td>58</td>
<td>51.5</td>
<td>2.986</td>
<td>15.6</td>
<td></td>
</tr>
<tr>
<td>Open Habitats</td>
<td>47</td>
<td>67.3</td>
<td>3.163</td>
<td>16.5</td>
<td></td>
</tr>
<tr>
<td>dry habitats</td>
<td>43</td>
<td>47.8</td>
<td>2.054</td>
<td>10.7</td>
<td></td>
</tr>
<tr>
<td>moist/wet habitats</td>
<td>19</td>
<td>58.4</td>
<td>1.109</td>
<td>5.8</td>
<td></td>
</tr>
</tbody>
</table>
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\(^2\)adj. = 0.397), dispersal by wind (r\(^2\)adj. = 0.334), dispersal by unassisted means (r\(^2\)adj. = 0.317), and dispersal by multiple modes (r\(^2\)adj. = 0.246)(Table 4.8). Modes with intermediate explanatory power were dispersal by prolonged dormancy (r\(^2\)adj. = 0.199), dispersal by ants (r\(^2\)adj. = 0.152), and dispersal by animal adhesion (r\(^2\)adj. = 0.114). Modes with minimal explanatory power were dispersal by mechanical expulsion (r\(^2\)adj. = 0.060) and dispersal by vegetative expansion (r\(^2\)adj. = 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>$r^2$ adj.</th>
<th>p&lt;$W^1$</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. MODE OF DISPERAL(^2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>animal ingestion(^3,8,9,10,15,17,18,19,22,23,25,29,33,34,36,43)</td>
<td>sqrt # spp</td>
<td>126.67</td>
<td>0.0001</td>
<td>0.3969</td>
<td>0.81</td>
<td>negative</td>
</tr>
<tr>
<td>animal adhesion(^3,6,7,10,11,15,16,17,18,19,24,28,31,35,36,37,39)</td>
<td>sqrt # spp</td>
<td>25.65</td>
<td>0.0001</td>
<td>0.1143</td>
<td>0.22</td>
<td>positive</td>
</tr>
<tr>
<td>ants(^3,8,11,15,17,25,28,29,34,35,36,37,42,43)</td>
<td>sqrt # spp</td>
<td>35.23</td>
<td>0.0001</td>
<td>0.1520</td>
<td>0.57</td>
<td>negative</td>
</tr>
<tr>
<td>wind(^4,10,15,16,17,21,24,31,36,37,41,42,43)</td>
<td>sqrt # spp</td>
<td>96.76</td>
<td>0.0001</td>
<td>0.3339</td>
<td>0.79</td>
<td>positive</td>
</tr>
<tr>
<td>prolonged dormancy(^4,5,8,9,15,16,17,18,19,24,26,31,37,43)</td>
<td>sqrt # spp</td>
<td>38.56</td>
<td>0.0001</td>
<td>0.1992</td>
<td>0.80</td>
<td>positive</td>
</tr>
<tr>
<td>mechanical expulsion(^4,5,7,11,15,16,17,18,19,28,31,39,40,41,42,43)</td>
<td>ln sqrt # spp</td>
<td>9.41</td>
<td>0.0026</td>
<td>0.0603</td>
<td>0.23</td>
<td>negative</td>
</tr>
<tr>
<td>unassisted means(^7,21,23,31)</td>
<td>sqrt # spp</td>
<td>89.69</td>
<td>0.0001</td>
<td>0.3171</td>
<td>0.37</td>
<td>positive</td>
</tr>
<tr>
<td>multiple modes(^3,8,11,15,16,17,18,19,20,22,24,28,31,37,39,40,41,42,43)</td>
<td>sqrt # spp</td>
<td>63.37</td>
<td>0.0001</td>
<td>0.2462</td>
<td>0.82</td>
<td>positive</td>
</tr>
<tr>
<td>vegetative expansion(^4,5,8,10,15,17,26,28,29,39,41,42,43)</td>
<td>sqrt # spp</td>
<td>10.94</td>
<td>0.0011</td>
<td>0.0495</td>
<td>0.59</td>
<td>negative</td>
</tr>
<tr>
<td>MODEL 1 (HERBS)(^12): unassisted means + prolonged dormancy + ant + animal ingestion</td>
<td># spp</td>
<td>61.35</td>
<td>0.0001</td>
<td>0.5583</td>
<td>0.95</td>
<td></td>
</tr>
<tr>
<td>MODEL 2 (ALL LIFE FORMS)(^11): unassisted means + animal conveyance (ants + seed caching by birds and mammals) + prolonged dormancy</td>
<td># spp</td>
<td>83.61</td>
<td>0.0001</td>
<td>0.5647</td>
<td>0.67</td>
<td></td>
</tr>
</tbody>
</table>
Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt; W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. LIFE HISTORY¹⁴</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>annual¹,³,⁴,⁵,⁶,⁷,⁸,¹⁰,¹⁶,¹⁷,¹⁸,¹⁹,²²,²³,²⁴,²⁵,²⁸,²⁹,³³,³⁵,³⁷,³⁹,⁴⁰,⁴¹,⁴²,⁴³</td>
<td>sqrt # spp</td>
<td>9.52</td>
<td>0.0023</td>
<td>0.0427</td>
<td>0.80</td>
<td>positive</td>
</tr>
<tr>
<td>biennial¹⁴,⁶,⁷,⁸,¹⁰,¹⁵,¹⁷,¹⁸,¹⁹,²⁰,²¹,²²,²⁴,³¹,³⁶,³⁷</td>
<td>sqrt # spp</td>
<td>35.63</td>
<td>0.0001</td>
<td>0.1535</td>
<td>0.03</td>
<td>positive</td>
</tr>
<tr>
<td>perennial¹³,⁴,⁵,⁶,⁷,⁸,¹⁰,¹¹,¹³,¹⁵,¹⁶,¹⁸,¹⁹,²¹,²³,²⁴,²⁸,³⁹,³¹,³⁵,³⁷,³⁹,⁴⁰,⁴¹,⁴²,⁴³</td>
<td>sqrt # spp</td>
<td>29.91</td>
<td>0.0001</td>
<td>0.1315</td>
<td>0.51</td>
<td>negative</td>
</tr>
<tr>
<td>MODEL: % taxa perennial</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>sqrt # spp</td>
<td>29.91</td>
<td>0.0001</td>
<td>0.1315</td>
<td>0.51</td>
<td>negative</td>
</tr>
<tr>
<td>3. PROVENANCE¹⁴</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>native¹,³,⁴,⁷,⁸,¹⁰,¹⁵,¹⁶,¹⁷,²¹,²³,²⁴,²⁵,²⁸,³⁰,³¹,³³,³₆</td>
<td># spp</td>
<td>70.82</td>
<td>0.0001</td>
<td>0.2677</td>
<td>0.67</td>
<td>negative</td>
</tr>
<tr>
<td>alien¹,³,⁴,⁷,⁸,¹⁰,¹⁵,¹₆,¹⁹,²¹,²₃,²⁴,²⁵,²⁸,³₀,³₁,³₃,³₆</td>
<td># spp</td>
<td>66.54</td>
<td>0.0001</td>
<td>0.2555</td>
<td>0.36</td>
<td>positive</td>
</tr>
<tr>
<td>MODEL: % taxa native</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td># spp</td>
<td>70.82</td>
<td>0.0001</td>
<td>0.2677</td>
<td>0.67</td>
<td>positive</td>
</tr>
<tr>
<td>4. LIFE FORM¹⁴</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>tree¹⁰,¹⁵,¹₆,¹₉,₂₃,₂₄,₂₅,₂₈,₃₀,₃₁,₃₃,₃₆</td>
<td>sqrt # spp</td>
<td>69.23</td>
<td>0.0001</td>
<td>0.2632</td>
<td>0.76</td>
<td>negative</td>
</tr>
<tr>
<td>shrub¹⁰,¹₅,¹₆,¹₇,₁₉,₁₉,₂₄,₂₉,₃₀,₃₁,₃₆</td>
<td>sqrt # spp</td>
<td>7.03</td>
<td>0.0087</td>
<td>0.0306</td>
<td>0.14</td>
<td>negative</td>
</tr>
<tr>
<td>vine¹₀,¹⁰,₁₅,₁₆,₂₈,₂₉,₃₀,₃₃,₃₆,₃₉,₄₁,₄₂,₄₃</td>
<td>sqrt # spp</td>
<td>32.91</td>
<td>0.0001</td>
<td>0.1783</td>
<td>0.04</td>
<td>positive</td>
</tr>
<tr>
<td>fern¹₃,₁₅,₁₇,₁₈,₁₉,₂₀,₂₈,₃₄,₃₅,₄₃</td>
<td>sqrt # spp</td>
<td>11.40</td>
<td>0.0009</td>
<td>0.0549</td>
<td>0.03</td>
<td>negative</td>
</tr>
<tr>
<td>fern ally¹,⁴,⁶,₇,₉,₁₀,₁₅,₁₇,₁₈,₁₉,₂₀,₂₁,₂₆,₃₄,₃₅,₃₉,₄₀,₄₁,₄₂,₄₃</td>
<td>ln sqrt # spp</td>
<td>3.10</td>
<td>0.0800</td>
<td>0.0109</td>
<td>0.003</td>
<td>positive</td>
</tr>
<tr>
<td>grass³,₅,₉,₁₅,₁₆,₁₉,₂₀,₂₆,₂₈,₃₅</td>
<td>sqrt # spp</td>
<td>72.72</td>
<td>0.0001</td>
<td>0.2730</td>
<td>0.33</td>
<td>positive</td>
</tr>
</tbody>
</table>
Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>herb⁷,11,24,25,30,31,33,36,39,42</td>
<td>sqrt # spp</td>
<td>31.37</td>
<td>0.0001</td>
<td>0.1372</td>
<td>0.73</td>
<td>positive</td>
</tr>
<tr>
<td>MODEL (ALL TAXA)²⁷: % tree⁺%vine</td>
<td># spp</td>
<td>38.41</td>
<td>0.0001</td>
<td>0.3373</td>
<td>0.56</td>
<td></td>
</tr>
</tbody>
</table>

5. HABITAT AFFINITY¹⁴

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>forest⁴,5,8,10,11,15,17,20,22,23,25,29,30,33,34,36</td>
<td># spp</td>
<td>68.63</td>
<td>0.0001</td>
<td>0.2615</td>
<td>0.45</td>
<td>negative</td>
</tr>
<tr>
<td>forest + open⁴,5,11,15,17,18,19,21,22,28,30,31,35,39,40,42,43</td>
<td>sqrt # spp</td>
<td>16.04</td>
<td>0.0001</td>
<td>0.0730</td>
<td>0.07</td>
<td>negative</td>
</tr>
<tr>
<td>open + forest (sqrt % &quot;open + forest&quot;)¹⁸,19,20,21,22,28,29,34,35</td>
<td>sqrt # spp</td>
<td>47.06</td>
<td>0.0001</td>
<td>0.1943</td>
<td>0.10</td>
<td>positive</td>
</tr>
<tr>
<td>open⁴,6,7,8,10,16,17,18,19,20,26,29,34,37,43</td>
<td># spp</td>
<td>121.85</td>
<td>0.0001</td>
<td>0.3875</td>
<td>0.04</td>
<td>positive</td>
</tr>
<tr>
<td>MODEL (ALL TAXA)²⁷: % open + % forest</td>
<td># spp</td>
<td>68.56</td>
<td>0.0001</td>
<td>0.4143</td>
<td>0.03</td>
<td></td>
</tr>
</tbody>
</table>

6. SHADE TOLERANCE¹¹

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>shade tolerance class 1 (very shade tolerant)¹⁹,23,24,25,29,30,31,33,36</td>
<td>sqrt # spp</td>
<td>53.02</td>
<td>0.0001</td>
<td>0.2140</td>
<td>0.14</td>
<td>negative</td>
</tr>
<tr>
<td>shade tolerance class 2³,5,23,24,28,30,31,33,36</td>
<td>sqrt # spp</td>
<td>40.18</td>
<td>0.0001</td>
<td>0.1702</td>
<td>0.28</td>
<td>negative</td>
</tr>
<tr>
<td>shade tolerance class 3³,5,15,17,23,24,25,29,30,31,36,37</td>
<td>sqrt # spp</td>
<td>5.20</td>
<td>0.0237</td>
<td>0.0215</td>
<td>0.19</td>
<td>negative</td>
</tr>
<tr>
<td>shade tolerance class 4³,5,6,10,16,18,19,20,21,22,26,28,33,35,37</td>
<td>sqrt # spp</td>
<td>20.19</td>
<td>0.0001</td>
<td>0.0913</td>
<td>0.01</td>
<td>positive</td>
</tr>
<tr>
<td>shade tolerance class 5 (very shade intolerant)⁵,6,7,10,16,17,31,35,36</td>
<td>sqrt # spp</td>
<td>80.27</td>
<td>0.0001</td>
<td>0.2933</td>
<td>0.46</td>
<td>positive</td>
</tr>
</tbody>
</table>
Table 4.8. Plant trait correlates of species richness in 10m x 10m quadrats (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p≤W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>MODEL (ALL TAXA)¹⁴: % shade tolerance class 5 + % shade tolerance class 1</td>
<td>sqrt # spp</td>
<td>46.92</td>
<td>0.0001</td>
<td>0.3247</td>
<td>0.47</td>
<td></td>
</tr>
</tbody>
</table>

7. MOISTURE AFFINITY¹⁴

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p≤W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>obligate upland¹⁴, 15, 17, 22, 24, 26, 29, 30, 42, 43</td>
<td>sqrt # spp</td>
<td>66.52</td>
<td>0.0001</td>
<td>0.2554</td>
<td>0.77</td>
<td>negative</td>
</tr>
<tr>
<td>facultative upland¹⁴, 8, 10, 15, 17, 22, 24, 29, 30, 41, 42, 43</td>
<td>sqrt # spp</td>
<td>71.35</td>
<td>0.0001</td>
<td>0.2692</td>
<td>0.65</td>
<td>negative</td>
</tr>
<tr>
<td>facultative ⁶, 10, 11, 15, 17, 22, 24, 33, 40, 42, 43</td>
<td>sqrt # spp</td>
<td>0.06</td>
<td>0.8730</td>
<td>0.0051</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>facultative wetland ⁵, 6, 8, 10, 11, 15, 17, 22, 24, 33, 40, 41, 43</td>
<td>sqrt # spp</td>
<td>83.38</td>
<td>0.0001</td>
<td>0.3014</td>
<td>0.83</td>
<td>positive</td>
</tr>
<tr>
<td>obligate wetland ⁴, 5, 6, 7, 8, 10, 11, 15, 17, 22, 24, 39, 40, 41, 42</td>
<td>sqrt # spp</td>
<td>52.92</td>
<td>0.0001</td>
<td>0.2137</td>
<td>0.34</td>
<td>positive</td>
</tr>
<tr>
<td>MODEL:: % taxa facultative wetland</td>
<td>sqrt # spp</td>
<td>83.38</td>
<td>0.0001</td>
<td>0.3014</td>
<td>0.83</td>
<td>positive</td>
</tr>
</tbody>
</table>

8. OVERALL MODEL:: PLANT ATTRIBUTES¹⁴

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>F</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p≤W¹</th>
<th>relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>% taxa herbs dispersed by unassisted means + % taxa herbs dispersed by prolonged dormancy + % taxa herbs dispersed by ants + % taxa herbs dispersed by animal ingestion¹²</td>
<td># spp</td>
<td>61.35</td>
<td>0.0001</td>
<td>0.5583</td>
<td>0.95</td>
</tr>
</tbody>
</table>

Notes:
1. Shapiro-Wilk W test for normality of residuals (residuals normal when p≥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.

261
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. 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 unassisted 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 (r²adj.=0.154) or perennial (r²adj.=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 (r²adj.=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 ($r^2_{adj.} = 0.268$ 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 ($r^2_{adj.} = 0.273$) and trees ($r^2_{adj.} = 0.263$) (Table 4.8). Variables with intermediate explanatory power were the percentage of taxa that were vines ($r^2_{adj.} = 0.178$) and herbs ($r^2_{adj.} = 0.137$). The percentage of taxa that were ferns ($r^2_{adj.} = 0.055$) and shrubs ($r^2_{adj.} = 0.031$) 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
fern.

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 (r²adj. = 0.388) and forested (r²adj. = 0.214) habitats (Table 4.8). The percentage of taxa with an affinity for "open + forest" habitats (r²adj. = 0.194) explained more than twice as much variance in species richness as taxa with an affinity for "forest + open" habitats (r²adj. = 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 x 10m 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 (r²adj. = 0.293), shade tolerance class 1 (r²adj. = 0.214), and, shade tolerance class 2 (r²adj. = 0.170) (Table 4.8). The
percentage of taxa classified as shade tolerance 4 \( (r^2\text{adj.}=0.091) \) explained more variance than taxa classified as shade tolerance class 3 \( (r^2\text{adj.}=0.024) \).

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 \( (r^2\text{adj.}=0.301) \), facultative upland species \( (r^2\text{adj.}=0.269) \), obligate upland species \( (r^2\text{adj.}=0.255) \), and obligate wetland species \( (r^2\text{adj.}=0.214) \) (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 x 10m 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<\text{W} = 0.67 versus p<\text{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<\text{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<\text{W} = 0.88, 0.95, 0.89, respectively) and strong explanation of variance (r^2\text{adj.} = 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Attribute</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
</tr>
<tr>
<td>I. ENVIRONMENTAL VARIABLES</td>
<td></td>
</tr>
<tr>
<td>MODEL E1: ln # tree species (&gt;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</td>
<td>39.00</td>
</tr>
<tr>
<td>MODEL E2: % canopy closure (ln p/q) + sqrt # stems 0-4 cm dbh + soil moisture class + soil parent material²</td>
<td>33.93</td>
</tr>
<tr>
<td>II. DISPERsal VARIABLES</td>
<td></td>
</tr>
<tr>
<td>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 dormancy¹</td>
<td>83.61</td>
</tr>
<tr>
<td>MODEL D2 (HERBS ONLY): % taxa dispersed by unassisted means + % taxa dispersed by prolonged dormancy + % taxa dispersed by ants + % taxa dispersed by animal ingestion¹</td>
<td>74.10</td>
</tr>
<tr>
<td>III. MIXED VARIABLES</td>
<td></td>
</tr>
<tr>
<td>MODEL M1. % stems sugar maple + % taxa herbs dispersed by unassisted means + % taxa dispersed by prolonged dormancy (all life forms)³</td>
<td>123.54</td>
</tr>
</tbody>
</table>
Table 4.9. Comparison of selected GLM models of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Attribute</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th></th>
<th>F</th>
<th>r^2adj</th>
<th>MSE</th>
<th>p&lt;W</th>
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</thead>
<tbody>
<tr>
<td>III. MIXED VARIABLES (cont’d)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MODEL M2: ln # tree species (&gt;1 m) + % canopy closure (ln p/q) + forest cover type + % taxa dispersed by unassisted means (all life forms)*</td>
<td>56.51</td>
<td>0.6716</td>
<td>0.6692</td>
<td>0.61</td>
</tr>
<tr>
<td>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^</td>
<td>53.18</td>
<td>0.7119</td>
<td>0.5870</td>
<td>0.95</td>
</tr>
<tr>
<td>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^</td>
<td>44.89</td>
<td>0.6732</td>
<td>0.6660</td>
<td>0.22</td>
</tr>
<tr>
<td>MODEL M5: % taxa herbs dispersed by wind + sqrt # stems 0-4 cm dbh + soil moisture class + % canopy closure (ln p/q) + soil parent material^</td>
<td>43.63</td>
<td>0.6422</td>
<td>0.7291</td>
<td>0.89</td>
</tr>
</tbody>
</table>

Notes:
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.
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.

<table>
<thead>
<tr>
<th>Model</th>
<th>DCA Ordination Space</th>
<th>Degree of Overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1 vs E2</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D1 vs D2</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>M1 vs M2</td>
<td>overlap</td>
<td>minor</td>
</tr>
<tr>
<td>M1 vs M3</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>M1 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>M1 vs M5</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>M2 vs M3</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>M2 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>M2 vs M5</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>M3 vs M4</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>M3 vs M5</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>M4 vs M5</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>E1 vs D1</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E1 vs D2</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>E1 vs M1</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>E1 vs M2</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E1 vs M3</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>E1 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E1 vs M5</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E2 vs D1</td>
<td>overlap</td>
<td>minor</td>
</tr>
<tr>
<td>E2 vs D2</td>
<td>overlap</td>
<td>minor</td>
</tr>
<tr>
<td>E2 vs M1</td>
<td>separate</td>
<td>none</td>
</tr>
<tr>
<td>E2 vs M2</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E2 vs M3</td>
<td>overlap</td>
<td>major</td>
</tr>
</tbody>
</table>
Table 4.10. Summary of graphical evaluation of leading models of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>DCA Ordination Space</th>
<th>Degree of Overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td>E2 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>E2 vs M5</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D1 vs M1</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>D1 vs M2</td>
<td>overlap</td>
<td>minor</td>
</tr>
<tr>
<td>D1 vs M3</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D1 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D1 vs M5</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D2 vs M1</td>
<td>overlap</td>
<td>major</td>
</tr>
<tr>
<td>D2 vs M2</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D2 vs M3</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D2 vs M4</td>
<td>overlap</td>
<td>moderate</td>
</tr>
<tr>
<td>D2 vs M5</td>
<td>overlap</td>
<td>moderate</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model(s)</th>
<th>Partial F</th>
<th>p&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td># tree species</td>
<td>E1</td>
<td>66.16</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M2</td>
<td>75.51</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% canopy closure</td>
<td>E1</td>
<td>18.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>E2</td>
<td>43.19</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M2</td>
<td>20.33</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>9.02</td>
<td>0.0030</td>
</tr>
<tr>
<td></td>
<td>M4</td>
<td>8.51</td>
<td>0.0040</td>
</tr>
<tr>
<td></td>
<td>M5</td>
<td>12.64</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>forest cover type</td>
<td>E1</td>
<td>17.96</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M2</td>
<td>4.29</td>
<td>0.0024</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>6.99</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>open microhabitats</td>
<td>E1</td>
<td>15.09</td>
<td>0.0001</td>
</tr>
<tr>
<td># stems 0-4 cm dbh</td>
<td>E2</td>
<td>31.08</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>48.79</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M4</td>
<td>36.40</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M5</td>
<td>29.75</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>soil moisture class</td>
<td>E2</td>
<td>22.85</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M5</td>
<td>22.41</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>soil parent material</td>
<td>E2</td>
<td>8.10</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M5</td>
<td>7.28</td>
<td>0.0001</td>
</tr>
<tr>
<td>% unassisted means (ALF)</td>
<td>D1</td>
<td>59.36</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M2</td>
<td>69.64</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% animal conveyance (ALF)</td>
<td>D1</td>
<td>46.15</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M4</td>
<td>22.66</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% prolonged dormancy (ALF)</td>
<td>D1</td>
<td>25.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M1</td>
<td>57.99</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% unassisted means (H)</td>
<td>D2</td>
<td>32.63</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M1</td>
<td>58.19</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% prolonged dormancy (H)</td>
<td>D2</td>
<td>22.39</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>18.00</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>M4</td>
<td>31.46</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% ants (H)</td>
<td>D2</td>
<td>19.99</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Table 4.11. Explanatory variables included in leading models of species richness (cont’d).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model(s)</th>
<th>Partial F</th>
<th>p&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>% animal ingestion (H)</td>
<td>D2</td>
<td>14.38</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td>M3</td>
<td>15.65</td>
<td>0.0001</td>
</tr>
<tr>
<td>% stems sugar maple</td>
<td>M1</td>
<td>92.36</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>% grasses</td>
<td>M3</td>
<td>34.58</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>soil order</td>
<td>M4</td>
<td>5.08</td>
<td>0.0007</td>
</tr>
<tr>
<td>open regenerating fields</td>
<td>M4</td>
<td>4.53</td>
<td>0.0347</td>
</tr>
<tr>
<td>% wind (H)</td>
<td>M5</td>
<td>49.10</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
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); Al = % 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; 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.

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F Statistic</th>
<th>p-Value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>MODEL M1 - SPECIES: % stems sugar maple + % taxa herbs dispersed by unassisted means + % taxa dispersed by prolonged dormancy (all life forms)¹</td>
<td>sqrt # spp</td>
<td>123.54</td>
<td>0.0001</td>
<td>0.6593</td>
<td>0.88</td>
<td>no</td>
</tr>
<tr>
<td>MODEL M1 - GENUS: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means²</td>
<td># genera</td>
<td>94.68</td>
<td>0.0001</td>
<td>0.5996</td>
<td>0.42</td>
<td>no</td>
</tr>
<tr>
<td>MODEL M1 - FAMILY: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means³</td>
<td># families</td>
<td>63.77</td>
<td>0.0001</td>
<td>0.4977</td>
<td>0.002</td>
<td>ASACC x PDT ASACC x UNASS</td>
</tr>
<tr>
<td>MODEL M1 - ORDER: % taxa dispersed by prolonged dormancy (all life forms) + % stems sugar maple + % taxa herbs dispersed by unassisted means⁴</td>
<td># orders</td>
<td>59.16</td>
<td>0.0001</td>
<td>0.4787</td>
<td>0.06</td>
<td>ASACC x PDT</td>
</tr>
<tr>
<td>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 type⁵</td>
<td>sqrt # spp</td>
<td>53.18</td>
<td>0.0001</td>
<td>0.7119</td>
<td>0.95</td>
<td>no</td>
</tr>
</tbody>
</table>

282
Table 4.12. Contribution of phylogeny to superior models of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F Statistic</th>
<th>p-Value</th>
<th>r^2 adj.</th>
<th>p&lt;W</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>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</td>
<td># genera</td>
<td>47.07</td>
<td>0.0001</td>
<td>0.6857</td>
<td>0.77</td>
<td>PDH x GRASS</td>
</tr>
<tr>
<td>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.)</td>
<td># families</td>
<td>25.65</td>
<td>0.0001</td>
<td>0.5387</td>
<td>0.26</td>
<td>PDH x 0-4 cm dbh CC x 0-4 cm dbh PDH x GRASS PD x A1</td>
</tr>
<tr>
<td>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.)</td>
<td># orders</td>
<td>23.58</td>
<td>0.0001</td>
<td>0.5168</td>
<td>0.81</td>
<td>CC x 0-4 cm dbh PDH x GRASS A1 x GRASS</td>
</tr>
<tr>
<td>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</td>
<td>sqrt # spp</td>
<td>-43.63</td>
<td>0.0001</td>
<td>0.6422</td>
<td>0.89</td>
<td>no</td>
</tr>
<tr>
<td>MODEL M5 - GENUS: % taxa herbs dispersed by wind + canopy closure (ln p/q) + sqrt # stems 0-4 cm dbh + moisture class + soil parent material</td>
<td># genera</td>
<td>36.00</td>
<td>0.0001</td>
<td>0.5957</td>
<td>0.12</td>
<td>MC x 0-4 cm dbh CC x 0-4 cm dbh</td>
</tr>
<tr>
<td>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.)</td>
<td># families</td>
<td>30.09</td>
<td>0.0001</td>
<td>0.5505</td>
<td>0.40</td>
<td>CC x 0-4 cm dbh</td>
</tr>
</tbody>
</table>
Table 4.12. Contribution of phylogeny to superior models of species richness (cont’d).

<table>
<thead>
<tr>
<th>Model</th>
<th>Response Variable</th>
<th>F</th>
<th>p-value</th>
<th>r² adj.</th>
<th>p&lt;W¹</th>
<th>Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>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</td>
<td># orders</td>
<td>32.06</td>
<td>0.0001</td>
<td>0.5667</td>
<td>0.07</td>
<td>SPM x WIND</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>SPM x CC</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>CC x 0-4 cm dbh</td>
</tr>
</tbody>
</table>

Notes:
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.
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.
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.

<table>
<thead>
<tr>
<th>Taxonomic Rank</th>
<th># classified taxa</th>
<th># Attribute Categories</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
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</tr>
<tr>
<td><strong>MOISTURE AFFINITY</strong></td>
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<tr>
<td>Species</td>
<td>387</td>
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<tr>
<td>Genus</td>
<td>204</td>
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<td>28.9</td>
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<td><strong>LIGHT AFFINITY</strong></td>
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<td>Order</td>
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<td><strong>MODE OF DISPERSAL</strong></td>
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<tr>
<td>Species</td>
<td>413</td>
<td>88.1</td>
</tr>
<tr>
<td>Genus</td>
<td>208</td>
<td>86.5</td>
</tr>
<tr>
<td>Family</td>
<td>77</td>
<td>66.2</td>
</tr>
<tr>
<td>Order</td>
<td>45</td>
<td>42.2</td>
</tr>
</tbody>
</table>
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
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 to 1378m, 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 x 10m quadrat, was a significant but weak contributor to species richness (p=0.0007, $r^2$adj = 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 4.4.5.6). 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, 32.3 cm and 32.3 cm respectively, \( p > \chi^2 = 0.0097 \); mean maximum height = 76.6 cm, 133.2 cm, 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 \((r^2 \text{ adj.} = 0.6285, \text{Model D1. versus} \ r^2 \text{ adj.} = 0.5833, \text{Model E1. Table 4.9})\). Plant attributes that maximally explained differences in species richness were mode of dispersal \((r^2 \text{ adj.} = 0.5583)\), habitat affinity \((r^2 \text{ adj.} = 0.4143\)), life form \((r^2 \text{ adj.} = 0.3373\)), shade tolerance \((r^2 \text{ adj.} = 0.3247)\) and moisture affinity \((r^2 \text{ adj.} = 0.3014)\) (Table 4.8). In contrast, environmental attributes that maximally explained differences in species richness were stand structure \((r^2 \text{ adj.} = 0.5485)\) and soils \((r^2 \text{ adj.} = 0.3557)\) (Table 4.1). Significant but weak predictors of species richness were life history \((r^2 \text{ adj.} = 0.1315)\), human disturbance \((r^2 \text{ adj.} = 0.1280)\), landscape variables \((r^2 \text{ adj.} = 0.0658)\) and environmental heterogeneity \((r^2 \text{ adj.} = 0.0537)\) (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

290
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 A1 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 A1 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
   (r²adj. = 0.253), soil moisture (r²adj. = 0.247), and soil parent material (r²adj. = 0.220).

2. Stand structure variables explained 54.9% of the variance in species richness in 10m x 10m
   quadrats. The variables that maximally explained differences in richness were forest cover
   type (r²adj. = 0.277), # tree species >1m (r²adj. = 0.268), % stems sugar maple (r²adj. =
   0.256), % stems sugar maple 0-4 cm dbh (r²adj. = 0.254), # wet-mesic. wet tree species >1m
   (r²adj. = 0.224), and, # live tree stems 0-4 cm dbh (r²adj. = 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

301
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 ($r^2$adj. = 0.089), open trails ($r^2$adj. = 0.089), and open regenerating fields ($r^2$adj. = 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° 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 ($r^2$adj. = 0.397), ants ($r^2$adj. = 0.333), and the wind ($r^2$adj. = 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 ($r^2_{adj.} = 0.132$).

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 ($r^2_{adj.} = 0.268$).

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 ($r^2_{adj.} = 0.273$) and trees ($r^2_{adj.} = 0.263$).

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 ($r^2_{adj.} = 0.388$ 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 ($r^2_{adj.} = 0.293$ 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 ($r^2_{adj.} = 0.301$), and the percentages of taxa classified as having a facultative or obligate affinity for upland habitats ($r^2_{adj.} = 0.269$ and 0.255, 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 siliqua 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 siliqua, 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

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 tricocum, 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 tricocum, 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 \textit{b} relative to chlorophyll \textit{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 \textit{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 \textit{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 \textit{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.

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 \textit{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 (>1 m) 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.

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 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 ($r^2_{adj.} = 0.6285$. Model D1 versus $r^2_{adj.} = 0.5833$, 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.
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-Brown 1977), 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

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 ≤25% stems (>1m) sugar maple to 27.1 species in quadrats with ≥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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360


365


APPENDICES
APPENDIX 1

LOCATION OF STUDY SITES
Appendix 1. Location of Study Sites.

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APPENDIX 2

SUMMARY OF PLANT ATTRIBUTES BY SPECIES
Appendix 2. Summary of Plant Attributes by Species.


Appendix 2. Summary of plant attributes by species.

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Appendix 2. Summary of plant attributes by species.

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394
APPENDIX 3

SPECIES CODES
## Appendix 3. Species codes.

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398
### Appendix 3. Species codes.

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<th>Species Code</th>
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Appendix 3. Species codes.

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APPENDIX 4

DISTRIBUTION OF SPECIES BY SOIL PARENT MATERIAL, SOIL ORDER, SOIL MOISTURE AND CANOPY CLOSURE
### Legend

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**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 microhabitats in the same quadrat.
Appendix 4. Distribution of species by soil parent material, soil order, soil moisture and canopy closure.

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APPENDIX 5

LISTING OF SPECIES BY MICROHABITAT
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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425
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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|               | ARCTMINU       | CRAT_SP        | MATTSTRU       | SOLIGIGA       |
|               | ARISTRIP       | CYPRCALC       | MENTARVE       | SOLIRUGO       |
|               | ASARCA       | CYSTBULB       | MITEDIHP       | SPHEINTE       |
|               | ASCLSYRI       | DRYOCART       | MUHLMEXI       | STELLONG       |
|               | ASTELATE       | DRYOCRIS       | ONOCSENS       | TARAOFFI       |
|               | ASTENOVE       | DRYOINTE       | OSTRVIRG       | TAXBUCANA       |
|               | ASTEPUNI       | DRYOMARG       | PARTINSE       | THALDIOI       |
|               | ATHYFILI       | ELYMVIRG       | PHRYLEPT       | THALPUBE       |
|               | BETUALLE       | EPILCLI        | PILEPUMI       | THELPALU       |
|               | BETUPURY       | EPILCOLO       | PINUSTRO       | THUJOCCI       |
|               | BIDEFRON       | EPILEPT        | PLANMAJO       | TIRACORD       |
|               | BOEHCYLI       | EPILPARV       | PLANRUGE       | TILIAMER       |
|               | BOTRVALG       | EPIPHEL        | POA_ALSO       | TRIBORE       |
|               | CARDIDPH       | EQUARVE        | POA_PALU       | TRILEREC       |
|               | CARDPENS       | ERIGPHIL       | POA_PRAT       | TRILGRAN       |
|               | CAREALOP       | ERIGSTRI       | POLYACRO       | TSUGCANA       |
|               | CAREBEBB       | ERYTAMER       | POPUBALS       | ULMUAMER       |
|               | CAREBLAN       | EUPAMACU       | POPUTREM       | UNKN_751       |
|               | CAREBLAN       | EUPAPERF       | PRUNSERO       | URTIDIOI       |
|               | CAREBREV       | EUPARUGO       | PRUNVIRG       | VIBULENT       |
|               | CARECEPH       | FAGUGRAN       | PRUNVULG       | VIBUTRIL       |
|               | CARECRIS       | FESTSUBV       | QUERMACR       | VIOAFFI       |
|               | CAREDEWE       | FRAGVIRG       | RANABOR        | VIOBLAN       |
|               | CAREGARAC      | FRAXAMER       | RANUACRI       | VIOCANA       |
|               | CAREINTU       | FRAXNIGR       | RANURECU       | VIOCCU       |
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|               | CAREPEDU       | GALETETR       | RHURSADI       | VIOLPUBE       |
|               | CAREPENS       | GALIASPR       | RIBEAMER       | VIOL_SP       |
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|               | CAREROSE       | GALITRIF       | RIBEGLAN       | WALDFRAG       |
|               | CARETENE       | GENTANDR       | RIBERUBR       |               |
|               | CARETIB        | GERAROBE       | RIBETRIS       |               |
|               | CAREVULP       | GEUMCANA       | ROSABLAM       |               |
|               | CARPCARO       | GEUMLACI       | ROSAPALU       |               |
|               | CARYCORD       | GEUM_SP        | RUBULALE       |               |
|               | CAULHAL        | GLYCSTRI       | RUBUADE       |               |
|               | CERAFONT       | GYMNDRYO       | RUBUODR       |               |
|               | CIRCALPI       | HIERCAES       | RUBUPUBE       |               |
|               | CIRCUTE        | HYPEPERF       | SALIBEBB       |               |
|               | CIRSAVE        | IMPACAPE       | SALIDISC       |               |
|               | CLEMVRG       | LAPOCANA       | SALIERIO       |               |
|               | CLINBORE       | LIPPOLOES      | SAMBRAPU       |               |
|               | CORNALTE       | LYCOAMER       | SCHIPURP       |               |
|               | CORNFEOI       | LYCONUNIF      | SCIRATRO       |               |
|               | CORNROGU       | LYSICILI       | SCUTLATE       |               |
|               | TSUGCANA       | LYSINUMM       | SOLADULC       |               |
|               | ULMUAMER       | MAJACANA       | SOLIALTI       |               |

2. Moist Floors
(n=197 species)

| ACIIBALS       | ABIEBALS       | ACERENGU       | ACERRUBR       | ACERSACC       |
|               | ACEREURO       | ACERSACN       | ACERSANI       | ACERSPIC       |
|               | ACERRUBR       | ACERVULP       | ACTARUBR       | ACTA_SP        |
|               | ADIAPEDA       | ADIPEDA        | AGRIGRYP       | AGROGIGA       |
|               | AGROGIGA       | AGROGIGA       | AMLABRO        | AMELABRO       |
|               | AMPHBRAC       | AMPHBRAC       | ANEMCANA       | ANEMCANA       |
|               | ANEMVIIRG      | ANEMVIIRG      |               |               |

3. Wet Floors
(n=152 species)

| ACERRUBR       | ACERASCN       | ACERSANI       | ACERSPIC       | ACHIMILL       |
|               | ACISACN       | ACTARUBR       | ACTA_SP        | ACTA_SP       |
|               | ADIAPEDA       | AGRIGRYP       | AGROGIGA       | AGROGIGA       |
|               | AGROGIGA       | AGROGIGA       | AMELABRO       | AMELABRO       |
|               | AMPHBRAC       | AMPHBRAC       | ANEMCANA       | ANEMCANA       |
|               | ANEMVIIRG      | ANEMVIIRG      |               |               |
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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4. Moist Depressions (n=136 species)

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427
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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8. Moist Gap
\(n=68\) species

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9. MOUND
\(n=165\) species

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429
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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14. Raised Root Mat
(n=138 species)

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17. Ditch (n=68 species)

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| ACERSACN | ACERSACN |
| ACHIMILL | ACHIMILL |
| AGROGIGA | AGROGIGA |
| ANEMCANA | ANEMCANA |
| ASTELATE | ASTELATE |
| ASTEPUNI | ASTEPUNI |

18. Regenerating Field (n=125 species)

| ABIEBALS | ABIEBALS |
| ACERRUBR | ACERRUBR |
| ACERSACC | ACERSACC |
| ACERSACN | ACERSACN |
| ACHIMILL | ACHIMILL |
| ACTARUBR | ACTARUBR |
| AGRIGRYP | AGRIGRYP |
| AGROGIGA | AGROGIGA |
| AGROSTOL | AGROSTOL |
| AMELINTE | AMELINTE |
| ANEMVIRG | ANEMVIRG |
| APOCANDR | APOCANDR |
| AQUICANA | AQUICANA |
| ASCILSYRI | ASCILSYRI |
| ASTECILI | ASTECILI |
| ASTELATE | ASTELATE |
| ASTERNOVE | ASTERNOVE |
| ASTEPUNI | ASTEPUNI |
| BETUPAY | BETUPAY |
| BOTRVIRG | BOTRVIRG |
| BROMER | BROMER |
| CAREBLAN | CAREBLAN |
| CARECRIS | CARECRIS |
| CAREGRAC | CAREGRAC |
| CAREGRAN | CAREGRAN |
| CARELANU | CARELANU |
| CAREPENS | CAREPENS |
| CARERADI | CARERADI |
| CARESTIP | CARESTIP |
| CARETENE | CARETENE |
| CARE_.719 | CARE_.719 |
| CARPCARO | CARPCARO |

19. Dry Floors

| CARYCORD | CARYCORD |
| CELASCAN | CELASCAN |
| CERAFONT | CERAFONT |
| CHRYLEUC | CHRYLEUC |
| CIRASARV | CIRASARV |
| CORNSTOL | CORNSTOL |
| CORVCORN | CORVCORN |
| CRAT _SP | CRAT _SP |
| DAUCCARO | DAUCCARO |
| DESMGLUT | DESMGLUT |
| ELYMVIRG | ELYMVIRG |
| EPILOCIL | EPILOCIL |
| EPIILLEPT | EPIILLEPT |
| EPIPHELL | EPIPHELL |
| ERIARVIE | ERIARVIE |
| ERIGRPHL | ERIGRPHL |
| ERIGSTRI | ERIGSTRI |
| EUPAMACU | EUPAMACU |
| EUPAPERF | EUPAPERF |
| EUTHGRAM | EUTHGRAM |
| FRAVIRG | FRAVIRG |
| FRAXAMER | FRAXAMER |
| FRAXNIGR | FRAXNIGR |
| FRAXPENN | FRAXPENN |
| GALICIRC | GALICIRC |
| GALIOBTU | GALIOBTU |
| GALITRIF | GALITRIF |
| GENTANDR | GENTANDR |
| HIERCAES | HIERCAES |
| HYPERPERF | HYPERPERF |
| IMPACAPE | IMPACAPE |
| IRIS _SP | IRIS _SP |
| LACTCANA | LACTCANA |
| LIPALOES | LIPALOES |
| LYCOAMER | LYCOAMER |
| LYOXUNC | LYOXUNC |
| MELIOMIF | MELIOMIF |
| MELIOMIF | MELIOMIF |
| MHFRON | MHFRON |
| ONOCSENS | ONOCSENS |
| OXALSTR | OXALSTR |
| PANKACUM | PANKACUM |
| PARTNSE | PARTNSE |
| PHALARUN | PHALARUN |
| PILEPUMI | PILEPUMI |
| PLANLANC | PLANLANC |
| PLANRUGE | PLANRUGE |
| POA_COMP | POA_COMP |
| POA_PALU | POA_PALU |
| POA_PRAT | POA_PRAT |
| POPUBALS | POPUBALS |
| POPUTREM | POPUTREM |
| POTERECT | POTERECT |
| PRUNEREO | PRUNEREO |
| PRUNVIRG | PRUNVIRG |
| RANUACRI | RANUACRI |
| RUBUALLE | RUBUALLE |
| RUBUIDAE | RUBUIDAE |
| RUBUPUBE | RUBUPUBE |
| RUBUPUBE | RUBUPUBE |
| RUBUALLE | RUBUALLE |
| RUBUIDAE | RUBUIDAE |
| SALIBEBB | SALIBEBB |
| SALIDIES | SALIDIES |
| SALIERIO | SALIERIO |
| SISYMONT | SISYMONT |
| SMILHERB | SMILHERB |
| SOLIALTI | SOLIALTI |
| SOLICANA | SOLICANA |
| SOLIGIGA | SOLIGIGA |
| SOLINEMO | SOLINEMO |
| TARAOFFI | TARAOFFI |
| THUJOCCI | THUJOCCI |
| TILIAME | TILIAME |
| TRAGDUBI | TRAGDUBI |
| TRIFREPE | TRIFREPE |
| TRILGRAN | TRILGRAN |
| ULMUAMER | ULMUAMER |
| VIBUACER | VIBUACER |
| VIBULENT | VIBULENT |
| VICIRCAC | VICIRCAC |
| VIOLAFFI | VIOLAFFI |
| VIOL_.SP | VIOL_.SP |
| VITIRIPA | VITIRIPA |

OPEN CANOPY

19. Dry Floors
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

| OPEN CANOPY | GENTANDR | GERAROBE | GEUMCANA | GEUMLACI | GEUM_SP | GLYCSTR | HIERCAES | IMPACAPE | INULHELI | IRISVERS | LACT_SP | LAPOCANA | LEERVIRG | LIPALOES | LYCOUNIF | LYSICILI | MAIACANA | MATTSTRU | MEDILUPU | MENTARVE | MITEDIP | ONOCSENS | OSMOCLAY | PARTINSE | PHELEPRAT | PILEPUMI | PLANMAJO | PLANRUGE | POA_ALSO | POA_PALU | POA_PRAT | POLYPUBE | POPBALS | POPTREM | PRUNVIRG | PRUNVULG | RANUAROB | RANUACRI | RANURECU | RHAMCATH | RHUSRADI | RIBEAMER | RIBECYNO | RIBETRIS | RUBUOCCI | SALIERIO | SAMBCANA | SCUTRATE | SOLADULC | SOLICANA | SOLIGIGA | SPHEINTE | TARAOFFI | THUOCOCI | TILIAMER | ULMUAMER | VIOLUCUC | VITIRIPA |
|-------------|----------|----------|----------|----------|---------|---------|----------|---------|----------|----------|---------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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<th>Species Codes</th>
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<td><strong>22. (cont’d) ONOCSENS PARTINSE POA_PALU PRUNVIRG RANUACRI RANURECU RHAMCATH RIBETRIS RUBUIDAE RUBUPUBE SAMBCANA SOLADULC TARAOFFI TiarCord ULMUAMER</strong></td>
<td>ADIAPEDA, ARALNUDI, ARISTRIp, ASARCANA, ASTELATE, CARDDIPH, CAREARCT, CAREBLAN, CAREDIGI, CAREPEDU, CAREPENS, CAREPERS, CAREROSE, CARYCORD, CAULTHAL, CIRCLUTE, CIRSAVE, CIRSVULG, CONYCANA, CORNOEM, CORNRUGO, CYSTTENU, DICECANA, DIERLONI, DRYOCART, DRYPOL, EPIFVRG, EPIICOLO, EPIPHELL, ERYTAMER, EURTHRAM, FRAGVESC, FRAXAMER, GALITRIF, GERMAMACU, GERAROBE, GYMNDROYO, HACKVIRG, MAIAACANA, MAIARACE, MITCREPE, ONOPACAN, OJRZASPE, OSMOCLAY, OSTRVIRG, PHYRLEPT, POA_PRAT, POLYAUC, POLYPUKE, PRUNVIRG, QUERRUBR, RANUABOR, RHAMCATH, RUBUIDAE, RUBUOCCI, SAMBRAPU, SOLADULC, TARAOFFI</td>
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<td><strong>24. Seep (n=25 species)</strong></td>
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<td><strong>25. Mound (n=76 species)</strong></td>
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<td><strong>26. Dry Pit (n=26 species)</strong></td>
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<td><strong>27. Wet Pit (n=1 species)</strong></td>
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<td><strong>28. Log (n=64 species)</strong></td>
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<td><strong>29. Wet Pit (n=1 species)</strong></td>
<td>IMPACAPE</td>
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435
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

| CANOPY | PARTINSE | PHALARUN | PHELEPRAT | PIHYLEPT | PILEPUMI | PLANLANC | PLANMAJO | PLANRUGE | P0A_ALSO | POA_COMP | POA_PALU | POA_PRAI | P0LYPERS | P0LYPUBE | P0LYPUBE_P | P0LYPUB0 | P0LYPUBE_R | P0LYPUBE_S | P0LYPUBE_T | P0LYPUBE_U | P0LYPUBE_V | P0LYPUBE_W | P0LYPUBE_X | P0LYPUBE_Y | P0LYPUBE_Z | URTIDIGR | URTIDIOI | VERBHASt | VERBURI | VEROSERP | VIBUACER | VICIRCAC | VIOLAFFI | VIOLBLAN | VIOLCANA | VIOLCUCU | VIOLSIBE | VIOLSIBO | VITISIBO | VITIRIPA |
|--------|----------|----------|-----------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| 31. (cont’d) | EUPAMACU | EUPAPERF | EUPARUGO | FESTPRAT | FRAGVESC | FRAGVIRG | FRAXAMER | FRAXNIGR | FRAXPENN | GALIOBTU | GALITRIF | GERAROBExE | GEUMLACI | GEUM_SP | GLYCSTRI | GYMNDRYO | HACKVIRG | HEPAACUT | HIERCAES | HYPERPERF | HISTPATU | IMPACAPE | IRIS_SP | JUNCTENU | LACTCANA | LACTSERR | LEERORYZ | LEONCARD | LOBE_SP | LYCOAMER | LYCOHINIF | LYSICILI | MAIACANA | MATTSTRU | MEDILIPU | MELIALBA | MENICANA | MENTARVE | MUHLMEXI | ONOCSENS | ONOPACAN | OSMOCLAY | OSTRVIRG | OXALSTRI | PANI_SP | 33. Regenerating Field (n=147 species) | ACERRUBR | ACERSACC | ACERSACN | ACHIMILL | AGRIGRYP | AGROGIGA | AMPHBRAC | ANEMCANA | ANEMVIRG | ANTEMENG | APOCANDR | AQUICANA | ASCLINCA | ASCLSRYI | ASTICL | ASTIEER | ASTELANC | ASTELATE | ASTEPUNI | ASTCANCE | BETUPAPY | BOTRMAHR | BOTRVIRG | BROMINE | CAREALOP | CAREBEBB | CAREBLAN | CAREBREV | CARECRIS | CASEDEWE | CAREGAC | CAREGRAN | CARELANU | CAREPENS | CAREPRAI | CAREPROJ | CARERADI | CARESTIP | CARETENE | CAREVULP | CARE_879 | CARYCORD | CERAFONT | CHYRELUC | CIRSSARVE | CIRSVULG | CORRUGO | CORNSTOL | CRAT_SP | DAUSTSPIC | DAUCCARO | DIANARME | ELYRREPE | ELYMVIRG | EPICTIL | EPILEPT | EPIHELL | EQUARVE | EQUHIYEM | ERIHPHIL | ERIGSTRI | EUPAMACU | EUPAPERF | EUTHGRAM | FASUGRAN | FESTARUN | FESTRUHR | FESTUSB | FRAVIRG | FRAXAMER | FRAXNIGR | FRAXPENN | GALIOBTU | GALITRIF | GENTANDR | GEUM_SP | GLYCSTRI | HIERCAES | HYPERPERF | LACTCANA | LYCOTHRIS | LYMOUNIF | LYSICILI | MAIACANA | MATTSTRU | MEDILIPU | MELIALBA | MELIOFFI | MENTARVE | MUHLFRON | MUHLMEXI | 437 |
Appendix 5. Listing of species by microhabitat. Species codes presented in Appendix 3.

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34. Riparian Marsh (n=46 species)

35. Riparian Meadow (n=75 species)

36. Riparian Thicket (n=37 species)
APPENDIX 6

DISTRIBUTION OF SPECIES BY MICROHABITAT:
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| FRAGVIRG         | 3    | 1    | 1    | 4    | -    | -    | 1    | -    | -    | -    | 1    | 1   | 4    | -    | -    | 1    | 4    | -   |
| FRAXAMER         | 7    | 3    | -    | 1    | 4    | -    | 1    | 5    | -    | 1    | -    | 1   | 5    | -    | 2    | -    | 2    | 2   |
| FRAXNIGR         | 1    | 2    | 1    | 3    | 1    | -    | 2    | 2    | -    | 1    | -    | 2   | -    | 2    | 1    | -    | -    | 2   |
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APPENDIX 7

DISTRIBUTION OF SPECIES BY MICROHABITAT:
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Appendix 7. Distribution of species by microhabitat: open canopy.

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APPENDIX 9

ENVIRONMENTAL DATA SUMMARY BY QUADRAT (II)
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Appendix 9. Environmental data summary by quadrat (II).

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Appendix 9. Environmental data summary by quadrat (II).

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| 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   | 5    | 20 | 13  | 6   | 0  | 3  | 102 | 94    | 6     | 1     | 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     |
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| 11  | 88 | 88   | 54   | 32   | 2    | 0    | 86   | 74   | 12   | 4  | 22  | 46  | 7  | 5  | 114 | 94    | 18    | 2     | 0     |
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Appendix 9. Environmental data summary by quadrat (II).

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| 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  | 16 | 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 | 15 | 3  | 9   | 5   | 5    | 2    | 0    | 2    |
| 18  | 137| 32   | 27   | 20   | 0    | 0    | 32   | 31   | 1   | 14 | 8   | 4  | 0  | 2  | 63  | 27  | 12   | 0    | 0    | 0    |
| 18  | 138| 21   | 17   | 12   | 0    | 0    | 21   | 20   | 1   | 6  | 5   | 4  | 0  | 2  | 36  | 19  | 8    | 0    | 0    | 0    |
| 18  | 139| 22   | 18   | 14   | 0    | 0    | 22   | 21   | 1   | 6  | 7   | 4  | 0  | 2  | 42  | 9   | 25   | 8    | 0    | 0    |
| 18  | 140| 22   | 19   | 13   | 0    | 0    | 22   | 21   | 1   | 8  | 3   | 5  | 0  | 2  | 47  | 15  | 19   | 13   | 0    | 0    |
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| 19  | 147| 59   | 41   | 27   | 0    | 0    | 59   | 54   | 5   | 20 | 18  | 8  | 2  | 3  | 46  | 30  | 12   | 4    | 0    | 0    |
| 19  | 148| 40   | 30   | 24   | 0    | 0    | 40   | 39   | 1   | 14 | 13  | 5  | 0  | 3  | 53  | 43  | 4    | 6    | 0    | 0    |
| 19  | 149| 76   | 50   | 36   | 2    | 1    | 73   | 70   | 6   | 16 | 31  | 16 | 1  | 4  | 66  | 56  | 4    | 6    | 0    | 0    |
| 19  | 150| 58   | 48   | 33   | 2    | 1    | 55   | 53   | 5   | 14 | 18  | 14 | 1  | 4  | 66  | 56  | 4    | 6    | 0    | 0    |
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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:


<table>
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<tr>
<th>Species</th>
<th>Mean (m)</th>
<th>Median (m)</th>
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<th>Range (m)</th>
<th>Terminal Velocity (cm/s)</th>
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<td>trees, shrubs, vines, herbs (n=13 spp)</td>
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Appendix 11. Representative seed dispersal distances of native and alien species in N. America.

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<th>Terminal Velocity (cm/s)</th>
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<td><em>Prunus avium</em></td>
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<td><em>Toxicodendron radicans</em></td>
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<td><em>Vitis vulpina</em></td>
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<td><strong>Herbs (n=1)</strong></td>
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<td><em>Juglans nigra</em></td>
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<td><em>Quercus palustris</em></td>
<td>1.1 km</td>
<td>1.9 km</td>
<td>0.1-1.9 km</td>
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<td></td>
<td>25 42 (25)</td>
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<td><strong>Adhesive Fruits</strong></td>
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<td><strong>Herbs (n=4)</strong></td>
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<tr>
<td><em>Achyranthes aspera</em> (Costa Rica)</td>
<td>24.7m - 2.4 km</td>
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<td><em>Bidens sp.</em> (Costa Rica)</td>
<td>12.4-108.8</td>
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<td><em>Daucus carota</em></td>
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<tr>
<td><em>Petiveria alliacea</em> (Costa Rica)</td>
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<td><strong>Elaíosome Seeds/Fruits</strong></td>
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<td><strong>Trees (n=2)</strong></td>
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<td><em>Acacia suaveolens</em> (Australia)</td>
<td>2.0-6.5</td>
<td>10.9</td>
<td>0.4-10.9</td>
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Appendix 11. Representative seed dispersal distances of native and alien species in N. America.

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<td>Dendromecon harfordii</td>
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<tr>
<td>Dendromecon rigida</td>
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<td>4.8</td>
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<tr>
<td>Dillwynia retorta (Australia)</td>
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<td>Fremontodendron decumbens</td>
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<td>Asarum canadense</td>
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<td>Carex pilulifera (Denmark)</td>
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<td>Crotalaria rotundifolia</td>
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<td>Datura discolor</td>
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<td>Dicentra formosa</td>
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<tr>
<td>Erythronium grandiflorum</td>
<td>0.3</td>
<td>&lt;1 (mtd)</td>
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<td>Euphorbia esula</td>
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<td>25 (mtd)</td>
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<tr>
<td>Sanquinaria candensis</td>
<td>0.2-3.1</td>
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<td>Scleroaena dicantha (Australia)</td>
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<tr>
<td>Trillium grandiflorum</td>
<td>10.0</td>
<td>&lt;1-10.0</td>
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<tr>
<td>Trillium kamtschaticum (Japan)</td>
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<tr>
<td>Trillium ovatum</td>
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<tr>
<td>Trillium tschonoskii (Japan)</td>
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<td>0.4</td>
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<td>Viola odorata</td>
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Appendix 11. Representative seed dispersal distances of native and alien species in N. America.

<table>
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<th>Species</th>
<th>Seed Dispersal Distance</th>
<th>Ref.#</th>
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<td>Viola pensylvanica</td>
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<tr>
<td>Viola rostrata</td>
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<tr>
<td>Viola triloba</td>
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**Other Fruits** (n=3)

**Trees**

- Pinus spp
- Pinus edulis

**Herbs**

- Mimulus guttatus

**WIND DISPERSED**

**Trees** (n=31)

- Abies alba
- Acer griseum
- Acer negundo
- Acer platanoides
- Acer pseudoplatanus
- Acer rubrum
- Acer saccharum

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505
Table 11. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean (m)</th>
<th>Median (m)</th>
<th>Maximum (m)</th>
<th>Range (m)</th>
<th>Terminal Velocity (cm/s)</th>
<th>Ref.#</th>
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<td>55</td>
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<td><em>Catalpa bignoides</em></td>
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<td><em>Carpinus betulus</em></td>
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<td>47 (39)</td>
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<td>129</td>
<td>51</td>
<td></td>
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<tr>
<td><em>Cedrus atlantica var. glauca</em></td>
<td>68.8</td>
<td>112</td>
<td>51</td>
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<tr>
<td><em>Fraxinus spp</em></td>
<td>&gt;50</td>
<td>15% &gt; 50</td>
<td>120-170</td>
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<td>104</td>
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<td>131</td>
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<td><em>Larix laricina</em></td>
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<td>52</td>
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Appendix 1: Representative seed dispersal distances of native and alien species in N. America.

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<td><em>Thuja plicata</em></td>
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Appendix I1. Representative seed dispersal distances of native and alien species in N. America.

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<th>Maximum (m)</th>
<th>Range (m)</th>
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<td>101</td>
<td>69 19</td>
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<tr>
<td><em>Apocynum cannabinum</em></td>
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<td>51</td>
</tr>
<tr>
<td><em>Asclepias syriaca</em></td>
<td>13.8</td>
<td>45</td>
<td>150 (mtd)</td>
<td>4.2-25.3 2% &gt;150</td>
<td>24.9</td>
<td>67 58 58 51</td>
</tr>
<tr>
<td><em>Asclepias syriaca (cont’d)</em></td>
<td>15.6-43.7</td>
<td>75</td>
<td></td>
<td></td>
<td></td>
<td>70</td>
</tr>
<tr>
<td><em>Apocynum sibiricum</em></td>
<td>25.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Aster acuminatus</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Aster prenanthoides</em></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td><em>Carduus nutans</em></td>
<td>&lt;3°/0.1-100 (mtd)</td>
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<td><em>Carduus pyconcephalus</em></td>
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<td><em>Carduus tenuiflorus</em></td>
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<td>0.7-2.1</td>
<td></td>
<td></td>
<td></td>
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</tr>
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<td><em>Carlina vulgaris</em></td>
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<td>0.5-1.5</td>
<td></td>
<td></td>
<td></td>
<td>75</td>
</tr>
<tr>
<td><em>Centauria scabiosa</em></td>
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<td>0.5-1.6</td>
<td></td>
<td></td>
<td></td>
<td>75</td>
</tr>
<tr>
<td><em>Cirsium arvense</em></td>
<td>2 km (mtd) 11.4</td>
<td>3.8-11.4</td>
<td></td>
<td>26</td>
<td>21.6</td>
<td>6 75</td>
</tr>
<tr>
<td><em>Cirsium palustre</em></td>
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<td>2.3-6.8</td>
<td></td>
<td></td>
<td></td>
<td>75</td>
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<tr>
<td><em>Cirsium undulatum</em></td>
<td>18.4</td>
<td>35</td>
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<td></td>
<td></td>
<td>67</td>
</tr>
<tr>
<td><em>Cirsium vulgare</em></td>
<td>11.6 32 (mtd) &gt;&gt;km</td>
<td>50% &lt;1 16% 1-2 10% &gt;32</td>
<td></td>
<td>36</td>
<td></td>
<td>51 45 45 45</td>
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<tr>
<td><em>Cryptantha flava</em></td>
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<td></td>
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Appendix 11. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed Dispersal Distance</th>
<th>Ref. #</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (m)</td>
<td>Median (m)</td>
</tr>
<tr>
<td><strong>Erigeron acer</strong></td>
<td>2.4</td>
<td>1.2-2.4</td>
</tr>
<tr>
<td><strong>Erigeron annus</strong></td>
<td>2.5</td>
<td>1-25</td>
</tr>
<tr>
<td><strong>Eupatorium cannabinum</strong></td>
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<td><strong>Eupatorium rugosum</strong></td>
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</tr>
<tr>
<td><strong>Heterotheca latifolia</strong></td>
<td>1.1-1.7</td>
<td>20 (mtd)</td>
</tr>
<tr>
<td><strong>Hieracium aurantiacum</strong></td>
<td>2.0 (mtd)</td>
<td>8</td>
</tr>
<tr>
<td><strong>Hieracium umbellatum</strong></td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td><strong>Hypochoeris glabra</strong></td>
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<td></td>
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<td><strong>Hypochoeris radicata</strong></td>
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<td>0.7-2.0</td>
</tr>
<tr>
<td><strong>Leontodon autumnalis</strong></td>
<td>1.1</td>
<td>0.6-1.1</td>
</tr>
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<td><strong>Liatris aspera</strong></td>
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<td>9</td>
</tr>
<tr>
<td><strong>Mimulus guttatus</strong></td>
<td>4.8</td>
<td>44% &lt;0.3</td>
</tr>
<tr>
<td><strong>Physalis subglabrata</strong></td>
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<td></td>
</tr>
<tr>
<td><strong>Rumex obtusifolia</strong></td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td><strong>Senecio jacobea</strong></td>
<td>0.6-3.3</td>
<td>5.5</td>
</tr>
<tr>
<td>disk achenes</td>
<td>14</td>
<td>31% 1</td>
</tr>
<tr>
<td>disk achenes</td>
<td>58% 1-5</td>
<td></td>
</tr>
<tr>
<td><strong>Senecio squalidus</strong></td>
<td>1.8</td>
<td>0.6-1.8</td>
</tr>
<tr>
<td><strong>Senecio viscosus</strong></td>
<td>2.6</td>
<td>0.9-2.6</td>
</tr>
<tr>
<td><strong>Senecio vulgaris</strong></td>
<td>2.9</td>
<td>1.0-2.9</td>
</tr>
<tr>
<td><strong>Solidago altissima</strong></td>
<td>14.9</td>
<td>14.9</td>
</tr>
<tr>
<td>6-8 (mtd)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Solidago canadensis</strong></td>
<td>30.9</td>
<td>16.8-30.9</td>
</tr>
<tr>
<td><strong>Solidago gigantea</strong></td>
<td>23.8</td>
<td></td>
</tr>
</tbody>
</table>
Appendix 11. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed Dispersal Distance</th>
<th>Ref.#</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Mean (m)</td>
<td>Median (m)</td>
</tr>
<tr>
<td>Solidago graminifolia</td>
<td>21.1</td>
<td>12.0-21.1</td>
</tr>
<tr>
<td>Solidago missouriensis</td>
<td>29.4</td>
<td>16.2-29.4</td>
</tr>
<tr>
<td>Solidago nemoralis</td>
<td>39.0</td>
<td>27.9-39.0</td>
</tr>
<tr>
<td>Solidago rigida</td>
<td>4.9</td>
<td>15</td>
</tr>
<tr>
<td>Solidago speciosa</td>
<td>41.4</td>
<td>37.6-41.4</td>
</tr>
<tr>
<td>Sonchus arvensis</td>
<td>10.0</td>
<td>3.3-10.0</td>
</tr>
<tr>
<td>Sonchus oleraceus</td>
<td>0.1-0.9 (mode)</td>
<td>6.6</td>
</tr>
<tr>
<td>Sonchus oleraceus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Taraxacum officinale</td>
<td>2.3</td>
<td>0.8-2.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tragopogon dubius</td>
<td>2 (mode)</td>
<td>&gt;250</td>
</tr>
<tr>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tragopogon dubius</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tragopogon porrifolius</td>
<td>1.8</td>
<td>0.6-1.8</td>
</tr>
<tr>
<td></td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td>Trifolium arvense</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Tulipago farfara</td>
<td>4 km (mtd)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>4.4</td>
<td>1.5-4.4</td>
</tr>
<tr>
<td>Typha latifolia</td>
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</table>

**BALLISTIC DISPERSED**

<table>
<thead>
<tr>
<th>Shrubs (n=4)</th>
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</thead>
<tbody>
<tr>
<td>Ceanothenus cuneatus</td>
<td>10 (mtd)</td>
<td>1% = 9</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Ceanothenus leucodermis</td>
<td>10 (mtd)</td>
<td>1% = 9</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Dendromecon harfordii</td>
<td>3.6</td>
<td>5.1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Dendromecon rigida</td>
<td>1.3</td>
<td>4.8</td>
<td>2.9-4.8</td>
<td>9</td>
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</tbody>
</table>

510
Appendix 1. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed Dispersal Distance</th>
<th>Ref.#</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (m)</td>
<td>Median (m)</td>
</tr>
<tr>
<td><strong>Herbs (n=42)</strong></td>
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<td></td>
</tr>
<tr>
<td>Ballechores s.l.</td>
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</tbody>
</table>
| *Amphicarpa bracteata:*
  chasmogamous seeds    | 1.4       | 4.3        | 31% >2.0   |           |                         |
  aerial cleistogamous seeds | 1.3       | 3.8        | 25% >2.0   |           |                         |
| *Arceuthobium cryptopodum* |           |            | 14.6       |           |                         |
| *Cardamine hirsuta*   |           |            | 1.4        |           |                         |
| *Cassia fasciculata*  | 1.4-2.1   | 4.8        | 1.6% >4    |           |                         |
| *Chamaecrista fasciculata* | 0.3-0.7   |            |            |           |                         |
| *Chrysocephalum americanum* | 0.4       |            |            |           |                         |
| *Cnidoscolus stimulosus* | 0.6       | 1.2        | 0.0-0.9    |           |                         |
| *Crotalaria* sp       |           |            | 4.3        |           |                         |
| *Crotalaria rotundifolia* | 0.9       | 2.4        | 1.0-2.8    |           |                         |
| *Erodium moschatum*   | 0.6       | 0.9        | 0.0-0.9    |           |                         |
| *Euphorbia marginata* |           | 4.0        |            |           |                         |
| *Geranium carolinianum* | 3.3       | 4.2        | 1.8-4.2    |           |                         |
| *Geranium columbinum* |           | 1.5        |            |           |                         |
| *Geranium molle*      | 1.8       | 2.8        | 1.0-2.8    |           |                         |
| *Geranium maculatum*  | 3.0       | 4.8        | 1.8-4.8    |           |                         |
| *Impatiens capensis*  | 0.2       | 1.6        | 0.1-1.6    |           |                         |
|                       |           | 2.0        |            |           |                         |
|                       |           |            |            |           |                         |
|                       |           | 2         | 1.5-2      |           |                         |
|                       |           | 2.1        | most <0.2  |           |                         |
|                       |           |            | 15% >1.0   |           |                         |
| *Impatiens pallida*   |           | 2.0        |            |           |                         |
| *Impatiens parviflora*| 3.4       |            |            |           |                         |
| *Kalanchoe tubiflora* |           | 1.5        |            |           |                         |
| *Lepidium campestre*  | 0.3-0.8   | 2.0 (mtd)  |            |           |                         |
Appendix II. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean (m)</th>
<th>Median (m)</th>
<th>Maximum (m)</th>
<th>Range (m)</th>
<th>Terminal Velocity (cm/s)</th>
<th>Ref.#</th>
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</thead>
<tbody>
<tr>
<td><em>Lepidium vulgare</em></td>
<td></td>
<td></td>
<td>&gt;1.9</td>
<td></td>
<td></td>
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<tr>
<td><em>Lupinus texensis</em></td>
<td>0.6</td>
<td>4</td>
<td></td>
<td></td>
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<tr>
<td><em>Mitella diphylla</em></td>
<td>0.3</td>
<td>0.8</td>
<td>0.1-0.8</td>
<td></td>
<td></td>
<td>71</td>
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<tr>
<td><em>Montia fontana</em></td>
<td></td>
<td>2.0</td>
<td></td>
<td></td>
<td></td>
<td>60 (50)</td>
</tr>
<tr>
<td><em>Oenothera biennis</em></td>
<td>1.8</td>
<td>&lt;1</td>
<td>5</td>
<td>4</td>
<td>120</td>
<td>67 (34)</td>
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<tr>
<td><em>Oenothera rosea</em></td>
<td></td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
<td>12</td>
</tr>
<tr>
<td><em>Oxalis acerosella</em></td>
<td></td>
<td>2.3</td>
<td></td>
<td></td>
<td></td>
<td>60 (50)</td>
</tr>
<tr>
<td><em>Phlox drummondii</em></td>
<td>0.8</td>
<td>1.6</td>
<td>0.1-1.6</td>
<td></td>
<td></td>
<td>80</td>
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<tr>
<td><em>Phlox pilosa</em></td>
<td>1.2</td>
<td>3.6</td>
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<td>49</td>
</tr>
<tr>
<td><em>Sagina decumbens</em></td>
<td></td>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td>12</td>
</tr>
<tr>
<td><em>Salvia lyrata</em></td>
<td></td>
<td>2.0</td>
<td>0.5-2.0</td>
<td></td>
<td></td>
<td>13</td>
</tr>
<tr>
<td><em>Stillenia sylvatica</em></td>
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<td>3.0</td>
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<td></td>
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<td>81</td>
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<tr>
<td><em>Verbascum thapsus</em></td>
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<td>1</td>
<td>11</td>
<td></td>
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<td>34</td>
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<tr>
<td><em>Viola blanda</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chasmogamous seeds</td>
<td>1.0</td>
<td>3.0</td>
<td>2.4-3.0</td>
<td></td>
<td></td>
<td>16 (7)</td>
</tr>
<tr>
<td>cleistogamous seeds</td>
<td>0.8</td>
<td>3.8</td>
<td>2.2</td>
<td></td>
<td></td>
<td>7 (7)</td>
</tr>
<tr>
<td><em>Viola cucullata</em></td>
<td>1.5</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td><em>Viola eriocarpa</em></td>
<td>1.2</td>
<td>5.4</td>
<td></td>
<td></td>
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<tr>
<td><em>Viola fimbriatula</em></td>
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<tr>
<td><em>Viola papilionacea</em></td>
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</tr>
<tr>
<td>chasmogamous seeds</td>
<td>2.1</td>
<td>4.8</td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>cleistogamous seeds</td>
<td>1.0</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
<tr>
<td><em>Viola pedata</em></td>
<td>1.4</td>
<td>5.1</td>
<td></td>
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<td></td>
<td>7</td>
</tr>
<tr>
<td><em>Viola rostrata</em></td>
<td>1.2</td>
<td>4.2</td>
<td></td>
<td></td>
<td></td>
<td>7</td>
</tr>
</tbody>
</table>
Appendix 1. Representative seed dispersal distances of native and alien species in N. America.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed Dispersal Distance</th>
<th>Ref.#</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (m)</td>
<td>Median (m)</td>
</tr>
<tr>
<td>Viola striata</td>
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<td></td>
</tr>
<tr>
<td>chasmogamous seeds</td>
<td>1.5</td>
<td>1.1</td>
</tr>
<tr>
<td>cleistogamous seeds</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td><strong>UNASSISTED</strong></td>
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<td></td>
</tr>
<tr>
<td><strong>Grasses (n=3)</strong></td>
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<tr>
<td>Anthoxanthum odoratum</td>
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<td></td>
</tr>
<tr>
<td>Vulpia ciliata</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>Vulpia fasciculata</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td><strong>Herbs (n=11)</strong></td>
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</tr>
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<td>Chamaelaucium luteum</td>
<td>10.1</td>
<td>3.4</td>
</tr>
<tr>
<td>Chaenorrhinum minus</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>Dipsacus sylvestris</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>Echeveria gibbiflora</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>Heterotheca latifolia</td>
<td>0.5-0.9</td>
<td>12</td>
</tr>
<tr>
<td>ray achenes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lithospermum caroliniense</td>
<td>2.0 (mtd)</td>
<td>most &lt;1</td>
</tr>
<tr>
<td>Mimulus guttatus</td>
<td>4.8</td>
<td></td>
</tr>
<tr>
<td>Mirabilis hirsuta</td>
<td>0.4</td>
<td>1.6</td>
</tr>
<tr>
<td>Verbena stricta</td>
<td>1.0</td>
<td>3.5</td>
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APPENDIX 12

PRINCIPAL FRUGIVORES OF EASTERN NORTH AMERICA

<table>
<thead>
<tr>
<th>BIRDS (n=50)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern bluebird*</td>
<td>White-throated sparrow</td>
</tr>
<tr>
<td>Northern bobwhite</td>
<td>European starling*</td>
</tr>
<tr>
<td>Northern cardinal</td>
<td>Tree swallow</td>
</tr>
<tr>
<td>Gray catbird*</td>
<td>Summer tanager</td>
</tr>
<tr>
<td>Yellow-breasted chat</td>
<td>Brown thrasher*</td>
</tr>
<tr>
<td>American crow</td>
<td>Gray-cheeked thrush</td>
</tr>
<tr>
<td>Fish crow*</td>
<td>Hermit thrush</td>
</tr>
<tr>
<td>Purple finch</td>
<td>Swainson’s thrush</td>
</tr>
<tr>
<td>Northern flicker</td>
<td>Wood thrush*</td>
</tr>
<tr>
<td>Great-crested flycatcher</td>
<td>Tufted titmouse</td>
</tr>
<tr>
<td>Evening grosbeak</td>
<td>Eastern towhee</td>
</tr>
<tr>
<td>Pine grosbeak</td>
<td>Wild turkey</td>
</tr>
<tr>
<td>Rose-breasted grosbeak</td>
<td>Veery</td>
</tr>
<tr>
<td>Ruffed-grouse*</td>
<td>Red-eyed vireo</td>
</tr>
<tr>
<td>Spruce grouse</td>
<td>Warbling vireo</td>
</tr>
<tr>
<td>Eastern kingbird</td>
<td>Bay-breasted warbler</td>
</tr>
<tr>
<td>Ruby-crowned kinglet</td>
<td>Chestnut-sided warbler</td>
</tr>
<tr>
<td>Northern mockingbird*</td>
<td>Tennessee warbler</td>
</tr>
<tr>
<td>Baltimore oriole</td>
<td>Yellow-rumped warbler</td>
</tr>
<tr>
<td>Orchard oriole</td>
<td>Bohemian waxwing</td>
</tr>
<tr>
<td>Ring-necked pheasant</td>
<td>Cedar waxwing*</td>
</tr>
<tr>
<td>American robin*</td>
<td>Downy woodpecker</td>
</tr>
<tr>
<td>Yellow-bellied sapsucker</td>
<td>Pileated woodpecker</td>
</tr>
<tr>
<td>Fox sparrow</td>
<td>Red-bellied woodpecker</td>
</tr>
</tbody>
</table>
Appendix 12. Principal Frugivores of Eastern North America (cont’d).

<table>
<thead>
<tr>
<th>MAMMALS (n=14)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Black bear*</td>
<td>Moose</td>
</tr>
<tr>
<td>Eastern chipmunk</td>
<td>Deer mouse</td>
</tr>
<tr>
<td>Common cottontail</td>
<td>White-footed mouse</td>
</tr>
<tr>
<td>New England cottontail</td>
<td>Raccoon</td>
</tr>
<tr>
<td>White-tailed deer*</td>
<td>Eastern fox squirrel</td>
</tr>
<tr>
<td>Eastern red fox</td>
<td>Eastern gray squirrel</td>
</tr>
<tr>
<td>Gray fox</td>
<td>Eastern red squirrel</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>REPTILES (n=1)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Box Turtle</td>
<td></td>
</tr>
</tbody>
</table>

516
APPENDIX 13

KNOWN MYRMECOCHORES IN THE U.S. NORTHEAST

<table>
<thead>
<tr>
<th>Name</th>
<th>Reference</th>
<th>Nesting Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aphaenogaster rudis</em></td>
<td>4, 5, 6, 7, 11, 12, 13, 14, 15</td>
<td>majority of <em>Aphaenogaster</em> 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)</td>
</tr>
<tr>
<td><em>Aphaenogaster tennesseensis</em></td>
<td>12</td>
<td>usually nests on rotten stumps and fallen logs with few passages running into the soil (Creighton, 1950, p.139; Lynch et al. 1988)</td>
</tr>
<tr>
<td><em>Aphaenogaster texana</em></td>
<td>5</td>
<td>see <em>A. rudis</em>.</td>
</tr>
<tr>
<td><em>Camponotus nearticus</em></td>
<td>14</td>
<td>most species of <em>Camponotus</em> 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)</td>
</tr>
<tr>
<td><em>Camponotus pennsylvanicus</em></td>
<td>8, 14</td>
<td>see <em>C. nearticus</em>.</td>
</tr>
<tr>
<td><em>Cremaioagaster lineolata</em></td>
<td>7</td>
<td>nests in dead wood of standing or prostrate trunks (Wheeler 1960, p. 208)</td>
</tr>
<tr>
<td><em>Formica fusca</em></td>
<td>1</td>
<td>nests in soil beneath a covering object (Creighton 1950, p.328)</td>
</tr>
<tr>
<td><em>Formica integra</em></td>
<td>5, 13</td>
<td>nests in stumps and in soil under cover of stones, logs, or branches (Wheeler 1960, pp. 204-206).</td>
</tr>
<tr>
<td><em>Formica neogagates</em></td>
<td>8, 9</td>
<td>nests in soil beneath stones or other covering objects (Creighton 1950, p. 457)</td>
</tr>
<tr>
<td><em>Formica subsericea</em></td>
<td>1, 2, 5, 8, 13, 14</td>
<td>nests in soil where it forms mounds up to 30 cm high (Wheeler 1960, pp. 203-204)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Name</th>
<th>Reference</th>
<th>Nesting Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lasius alienus</em></td>
<td>1.5.8.9.13.14</td>
<td>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)</td>
</tr>
<tr>
<td><em>Leptothorax curvispinosus</em></td>
<td>5.13</td>
<td>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)</td>
</tr>
<tr>
<td><em>Leptothorax longispinosus</em></td>
<td>5.13</td>
<td>see <em>L. curvispinosus</em>.</td>
</tr>
<tr>
<td><em>Myrmecina americana</em></td>
<td>5</td>
<td>usually nests in moist shady areas, often under small stones (Creighton 1950, p.248)</td>
</tr>
<tr>
<td><em>Myrmica emeryana</em></td>
<td>9.14</td>
<td>most species in genus nest in soil under a covering object (Creighton 1950, p.91)</td>
</tr>
<tr>
<td><em>Myrmica fracticornis</em></td>
<td>8</td>
<td>see <em>M. emeryana</em>.</td>
</tr>
<tr>
<td><em>Myrmica punctiventris</em></td>
<td>1.2.3.10.13.14</td>
<td>see <em>M. emeryana</em>.</td>
</tr>
<tr>
<td><em>Myrmica spatulata</em></td>
<td>1</td>
<td>see <em>M. emeryana</em>.</td>
</tr>
<tr>
<td><em>Phrenolepis imparis</em></td>
<td>13.14</td>
<td>often nests in damp soil in shady positions (Creighton 1950, p.135)</td>
</tr>
<tr>
<td><em>Stenamma schmitti</em></td>
<td>5.13</td>
<td>habits little known; nests in wooded areas in leaf mould, under stones or logs or beneath thick, loose moss (Creighton 1950, p.135)</td>
</tr>
<tr>
<td><em>Tapinoma sessile</em></td>
<td>1.5.13</td>
<td>not particular; in soil with or without a covering object, under bark, and in preformed cavities of various kinds (Creighton 1950, p.351)</td>
</tr>
</tbody>
</table>
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 1\(^{st}\)); ML=mid to late season flowering (after June 1\(^{st}\)). Source: Curtis 1959, p.521.

<table>
<thead>
<tr>
<th>Species</th>
<th>W</th>
<th>P</th>
<th>Species</th>
<th>W</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actaea pachypoda</td>
<td>E</td>
<td></td>
<td>Geum canadense</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Adiantum pedatum</td>
<td>?</td>
<td></td>
<td>Hepatica acutiloba</td>
<td>•</td>
<td>E</td>
</tr>
<tr>
<td>Allium tricoccum</td>
<td>•</td>
<td>E</td>
<td>Hydrophyllum virginianum</td>
<td>•</td>
<td>E</td>
</tr>
<tr>
<td>Amphicarpa bracteata</td>
<td>ML</td>
<td></td>
<td>Laportea canadensis</td>
<td></td>
<td>ML</td>
</tr>
<tr>
<td>Arisaema triphyllum</td>
<td>E</td>
<td></td>
<td>Mutanthenium canadense</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Athyrium filix-femina</td>
<td>?</td>
<td></td>
<td>Osmorhiza claytonii</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Botrychium virginianum</td>
<td>E</td>
<td></td>
<td>Parthenocissus inserta</td>
<td>ML</td>
<td></td>
</tr>
<tr>
<td>Brachyelytrum erectum</td>
<td>E</td>
<td></td>
<td>Phryma leptostachya</td>
<td>ML</td>
<td></td>
</tr>
<tr>
<td>Carex laxiflora</td>
<td>E</td>
<td></td>
<td>Podophyllum peltatum</td>
<td>•</td>
<td>E</td>
</tr>
<tr>
<td>Carex pensylvanica</td>
<td>E</td>
<td></td>
<td>Polygonatum pubscens</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Caulophyllum thalictroides</td>
<td>•</td>
<td>E</td>
<td>Prenanthes alba</td>
<td>ML</td>
<td></td>
</tr>
<tr>
<td>Celastrus scandens</td>
<td>ML</td>
<td></td>
<td>Ribes cynosbati</td>
<td>ML</td>
<td></td>
</tr>
<tr>
<td>Circaea lutiana</td>
<td>ML</td>
<td></td>
<td>Sanguinaria canadensis</td>
<td>•</td>
<td>E</td>
</tr>
<tr>
<td>Claytonia caroliniana</td>
<td>E</td>
<td></td>
<td>Solidago flexicaulis</td>
<td>ML</td>
<td></td>
</tr>
<tr>
<td>Cryptotaenia canadensis</td>
<td>ML</td>
<td></td>
<td>Thalictrum dioicum</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Erythronium americanum</td>
<td>E</td>
<td></td>
<td>Trillium grandiflorum</td>
<td>•</td>
<td>E</td>
</tr>
<tr>
<td>Galium aparine</td>
<td>•</td>
<td>E</td>
<td>Uvularia grandiflora</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Galium triflorum</td>
<td>ML</td>
<td></td>
<td>Viola cucullata</td>
<td>E</td>
<td></td>
</tr>
<tr>
<td>Geranium maculatum</td>
<td>E</td>
<td></td>
<td>Viola pubescens</td>
<td>•</td>
<td>E</td>
</tr>
</tbody>
</table>

Notes:
Species prevalent in Wisconsin but absent from stands at Peterborough: *Erythronium albidum, Claytonia virginica, Galium concinnum, Sanicula gregaria, Smilax ecirrhata.*