# OLD-GROWTH NORTHERN HARDWOOD FORESTS: SPATIAL AUTOCORRELATION AND PATTERNS OF UNDERSTORY VEGETATION

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*Abstract.*    The goal of this research was to examine spatial patterns of forest understory vegetation at a fine resolution for future work on underlying processes. We used a cyclic, two-dimensional sampling design, sampling plants in 2100 quadrats (0.25 m$^2$), placing one 62 × 29.5 m grid within each of four old-growth northern hardwood (*Acer saccharum–Betula alleghaniensis*) stands. The specific plan used was designed to maximize spatial information and sampling efficiency. The study was done in the Sylvania Wilderness Area, Ottawa National Forest, Upper Michigan, USA.

Spatial patterns of ground-layer species vary with the environment, species ecological characteristics, and their interactions. Competition with maple saplings may be a strong determinant of understory spatial patterns of these forests. Based on 95% confidence intervals, spatial analysis showed that most ground-layer species were positively autocorrelated to distances of <2.5 m in stands with high sapling density, while many of these same species were autocorrelated at up to 21 m in stands with low sapling density. Most ground-layer species also had distributions indistinguishable from random at three other resolutions (9.0 × 10.5 m to 9.0 × 31.5 m blocks) in stands with high sapling density, but aggregated distributions in stands with low sapling density. Logistic regression analysis yielded direct and indirect negative correlations between ground-layer species and maple saplings.

Plant species temporal guilds were autocorrelated according to the following rank distances: spring ephemerals > evergreen ≥ early summer > late summer > dimorphic. More species were autocorrelated to greater distances on loamy soils than on sandy soils. Plant species dispersal guilds were autocorrelated according to the following rank distances: ballistic ≥ spores ≥ ant > ingested > adhesive. Thus there is a general inverse relationship between autocorrelation distance and migration rates of dispersal guilds. The spatial distribution of microtopography and decayed, coarse woody debris appears to be important for the maintenance of plant diversity and heterogeneity in old-growth stands. Forest managers can help maintain biological diversity by giving preferential management to those species that are rare and, if once locally extirpated, have poor re-colonization ability. This requires maintaining regional landscape diversity, as well as within-stand microhabitats.

*Key words:    competition; dispersion index; forest herb; forest understory; old-growth northern hardwood forest; resource management; sampling strategy and spatial analysis; seed dispersal; spatial autocorrelation; Sylvania Wilderness Area (Upper Michigan, USA); vegetation in forest understory.*

## Introduction

Increasingly, the public, the scientific community, and land managers are viewing biodiversity as an important consideration in the area of natural resource management (National Forest Management Act of 1976, Wilson 1988, Wisconsin Department of Natural Resources 1995). Concerns during the last decade over the cutting of old-growth forests in the Pacific Northwest (USA) have focused the need for a better understanding of the effects of forest management upon bio-

diversity. In the northern U.S. Lake States (Minnesota, Wisconsin, and Michigan), there is considerable interest in learning how to manage these forests consistent with the maintenance of individual species and ecosystem diversity (e.g., Crow et al. 1994, Wisconsin Department of Natural Resources 1995). Biodiversity has been linked in several studies to the stability of some ecosystem functions (e.g., Tilman and Downing 1994, McGrady et al. 1997), but other studies report results to the contrary (Wardle et al. 1997; also see Huston 1997).

The forest understory (herbs, shrubs, tree seedlings, and saplings) is an important component of biodiversity with both intrinsic and functional values. Herbs and shrubs, hereafter called the *ground layer,* account for the vast majority of vascular plant species in eastern North American forests (Curtis 1959, Whittaker 1966, Whitney and Foster 1988, Scheiner and Istock 1994). In addition, the understory serves as a "nursery" for

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future canopy trees, and provides both food and habitat for a wide array of animal species (Martin et al. 1951, Pough et al. 1987). Muller and Bormann (1976) suggested that forest herbs that are active in the spring reduce the loss of potassium and nitrogen from the ecosystem, but a more recent study found that microbial biomass may be a much larger nitrogen sink than these herbs (Zak et al. 1990).

Many recent landscape-ecology studies have identified links between pattern and process in areas that vary widely in size from one another (e.g., Swanson et al. 1988, Turner 1989, Mladenoff et al. 1993, 1995). Consequently, an understanding of patterns in terms of the processes that produce them can assist ecologically based resource management (Wiens et al. 1993). This study is part of a larger project to understand the effects of forest management on ecological aspects of hemlock–hardwood forests in Wisconsin (Goodburn 1996). Here we examine patterns of understory vegetation at old-growth sites in the region that are relatively unaltered by direct anthropogenic forces with the intention that this can serve as a baseline assessment for future work on processes.

It is necessary to examine biodiversity and ecological processes at an appropriate scale, where scale is characterized by study area *extent* and the *grain*, or resolution, used in sampling (Turner 1989). We chose a sample area or extent measured in meters for this study, with a sampling resolution (quadrat size) of 0.25 $m^2$ of the forest understory. The growth of many understory species is influenced by several processes that occur over small areas such as gap formation (Moore and Vankat 1986, Mladenoff 1987, 1990), microtopography (Bratton 1976, Thompson 1980), canopy composition (Hicks 1980, Crozier and Boerner 1984), and competition (Foster 1998). Also, the prevalence of vegetative propagation among forest herbs (Whitford 1949), and their slow rate of spread by seed (Matlack 1994), suggest that most species experience environmental heterogeneity at a process area (sensu Csillag et al. 2000) of <1 m.

The spatial pattern of a species may be useful as a diagnostic tool in forest management because it may reflect the ecology of the species being studied, including reproductive and dispersal behavior, response to its environment, disturbance, site history, and species interactions such as competition. In this paper, we relate the spatial patterns of individual species with several ecological factors. Since species vary in dispersal mode and distance, phenology, and whether or not they reproduce mainly from seed, we broadly hypothesize that different species will exhibit different spatial patterns within a given environment. Our second broad hypothesis is that the spatial pattern of a species is dependent upon its environment, both directly and through competition. Regression analysis can complement a spatial analysis by elucidating which biotic and abiotic factors are related to a species' distribution.

## Spatial autocorrelation

Positive spatial autocorrelation exists when the values of random variables at pairs of locations a certain distance apart are more similar than expected for randomly associated pairs of observations, resulting in patches or gradients (Legendre 1993). Of interest are both the magnitude of the autocorrelation and the distance, if any, at which autocorrelation vanishes. Autocorrelations can be of small or large extent, corresponding with the notion of small or large patches. Spatial autocorrelation is a widespread phenomenon in ecology (e.g., Fortin et al. 1989, Henebry 1995, Torgersen et al. 1995, Koenig 1998, Radeloff et al. 2000). The spread of plants by the processes of growth, vegetative reproduction, and limited seed dispersal produces spatial autocorrelation. Plant species respond individualistically to their environment (Gleason 1926), both directly and indirectly through species interactions. Autocorrelation can be used to compare the pattern of the same species in different environments, and the patterns of different species in the same environment. In this paper, we use the term "autocorrelation" to refer to positive spatial autocorrelation.

We hypothesize that over small areas (extents of up to a few tens of meters) clonal species (those that reproduce primarily by vegetative means, e.g., *Lycopodium*) are autocorrelated to shorter distances than species that reproduce primarily by seed (e.g., annuals) because of the slow rate of spread by clonal species.

Matlack (1994) found the following migration rates of plants by dispersal guilds from older second-growth forest into early successional forest: ingested > adhesive ≫ wind ≥ ants ≥ no disperser (see Table 1 for definitions of dispersal guilds). Similarly, Brunet and von Oheimb (1998) found that ant-dispersed species had lower migration rates than adhesive or ingested species. There is also genetic evidence that migration rates vary across dispersal guilds; populations of a species that is gravity dispersed are more genetically differentiated than populations of an adhesive species (Williams and Guries 1994). We predict that guilds with the least migration potential will be the most autocorrelated, producing the following trend in decreasing distances of autocorrelation: no disperser > ant-dispersed ≈ ballistic > adhesive > ingested. We assume that species that are dispersed short distances in a homogeneous, favorable environment will grow in continually expanding patches, and species that are dispersed greater distances across heterogeneous environment will be limited to the small patches of favorable environment.

We hypothesize that spring ephemerals will be autocorrelated to greater distances than other temporal guilds (see Table 1 for definitions of temporal guilds). First, spring ephemerals are typically dispersed short distances by ants, whereas species in the early-summer and late-summer guilds are more often dispersed by

TABLE 1. Guild types and understory species assignments to guilds.

A) Guild types and definitions

| Guild type | Definition |
|---|---|
| **Dispersal** | |
| No disperser | species with seeds lacking obvious adaptations for dispersal such as plumes, berries, or hooks; the seeds of these species simply fall off their stems when mature |
| Spore | clubmoss and fern species |
| Ant-dispersed | species with seeds having elaiosomes (oil bodies) attached that attract ants to serve as dispersers |
| Ballistic | species having seeds that are expelled forcefully when the fruit ripens |
| Ingested | species with seeds present in fleshy fruits that are generally eaten and dispersed by birds and mammals |
| Adhesive | species having seeds equipped with hooks that attach to the fur of passing mammals |
| **Temporal†** | |
| Spring ephemeral | leaf out in early spring and senesce before canopy closure |
| Early summer | emerge in early spring and persist through canopy closure for varying lengths of time, but reach peak coverage before midsummer |
| Late summer | emerge in mid to late spring and reach peak coverage after midsummer |
| Evergreen | maintain active leaves throughout the year |
| Evergreen dimorphic | hold two different sets of leaves or leaf positions at two different seasons |

B) Assignment of understory species (with frequency ≥9 quadrat occurrences in a plot) to guilds‡

| Species§ | Guild Temporal‖ | Guild Reproductive¶ | Guild Dispersal# |
|---|---|---|---|
| *Claytonia caroliniana* | spr. eph. | seed | a |
| *Dentaria laciniata* | spr. eph. | veg. | b |
| *Allium tricoccum* | spr. eph. | veg. | no disp. |
| *Osmunda claytoniana* | e. sum. | veg. | spore |
| *Athyrium filix-femina* | e. sum. | veg. | spore |
| *Gymnocarpium dryopteris* | e. sum. | veg. | spore |
| *Thelypteris phegopteris* | e. sum. | veg. | spore |
| *Actaea pachypoda* | e. sum. | seed | inges. |
| *Viola selkirkii* | e. sum. | veg. | a and b |
| *V. blanda* | e. sum. | veg. | a and b |
| *V. pubescens* | e. sum. | veg. | a |
| *Trientalis borealis* | e. sum. | veg. | no disp. |
| *Osmorhiza* sp. | e. sum. | seed | adhes. |
| *Galium triflorum* | e. sum. | veg. | adhes. |
| *Arisaema triphyllum* | e. sum. | veg. | inges. |
| *Streptopus roseus* | e. sum. | veg. | inges. |
| *Maianthemum canadense* | e. sum. | veg. | inges. |
| *Polygonatum pubescens* | e. sum. | veg. | inges. |
| *Circaea alpina* | l. sum. | seed | adhes. |
| *Brachyeletrum erectum* | l. sum. | seed | no. disp. |
| *Lycopodium lucidulum* | ev. | veg. | spore |
| *L. obscurum* | ev. | veg. | spore |
| *Dryopteris intermedia* | ev. dm. | veg. | spore |
| *Carex intumescens* | ev. dm. | seed | no disp. |
| *Rubus* sp. | shr./vin. | veg. | inges. |
| *Dirca palustris* | shr./vin. | seed | inges. |

  † Definitions from Givnish (1987).

  ‡ Frequency of species = the number of 0.5-m² quadrats in which the species was present per 29.5 × 62 m plot (out of a potential 525 quadrats/plot).

  § Species are listed by temporal guild; within a temporal guild species are listed in taxonomic order. Nomenclature generally follows Gleason and Cronquist (1991) except for *Dentaria laciniata*, for which the authority is Fernald (1950).

  ‖ Abbreviations: spr. eph. = spring ephemeral, e. sum. = early summer, l. sum. = late summer, ev. = evergreen, ev. dm. = evergreen dimorphic, shr./vin. = shrub/vine.

  ¶ Abbreviations: veg. = reproduces mainly by vegetative reproduction, seed = reproduces mainly by seed.

  # Abbreviations: a = ant-dispersed, adhes. = adhesive, b = ballistically dispersed, ingest. = ingested, no disp. = no disperser.

vertebrates (see Thompson 1980). Second, before canopy leafout, the forest environment is more homogeneous in terms of sunlight and soil moisture (see Anderson et al. 1969) than the same environment after canopy leafout (when other temporal guilds are active).

Our second broad hypothesis is that the spatial pattern of a species is a function of its abiotic environment, such as soil type, and indirectly through interactions such as competition for resources, including, for example, the influence of overstory structure on light. With other conditions favorable, we expect greater autocorrelation of plants in loamy soils than sandy soils

because the growth and reproduction of newly dispersed plants near the parent plant should be favored by a better soil. Similarly, we expect greater autocorrelation in stands with more favorable and homogeneous light environments. We hypothesize that overstory structure will also determine the understory plant community of each stand. Individual understory species pattern will be modified from these general response patterns in multi-species, understory communities, and especially under high competition, recent disturbance, or other factors operating over small areas.

The distribution of a species can be described as aggregated, regular, or random in a particular study area, but this is only relevant to a particular scale of analysis (i.e., resolution and extent) (Pielou 1969, Turner 1989). This description of a distribution is different from autocorrelation analysis of measurements taken at fixed locations (geostatistical data); autocorrelation analysis may reveal small patches on the landscape, but these patches themselves may be aggregated, regular, or random over different areas within the study area. We will test the hypothesis that the spatial pattern of a species at a range of resolutions is a function of its biotic and abiotic environment by examining whether individual species consistently exhibit one type of distribution in different stands.

## METHODS

### Study area

We chose the Sylvania Wilderness Area, Ottawa National Forest, in the Upper Peninsula of Michigan, USA (46°12′ N, 89°17′ W; Fig. 1) as our study area. This mesic, hemlock–northern hardwood landscape (6070 ha) is largely primary forest and has a species composition, spatial patterns, and disturbance dynamics believed to be representative of this portion of northern Lake States (northern Wisconsin and Upper Michigan) prior to European settlement (Mladenoff et al. 1993, Frelich 1995). Sylvania has a continental climate, with cold winters and moderate summers. Mean monthly temperatures are −12.2°C in January, and 18.6°C in July. The frost-free period averages 61 d. The average annual precipitation is 864 mm; half of this falls during the growing season (NOAA 1980).

Sylvania is situated on the Winegar terminal moraine, and is characterized by a thick layer of somewhat-sandy to loamy, glacial drift. Local relief is low, with above-sea-level elevations from 517 m to 567 m. The topography is irregular, with many kettle lakes and sandy ridges (Albert 1995). Slopes range from 0 to 40%, and average 10%. Two of the four stands in this study have coarse-loamy, Alfic Fragiorthod soils (a rich Spodosol underlain by a fragipan), and two have sandy Entic Haplorthods (a more nutrient-poor Spodosol lacking a fragipan; Bockheim 1997). These soils are typical in Sylvania (Jordan 1973). However, the soils
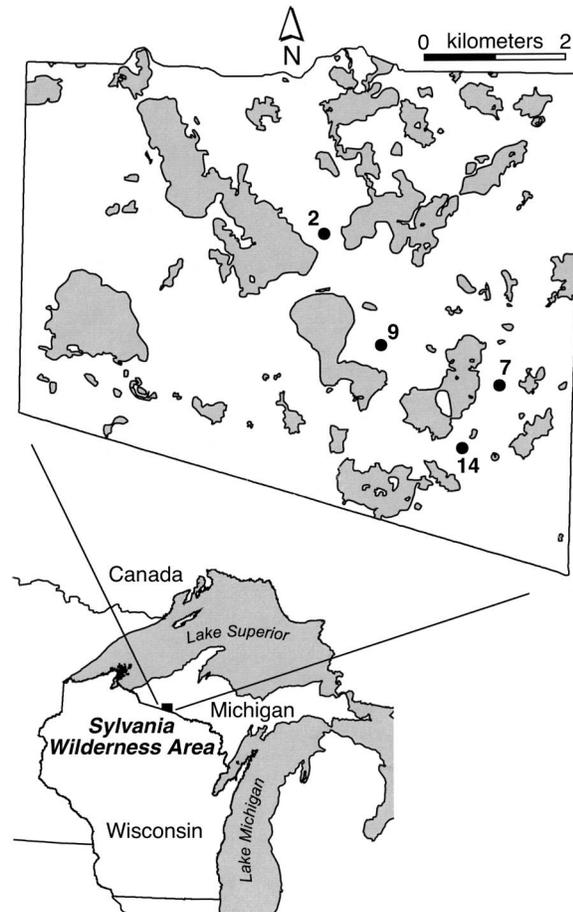


FIG. 1. Location of the Sylvania National Wilderness Area in the Upper Peninsula of Michigan, USA, and study stands within the Sylvania National Wilderness Area. This map shows most of Sylvania and includes some areas that are outside its boundaries. Shaded areas are water bodies. Numbers refer to stand numbers used by various researchers working on a larger interdisciplinary project, including Goodburn (1996) and Bockheim (1997): 2 = high-density, loamy soil; 7 = low-density, sandy soil; 9 = low-density, loamy soil; 14 = high-density, sandy soil (see Table 2).

in Sylvania are somewhat infertile for the mesic soils in the region (Foster 1998).

Sample plots were located in northern hardwood stands dominated by sugar maple (*Acer saccharum*). Other canopy species were American basswood (*Tilia americana*) and yellow birch (*Betula alleghaniensis*); eastern hemlock (*Tsuga canadensis*) accounted for <15% of the basal area of trees >2 cm in diameter at breast height (1.4 m) in all stands.

### Spatial autocorrelation and sampling design

We used a spatial sampling design designed to capture maximum spatial information with high efficiency. Sampling designs that have a greater number of distance classes (lags) between sampling points are better than others at detecting spatial patterns in ecological
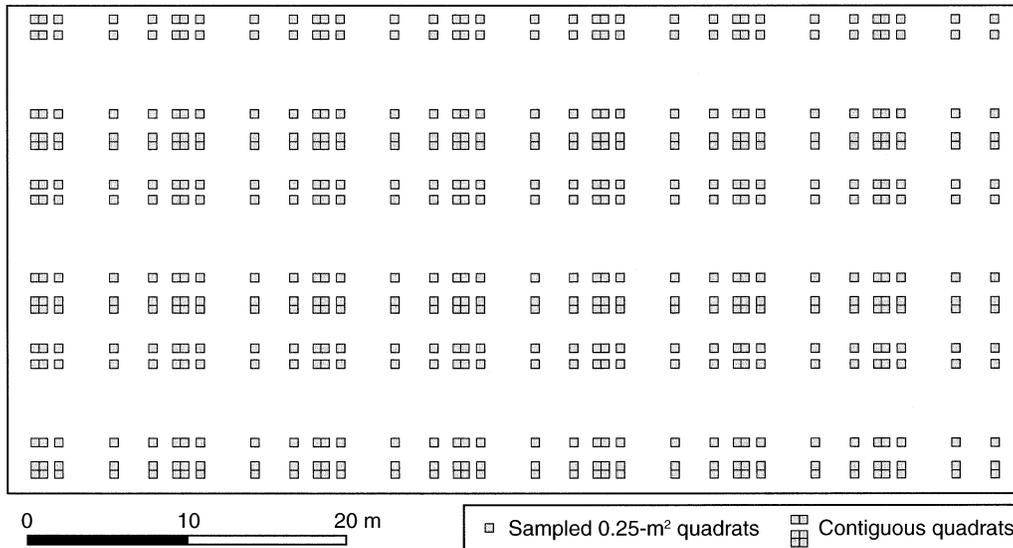
FIG. 2. Sampling design showing arrangement of 0.25-m² quadrats in a spatial adaptation of an irregular time series that produces every multiple of the smallest lag (i.e., in each cardinal direction that there are pairs of quadrats that are contiguous, other pairs that are two quadrat widths apart, other pairs that are three quadrat widths apart, etc.).

data (Fortin et al. 1989). The cyclic sampling design we used is derived from time-series analysis, and allows the estimation of autocorrelation at all multiples of the smallest lag with a minimum number of sampling points (Clinger and Van Ness 1976; Fig. 2).

We centered four plots (29.5 × 62 m) on preestablished 30 × 100 m plots, located in stands where forest structure and soils data had been collected as part of the larger interdisciplinary project (Goodburn and Lorimer 1998; Fig. 1). We chose a quadrat size of 0.25 m² to detect spatial patterns in understory vegetation over small areas related to factors such as microtopography, clonal growth, and species lacking obvious dispersal mechanisms. A 95% confidence interval for the autocorrelation function was chosen, which determined the sampling intensity (Clayton and Hudelson 1995). We chose a repeating series that sampled 5 of every 18 quadrats in the east-west direction and 5 of 21 quadrats in the north-south direction in each plot, resulting in lag distances of 0.5 m to 30 m, and a total of 525 quadrats per plot (Clinger and Van Ness 1976; Fig. 2). Because each plot was located in a distinct stand, the terms ''plot'' and ''stand'' are used interchangeably, hereafter.

### Data collection

We permanently marked the quadrats, and sampled them once each month during July and August 1996 and May 1997. This schedule is adequate to sample all temporal guilds at the height of their leaf cover. At each quadrat, we recorded percent cover of: (a) all ground-layer vascular plant species, tree seedlings (<30 cm tall), and small saplings (≥0.3 m and <1.4 m tall); (b) large sapling layer (≥1.4 m and <6.0 m tall), subcanopy layer (≥6.0 m and <12.0 m tall), and canopy layer (≥12.0 m tall), as estimated through a cylinder calibrated to view a 5-m radius overhead at average canopy height; (c) microtopography, classified as: forest floor, pit (>10 cm below matrix of forest floor), slope, and mound (>10 cm above forest floor); (d) coarse woody debris (≥20 cm diameter) in three stages of decay; and (e) exposed mineral soil (bare ground).

Photosynthetically active radiation (PAR) was measured directly at each quadrat under uniformly cloudy conditions as suggested by Parent and Messier (1996) using a ceptometer (AccuPAR Model Par-80 [Decagon Devices, Pullman, Washington, USA]) in as many of the quadrats, stands, and sampling periods as weather and time allowed.

### Data analysis

*Preliminary analysis.*—An important consideration in spatial analysis is whether the data are nonstationary (i.e., exhibit spatial trends or gradients). In preliminary analyses of each species and in each plot, data were examined for evidence of nonstationarity. There was no evidence of nonstationarity, and therefore all subsequent analyses assumed stationarity.

*Spatial autocorrelation.*—We chose correlograms instead of the more commonly used semivariograms to quantify the spatial dependence because a significance test has been derived for the former (see Eq. 4, below). We calculated correlograms for the data using the spatial data analysis software S+SPATIALSTATS (MathSoft, Seattle, Washington, USA) as follows:

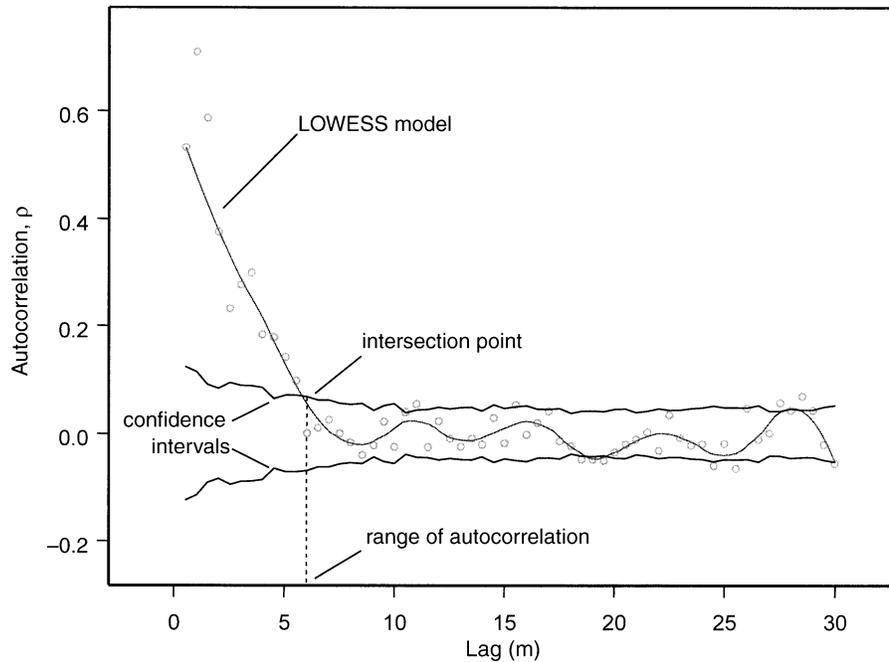$$\rho(h) = \frac{C(h)}{C(0)} \qquad (1)$$

FIG. 3. Correlogram fit with locally weighted scatterplot smoothing (LOWESS) regression model and 95% confidence intervals around the autocorrelation function. Points above the confidence interval indicate lags (all pairs of points separated by a given distance) that are significantly positively autocorrelated. The lag closest to the intersection of the LOWESS model and the confidence interval is used as the range (distance) of autocorrelation (in this example, 6.0 m).

where $C(h)$ is the covariance for pairs of points separated by distance $h$, and $C(0)$ is the finite variance of the random field. Correlograms are related to semivariograms as follows:

$$\rho(h) = 1 - \frac{\gamma(h)}{C(0)} \qquad (2)$$

where the semivariogram,

$$\gamma(h) = \frac{1}{2|N(h)|} \sum_{N(h)} (z_i - z_j)^2 \qquad (3)$$

and $N(h)$ is the set of all pairwise distances $i - j = h$, $|N(h)|$ is the number of distinct pairs in $N(h)$, and $z_i$ and $z_j$ are data values at spatial locations $i$ and $j$, respectively.

We plotted 95% confidence intervals for the autocorrelation function of each lag using the following equation derived by Clayton and Hudelson (1995):

$$0 \pm 1.96\sqrt{\text{var}[r(v)]} \qquad (4)$$

where

$$\sqrt{\text{var}[r(v)]} = \sqrt{\frac{1}{|N(h)|}}. \qquad (5)$$

Note that these confidence intervals are centered on zero and are derived under the assumption that the data are random. Therefore, any observed autocorrelation value that lies outside the confidence interval is considered statistically significant. A LOWESS (locally

weighted scatterplot smoothing) regression model (Cleveland 1979, Trexler and Travis 1993) was fit to the correlogram using S-PLUS 4.0 (span 0.2, degree 2; MathSoft), and the lag closest to the intersection of the model and the confidence interval was defined to be as the range of significant autocorrelation (Fig. 3). These values were used in all subsequent analyses. The model was unable to detect autocorrelation over small areas of species occurring in fewer than nine quadrats in a single plot. These species were omitted from further analysis.

*Index of dispersion.*—We used an index of dispersion to test species spatial distribution (regular, random, or aggregated) at several resolutions. We divided each plot into blocks of quadrats containing an equal number and spacing of quadrats. Blocks were $9.0 \times 10.5$ m ($n = 21$ blocks), $9.0 \times 15.5$ m ($n = 14$), and $9.0 \times 31.5$ m ($n = 7$). We used the mean and variance of quadrats of species frequency in each block to calculate an index of dispersion (ID) according to Upton and Fingleton (1985):

$$\text{ID} = (n - 1)s^2/\bar{x} \qquad (6)$$

where, $n =$ number of blocks. We performed a two-tailed $\chi^2$ test of this value.

*Guild analysis.*—Understory plant species were assigned to functional guilds based on dispersal mechanism (Handel et al. 1981, Willson 1993), reproduction (Bierzychudek 1982), and phenology (Givnish 1987;

TABLE 2. Understory species richness ($S$) and evenness ($E$) with respect to soil texture, stand characteristics, and dominance of saplings in a northern hardwood forest (Upper Michigan, USA).

| Dominance of maple saplings† | Soil type | | | |
|---|---|---|---|---|
| | Loamy | | Sandy | |
| | $S$ | $E$ | $S$ | $E$ |
| High density | 38‡ | 0.461 | 27§ | 0.557 |
| Low density‖ | 48 | 0.692 | 25 | 0.593 |

*Note:* Standard deviation of species richness for loamy soil = 7.4, for sandy soil = 1.4.

† Sapling size: 0.3 m < small ≤ 1.4 m; 1.4 m < large ≤ 6.0 m.

‡ Small saplings.

§ Large saplings.

‖ Low to moderate levels of both small and large saplings.

Table 1). We calculated mean autocorrelation distance for all species in each guild by stand to test for location differences. We also used the maximum autocorrelation distance for species to calculate averages for each guild. We used one-way ANOVA (analysis of variance) to determine if the differences among guilds within a stand were significant.

*Regression analysis.*—We checked for collinearity among independent variables, then calculated backwards, step-wise logistic regressions of small sugar maple saplings (the response variable) against the overstory, microtopography, bare ground, and coarse woody debris data using the LOGISTIC procedure of SAS (SAS Institute 1990). We checked for spatial autocorrelation in the residuals of the regression model before continuing, according to recent statistical theory (Cressie 1993). We modeled the autocorrelation of the residuals using semi-variograms in S+SPATIALSTATS, then used a generalized, linear mixed model (the MIXED procedure in SAS combined with the GLIMMIX macro) to perform logistic regressions that accounted for autocorrelation. We repeated this process for the nine most abundant ground-layer species, including small maple saplings and maple seedlings as additional independent variables.

We conducted a $\chi^2$ test to determine whether any plant species occurred on moderately and highly decayed logs more or less frequently than one would expect if they were randomly distributed. We limited this test to species with an expected frequency of ≥5 occurrences on these logs.

*Community analysis.*—We calculated the species richness in each stand. We calculated the evenness of species in each stand according to Pielou (1969):

$$E = H'/\ln S \qquad (7)$$

where $S$ is the species richness in each stand, $H'$ is the Shannon index of diversity:

$$H' = -\sum p_i \ln p_i \qquad (8)$$

and $p_i$ = the proportion of individuals found in the $i$th

species. For these calculations, we substituted species frequencies for the numbers of individuals of a species.

We used the Sørensen distance (also known as the Czekanowski or Bray-Curtis coefficient) to measure the dissimilarity between communities in different stands:

$$\text{Sørensen distance} = 1 - \frac{2W}{A + B} \qquad (9)$$

where $W$ is the sum of shared abundances, and $A$ and $B$ are the sums of abundances in each stand. We substituted frequencies for abundances, and we also used a general relativization on the data, a procedure that is appropriate when calculating the Sørensen distance (PC-ORD version 3.20 for Windows [MjM Software Design, Gleneden Beach, Oregon, USA]).

## RESULTS

The four stands varied with regard to soil texture (two loamy and two sandy) and the dominance of maple saplings (Table 2, Fig. 4a and b). Two stands (one of each soil type) are dominated by either small saplings



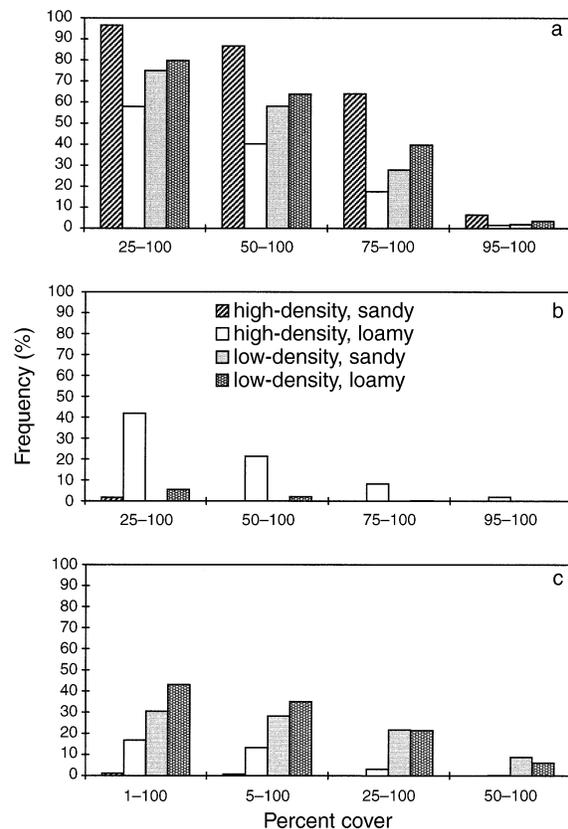FIG. 4. Frequency of percent cover above various thresholds for (a) deciduous large-sapling layer (1.4 − 6.0 m), (b) small sugar maple saplings (0.3 − 1.4 m), and (c) coniferous (95% hemlock) large-sapling layer (1.4 − 6.0 m); $n = 525$ quadrats. Hemlock in the subcanopy showed a similar pattern among stands as in the large-sapling layer and is not presented. In the histogram key, ''density'' refers to sapling density.
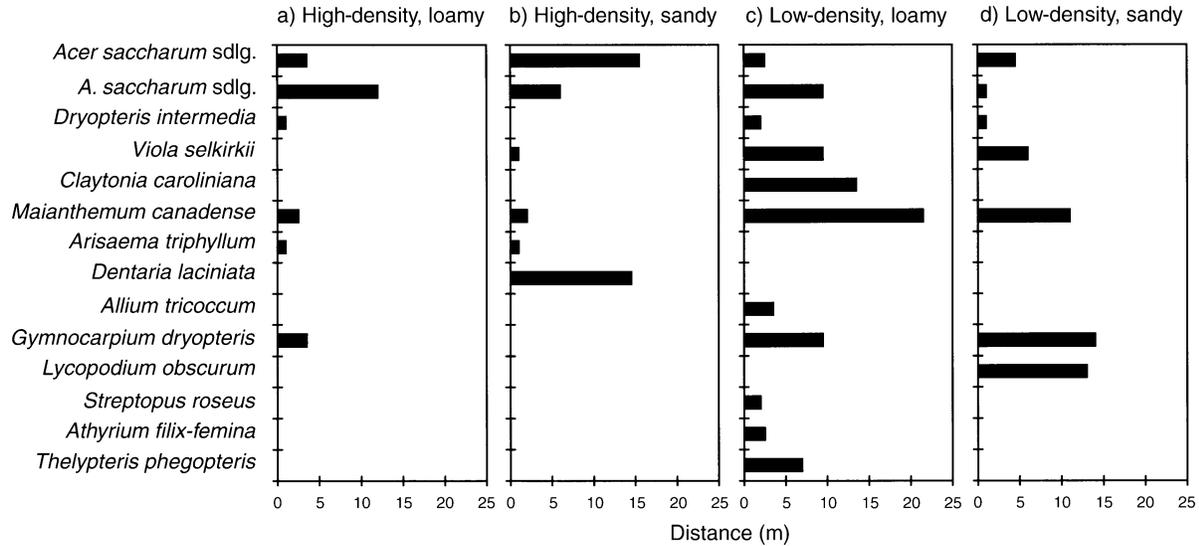
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Fɪɢ. 5. Autocorrelation of species by stand in (a) high-density, loamy; (b) high-density, sandy; (c) low-density, loamy, and (d) low-density, sandy stands. Species with a total frequency of ≥50 0.25-m² quadrats per study (out of a potential 2100-quadrats total from the four plots combined) are listed by decreasing frequency; see Table 3 for full species names. Abbreviations: sdlg, seedlings; splg, saplings.

or large saplings ("high density"). Two have low-to-moderate sapling density ("low density"). The four stands also varied with regard to hemlock frequency in the subcanopy and large sapling layers; the two stands dominated by saplings had much lower hemlock cover (Fig. 4c). A total of 63 species were recorded in the four stands, including two non-native species, *Galeopsis tetrahit* and *Veronica officinalis* in the high-density loamy stand (Miller 1999). Of the 63 species that were observed, 13 species occurred in all four stands, 8 species occurred in three stands, 20 species occurred in two stands, and 22 species occurred in only a single stand. Nearly half (30) of the species occurred only on loamy soils, while only 11% (7 species) occurred only on sandy soils. The mean herbaceous ground-layer cover was 9.3%. Small maple sapling cover was 8.7%; maple seedling cover averaged 9.5%. The average distance that photosynthetically active radiation (PAR) was significantly autocorrelated in the four plots was 22.8 m in the spring, 12.5 m in early summer, and 12.3 m in late summer; in the only stand where PAR was sampled at all three times (high-density sapling, sandy-soil stand), PAR was significantly autocorrelated to 24.0 m, 12.5 m, and 9.0 m in spring, early summer, and late summer, respectively.

### Comparison of patterns by species and by stands

*Spatial autocorrelation.*—Except for one spring ephemeral (*Dentaria laciniata*), there was little autocorrelation of herbaceous and shrub species in the two high-density stands, while there was considerable variation in autocorrelation among these species in the low-density stands (Fig. 5). Of the species analyzed in three or more stands, sugar maple *Viola selkirkii*,

*Maianthemum canadense*, and *Gymnocarpium dryopteris* varied considerably by stand in their autocorrelation, while the fern *Dryopteris intermedia*, and *Arisaema triphyllum* did not. Of species that occurred in both soil types, small maple saplings, *V. selkirkii*, and *M. canadense* were autocorrelated to considerably greater distances on loamy soils underlain by a fragipan than on sandy soils. A clubmoss (*Lycopodium obscurum*) was autocorrelated to a greater distance on sandy soils than on loamy soils.

*Index of dispersion.*—Sugar maple saplings were regularly distributed in all stands, and at every resolution (Table 3). Three vertebrate-ingested species and seedlings of the wind-dispersed American basswood were spatially random at every resolution and in all stands where they occurred at an adequate frequency for analysis. In all stands but the high-density, loamy stand, nearly all species other than sugar maple were aggregated at every resolution. In contrast, all except one species in the high-density, loamy stand were spatially random at one or more resolutions.

### Analysis of patterns by guilds

Species that reproduce primarily by vegetative means were autocorrelated to greater distances than species that reproduce mainly by seed, but the difference was not statistically significant (Fig. 6a). The greatest nonsignificant differences between these two guilds occurred in the low-density stands. In the high-density, loamy stand, there was virtually no difference between vegetative and seed guilds, and in the high-density, sandy stand, there were no seed species at all.

The distance ranking of dispersal-guild autocorrelation was: ballistic ≥ spore ≥ ant > vertebrate-in-

TABLE 3. Results from $\chi^2$ index of dispersion at three spatial resolutions for all species with a frequency $\geq$ 21 quadrats in at least one plot (29.5 × 62 m).

| | | High sapling density | | Low sapling density | |
|---|---|---|---|---|---|
| | *n* | Loamy soil | Sandy soil | Loamy soil | Sandy soil |
| *Acer saccharum* seedling | 7 | R | R | R | R |
| | 14 | R | R | R | R |
| | 21 | R | R | R | R |
| *A. saccharum* sapling | 7 | AAA | AA | AAA | SR |
| | 14 | AAA | AAA | AAA | A |
| | 21 | A | AAA | AAA | AAA |
| *Dryopteris intermedia* | 7 | SR | AAA | AAA | A |
| | 14 | A | AAA | AAA | A |
| | 21 | SR | AAA | AAA | AAA |
| *Viola selkirkii* | 7 | | AAA | AAA | AAA |
| | 14 | | AAA | AAA | AAA |
| | 21 | | AA | AAA | AAA |
| *Claytonia caroliniana* | 7 | | | AAA | |
| | 14 | | | AAA | |
| | 21 | | | AAA | |
| *Maianthemum canadense* | 7 | SR | AAA | AAA | AAA |
| | 14 | | AAA | AAA | AAA |
| | 21 | | AAA | AAA | AAA |
| *Arisaema triphyllum* | 7 | SR | SR | A | AAA |
| | 14 | A | SR | A | AAA |
| | 21 | SR | AAA | A | AAA |
| *Dentaria laciniata* | 7 | | AAA | | |
| | 14 | | AAA | | |
| | 21 | | AAA | | |
| *Allium tricoccum* | 7 | | | AAA | |
| | 14 | | | AAA | |
| | 21 | | | AAA | |
| *Gymnocarpium dryopteris* | 7 | AA | AAA | AAA | AAA |
| | 14 | AAA | | AAA | AAA |
| | 21 | AAA | | AAA | AAA |
| *Lycopodium obscurum* | 7 | | | AAA | AAA |
| | 14 | | | AAA | AAA |
| | 21 | | | | AAA |
| *Streptopus roseus* | 7 | | | SR | SR |
| | 14 | | | SR | |
| | 21 | | | SR | |
| *Athyrium filix-femina* | 7 | | | AA | |
| | 14 | | | AAA | |
| | 21 | | | AAA | |
| *Thelypteris phegopteris* | 7 | | | AAA | |
| | 14 | | | AAA | |
| | 21 | | | AAA | |
| *Polygonatum pubescens* | 7 | | SR | SR | SR |
| | 14 | | SR | | |
| | 21 | | SR | | |
| *Tilia americana* seedling | 7 | | SR | SR | |
| | 14 | | | SR | |
| | 21 | | | SR | |
| *Lycopodium lucidulum* | 7 | | AAA | | A |
| | 14 | | AAA | | AAA |
| | 21 | | | | AAA |
| *Dirca palustris* | 7 | | | | SR |
| | 14 | | | | SR |
| | 21 | | | | SR |
| *Betula alleghaniensis* sapling | 7 | | | SR | |
| | 14 | | | AA | |
| | 21 | | | AA | |

*Notes:* The three spatial resolutions are $n$ = 21 blocks of 9.0 × 10.5 m; $n$ = 14 blocks measuring 9.0 × 15.5 m; and $n$ = 7 blocks measuring 9.0 × 31.5 m. Distribution key: R = regular distribution, SR = spatially random distribution, A = aggregated distribution; a blank space means that the species was either absent or too infrequent to perform the analysis at that resolution. ''AAA'' indicates a significantly aggregated distribution at $P < 0.001$, ''AA'' indicates a significantly aggregated distribution at $0.01 < P \leq 0.001$, and ''A'' indicates a significantly aggregated distribution at $0.05 < P \leq 0.01$.
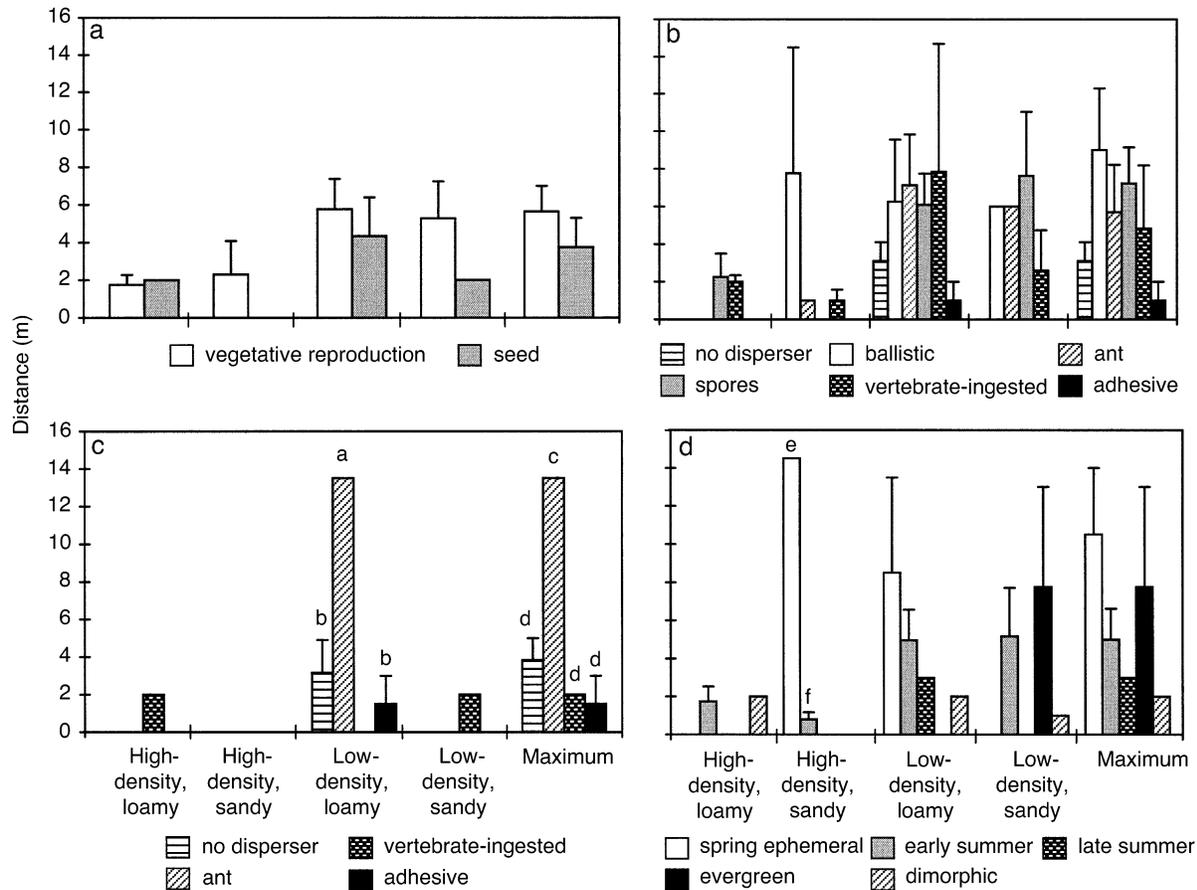
FIG. 6. Autocorrelation by stands of (a) reproductive guilds, (b) dispersal guilds, (c) dispersal guilds using only species that reproduce primarily by seed, and (d) temporal guilds. Only species with frequency ≥ 9 quadrats in a stand contributed to a guild's average in that stand. The maximum bars were calculated by using the maximum autocorrelation among the four stands for each species, then calculating the average for each guild. Data are means + 1 SE. Different letters above bars of the same guild within a stand indicate significant differences (ab, $P = 0.076$; cd, $P = 0.057$; ef, $P < 0.0001$).

gested > no disperser > adhesive (Fig. 6b). Of species that reproduce primarily by seed, ant-dispersed species were autocorrelated to significantly greater distances than the other guilds: ant ≫ no disperser ≥ vertebrate-ingested ≥ adhesive (Fig. 6c). The relationships among dispersal guilds generally remained the same within stands not dominated by saplings, with the exception that the vertebrate-ingested guild was slightly more autocorrelated than the ballistic, ant, and spore guilds in the low-density, loamy stand. In high-density stands, there was little difference among ground-layer dispersal guilds, except for the ballistically dispersed *Dentaria laciniata* in the high-density, sandy stand that was autocorrelated to a much greater distance than all other ground-layer species in this stand.

The distance rank of temporal-guild autocorrelation was: spring ephemerals > evergreen > early summer > late summer > dimorphic; although only in the high-density, sandy stand were there significant differences (Fig. 6d). The relationship among guilds remained the same when we compared them within stands.

*Correlates of understory vegetation distributions*

In the high-density, loamy stand, percent cover of small sugar maple saplings was negatively correlated with percent cover of treefall mounds and bare ground (Table 4a). Percent cover of three of the four ground-layer species analyzed in this stand (*G. dryopteris*, *M. canadense*, and *D. intermedia*) were either directly or indirectly negatively correlated with percent cover of small saplings. In the low-density, sandy stand, these same three ground-layer species were negatively correlated with small maple saplings via correlations (+) with the percent cover of conifers in the sapling layer; a clubmoss species was negatively correlated with deciduous large-sapling cover (Table 4d). Small sugar maple saplings and the same three ground-layer species were negatively correlated with the large-sapling layer in the low-density, loamy stand; more than half of the ground-layer species analyzed in this stand were positively correlated with either small saplings or seedlings (Table 4c). In the high-density, sandy stand, a

TABLE 4. Positive (+) or negative (−) regression coefficients (at $P < 0.05$) by stand, from multiple logistic regressions of the percent cover of the 10 most frequent species (response variables) against various biotic and abiotic factors, after accounting for autocorrelation.

| Species | Deciduous | | | | | Hemlock | | Conif. large sap. | Microtopography | | | | Bare ground |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Can. | Sub. | Large sap. | Small sap. | Sdlg. | Can. | Sub. | | Mound | Slope | Pit | Floor | |
| a) High-density, loamy stand | | | | | | | | | | | | | |
| *Acer saccharum* sapling | − | − | ... | ... | ... | ... | ... | ... | − | ... | ... | ... | − |
| *Dryopteris intermedia* | ... | ... | ... | ... | ... | ... | ... | ... | − | ... | ... | − | + |
| *Maianthemum canadense* | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | ... | ... | ... |
| *Arisaema triphyllum* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Gymnocarpium dryopteris* | − | ... | ... | − | ... | ... | ... | + | ... | ... | ... | ... | ... |
| b) High-density, sandy stand | | | | | | | | | | | | | |
| *Acer saccharum* sapling | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Dryopteris intermedia* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Viola selkirkii* | ... | ... | ... | + | + | ... | ... | ... | ... | ... | ... | ... | + |
| *Maianthemum canadense* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Arisaema triphyllum* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Dentaria laciniata* | ... | + | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Gymnocarpium dryopteris* | − | ... | ... | ... | + | ... | ... | ... | ... | ... | ... | ... | ... |
| c) Low-density, loamy stand | | | | | | | | | | | | | |
| *Acer saccharum* sapling | + | − | − | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Dryopteris intermedia* | ... | − | − | − | ... | ... | − | ... | ... | ... | ... | ... | ... |
| *Viola selkirkii* | ... | ... | ... | + | ... | ... | ... | + | ... | ... | + | ... | + |
| *Claytonia caroliniana* | + | ... | ... | + | + | ... | ... | + | ... | ... | ... | ... | ... |
| *Maianthemum canadense* | ... | ... | − | ... | + | − | ... | ... | + | ... | ... | ... | ... |
| *Arisaema triphyllum* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | + | ... | ... |
| *Allium tricoccum* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Gymnocarpium dryopteris* | ... | ... | − | + | + | ... | ... | ... | ... | ... | ... | ... | + |
| *Lycopodium obscurum* | − | − | ... | + | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| d) Low-density, sandy stand | | | | | | | | | | | | | |
| *Acer saccharum* sapling | − | ... | ... | ... | ... | ... | ... | − | ... | + | ... | ... | ... |
| *Dryopteris intermedia* | ... | ... | ... | ... | ... | ... | ... | + | ... | ... | ... | ... | ... |
| *Viola selkirkii* | ... | − | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Maianthemum canadense* | ... | ... | ... | ... | ... | ... | ... | + | + | ... | ... | ... | ... |
| *Arisaema triphyllum* | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| *Gymnocarpium dryopteris* | + | ... | ... | ... | ... | ... | ... | + | ... | ... | ... | ... | ... |
| *Lycopodium obscurum* | + | − | − | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |

*Note:* Abbreviations in column headings are as follows: Can. = canopy; Sub. = subcanopy layer; Large sap. = large-sapling layer; Small sap. = small maple sapling; Sdlg. = maple seedling; Conif. large sap. = coniferous large sapling layer.

spring ephemeral (*D. laciniata*) was indirectly correlated (negatively) with large saplings, and the early summer herb *V. selkirkii* was positively correlated with maple seedling and small-sapling cover (Table 4b).

Small maple saplings and the dominant fern (*Dryopteris intermedia*) were negatively correlated with mounds in the high-density, loamy stand. But small saplings were positively correlated with the slopes of mounds in another stand. *M. canadense* was positively correlated with treefall mounds in all but one stand, and two ground-layer species were positively correlated with treefall pits.

In all, a total of 20 species were found on logs, nearly one third of all species recorded in this study. Only six species were frequent enough to perform a $\chi^2$ test of their distributions in relation to moderately and highly decayed logs. Sugar maple seedlings and *M. canadense* occurred less frequently than one would expect at random ($P < 0.005$ and $P < 0.05$, respectively). *D. intermedia* and *V. selkirkii* occurred more frequently than expected ($P < 0.01$ and $P < 0.005$, respectively). *Clay-*

*tonia caroliniana* and *A. triphyllum* did not occur on logs more or less frequently than expected.

### Understory communities in relation to sapling density and soils

Stands with low densities of maple saplings had greater evenness of species than stands with high densities of maple saplings (Table 2). The stands with loamy soils had a higher mean and variance of species richness than the stands with sandy soils (Table 2). Plant communities in stands with different soil types (loamy vs. sandy) were the most dissimilar (Table 5). Plant communities on sandy soils were more similar to each other than plant communities on loamy soils were to each other.

### DISCUSSION

#### Comparison of patterns by species and by stands

Our first broad hypothesis, that various species exhibit distinct spatial patterns within a given environ-

TABLE 5. Dissimilarity matrix of stands, using species frequencies.

| Stand type | High density | | Low density | |
|---|---|---|---|---|
| | Loamy | Sandy | Loamy | Sandy |
| High density, loamy | 0 | | | |
| High density, sandy | 0.831 | 0 | | |
| Low density, loamy | 0.743 | 0.846 | 0 | |
| Low density, sandy | 0.750 | 0.654 | 0.817 | 0 |

*Notes:* Dissimilarity was measured in Sørensen distance, calculated as follows: $1 - 2W/(A + B)$, where $W$ is the sum of shared abundances, and $A$ and $B$ are the sums of frequencies in individual stands. A general relativization was applied to the data before the distances were calculated. Seedlings were used for *Acer saccharum*.

ment, is supported by the result that species autocorrelation varies considerably in the stands with a low density of sugar maple saplings. There is also considerable variation among species within loamy and sandy soils, but less than in the low-density stands. This hypothesis is contradicted by the consistently small distances at which species other than maple were autocorrelated in the high-density stands. The results suggest that competition from small maple saplings may be influencing spatial patterns in the understory by constraining the spread of all other species, while large maple saplings may constrain all species, including small maple saplings. Spring ephemerals are least affected by maple saplings of all ground-layer groups, but even these are affected to some degree. It would be interesting to test these results by experimentally removing maple saplings, or by reciprocal transplanting of ground-layer species into areas of high- and low-density maple saplings, then look at survivorship. The inference that competition from maple saplings may influence the spatial patterns of other plant species is consistent with the negative correlations of both herb cover and total understory species richness with sugar maple cover <2 m tall in the Sylvania Wilderness Area found by Ferrari (1993). Furthermore, the impact of

maple saplings on the ground layer may be long lived; Hett and Loucks (1971) noted that maple seedlings only 0.9 cm in diameter at root crown were more than 15 yr old, and Dahir and Lorimer (1996) noted that the tallest sugar maple trees in gaps in mature and old-growth hardwood stands had a mean D1.5 m of 10 cm (range: 3.4–26.0 cm) and a mean total age of 65 yr (range: 24–158 yr). Sugar maple sapling density generally has a negative effect on the ground layer, but this relationship is influenced by several biotic and abiotic factors (Fig. 7).

Competition, however, is somewhat symmetric; there are regions within the stands we studied, particularly areas with *Lycopodium obscurum* and *Gymnocarpium dryopteris* cover, where maple appears to be at a competitive disadvantage. Other correlative and experimental studies have also noted reductions in tree regeneration due to ground-layer vegetation (Maguire and Forman 1983; Davis et al. 1998).

The index of dispersion results, like the autocorrelation results, both support and contradict the hypothesis that different species will exhibit distinct spatial patterns within a given environment. In all stands except the high-density, loamy stand, some species are randomly distributed while others have aggregated distributions. However, in the high-density, loamy stand, all ground-layer species except one are randomly distributed at the resolutions measured. These results also point to an association of the spatial patterns of ground-layer species with small maple saplings.

Our second broad hypothesis, that the spatial patterns of individual species vary among different environments, is generally supported by both our autocorrelation and index of dispersion results, and is consistent with several other studies. Nearly half of the herb species studied in a maple forest in southern Wisconsin (USA) displayed distributions that were related to topography and microtopography (Struik and Curtis 1962). In an early study of plant distributions, Whitford (1949) found considerably different patterns of aggre-
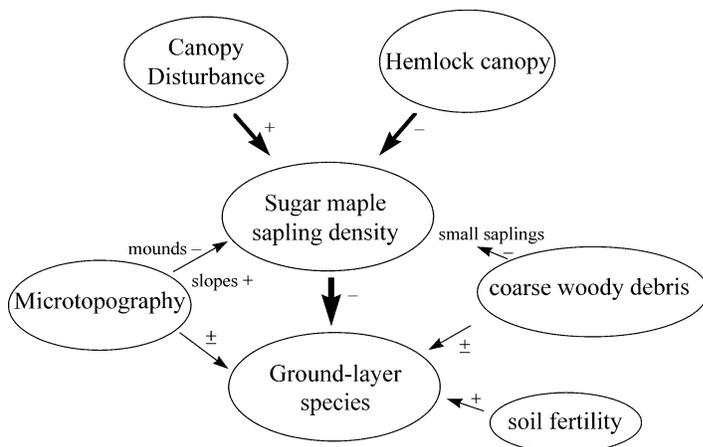


FIG. 7. Schematic representation of the relative effects of various biotic and abiotic factors on sugar maple sapling density and ground-layer species. The thickness of the arrows represents the approximate relative magnitude of the relationship.

gation for many of the same species occurring in both oak–hickory and maple–basswood stands in southern Wisconsin and northern Illinois (USA). Maslov (1989) also found different patterns for the same species in different forests outside Moscow, Russia. In Maine (USA), Collins (1988) found the distribution of *Maianthemum canadense* to vary along a successional forest gradient; it was aggregated in a later-successional forest dominated by a sugar maple canopy, but exhibited a regular distribution in an early successional hardwood forest. *M. canadense* was also regularly distributed in a mixed-deciduous forest in the same study (Collins 1988).

Maslov (1989) reached the conclusion that abundant species in heterogeneous environments will exhibit aggregated distributions, while the same species in homogeneous environments will exhibit more random distributions. Collins (1988) noted that most species exhibited aggregated distributions in two of the three stands he studied, but more species exhibited random or regular distributions in the stand where large ferns dominated the ground layer. This suggests that the ferns may have created a homogeneous (and, we suspect, unfavorable) environment with respect to the randomly distributed species. Similarly, our results show several species with aggregated distributions in all stands except the ones in which sugar maple saplings dominate the ground and large-sapling layers.

Maple seedlings were regularly distributed at all resolutions, and in all stands. Collins (1988) also found maple seedlings to exhibit a regular distribution. In our study, the regular distribution can be attributed to their ubiquitous occurrence. In one study of mesic forests in northern Wisconsin, the typical stand contained sugar maple seedlings (<30 cm) at 50 000 seedlings/ha (Curtis 1959). In contrast, we generally found maple saplings (<1.4 m) to be aggregated in areas away from taller saplings, as reported by Curtis (1959).

Despite the fact that only one of the four ground-layer species had the same distribution in all four stands, we expect that clonal species such as *Lycopodium* will have aggregated distributions where they occur, and others, such as *Polygonatum pubescens* and *Streptopus roseus* may have random distributions where they occur.

More species were autocorrelated to greater distances in loamy soil than sandy soil, supporting this specific hypothesis, as well as the broad hypothesis that the spatial pattern of a species is dependent upon its environment.

### Analysis of patterns by guilds

There were few statistically significant differences among guilds due in part to small sample sizes. For example, in the low-density, sandy stand, nine vegetative species contributed to the average autocorrelation distance (5.3 m), while there was only one seed species (2.0 m). In contrast, 32 species would be necessary for this difference to be significant. Nearly two thirds of the guilds in any one stand in this study were comprised of three species or fewer. Alternatively, if we had sampled many more plots where the ground layer was unconstrained by high sapling density, we could pool the plots to test for significant differences. Nevertheless, the results from the guild analysis are biologically consistent, and are generally consistent with the ecological literature, even where statistical significance is lacking.

Species reproducing primarily by vegetative means are autocorrelated to greater distances than species that reproduce by seed in this study, providing weak evidence against our hypothesis that clonal species would be autocorrelated to shorter distances than seed species. One explanation for this result is that given the extent of the study area investigated, seeds can be dispersed by vertebrates far enough away from the parent plant to no longer be autocorrelated, whereas new vegetative shoots cannot. However, other seed species are dispersed short distances either ballistically or by ants, and are autocorrelated to greater distances than strictly clonal species. Our results are consistent with some previous studies of spatial patterns in vegetation (e.g., Struik and Curtis 1962, Matlack and Good 1989). Maslov (1989) found that species that do not spread much vegetatively were generally not highly aggregated, while species that did spread vegetatively exhibited a variety of patterns, including high aggregation by species with long rhizomes. Matlack (1994), investigating the migration rates of understory flora from older second-growth forests into early successional stands in Pennsylvania (USA), found in two of his five study sites that species showing moderate or vigorous vegetative spread migrated more slowly than species showing little or no vegetative spread. He concluded that vegetative propagation was probably insignificant as a means of long-range colonization.

There was some evidence to support an alternative relationship than the one we hypothesized among dispersal guilds with regard to the distance that each is autocorrelated. Although we correctly hypothesized that short-distance dispersers such as species in the ant-dispersed guilds would be autocorrelated to greater distances than species in the adhesive and ingested guilds, the ant-dispersed guild was also autocorrelated to greater distances than the no-disperser guild. This suggests that ants are a better disperser than no agent at all, yet do not disperse the seed so far from the parent plant to be no longer autocorrelated. There is a general inverse relationship between the autocorrelation of dispersal guilds in our stands and the migration rates of dispersal guilds found by Matlack (1994) and Brunet and von Oheimb (1998). It appears that species that are adapted for long-distance dispersal migrate faster and occur in lower densities than species lacking such adaptations. Because of the relationship between spatial autocorrelation and density, the faster migrating

species are autocorrelated at shorter distances (over small areas) than species that migrate more slowly. Furthermore, our results suggest that there may be a threshold of species density below which autocorrelation is undetectable. Interestingly, the trend in autocorrelation among dispersal guilds observed in the low-density stands was not evident in the two stands dominated by maple saplings; plants may not disperse and establish well by seed in these stands due to greater competition for light with maple. In addition, the average distance that both seed and vegetative guilds were autocorrelated was smaller in the sapling-dominated stands than in the low-density stands.

Spring ephemerals were autocorrelated up to 3 times the distance of the early summer guild, supporting this specific hypothesis, as well as the broad hypothesis that different species will exhibit different spatial patterns within a given environment. This is not surprising given that the light environment in spring was autocorrelated twice the distance of the light environment in summer. Soil moisture and nutrients are probably also autocorrelated greater distances before leafout than after leafout when competition for resources increases (see Crozier and Boerner 1984). The remaining guilds were represented by only one or two species. Therefore, other trends (evergreen > late summer > dimorphic) should be regarded as anectodal.

### Correlates of understory vegetation distributions

Most species in the understory are negatively correlated with a moderately dense canopy of large saplings. Many ground-layer species are positively correlated with small saplings and maple seedlings in stands with both moderate and high densities of large sapling cover, probably because within these stands, most species attain the greatest growth in the few gaps in the large-sapling layer. Positive correlations in these stands should not be interpreted as a lack of competition, since absolute cover of ground-layer species coincident with maple in these stands may be lower than the absolute cover of the same species in other stands, where they occur in areas with less maple sapling and seedling cover.

Several species in this study were positively associated with pit and mound microtopography, an observation noted in other studies (e.g., Bratton 1976, Beatty 1984). Peterson and Campbell (1993) concluded that higher frequencies of herbaceous species on treefall mounds were primarily due to the lack of leaf litter. In stands with sparser large-sapling cover, most ground-layer species are negatively correlated with small maple saplings. Small maple saplings were negatively correlated with treefall mounds in the stand where the saplings were most numerous. In these stands, treefall mounds (and we suspect, pits) serve as refuges from maple sapling competition for some ground-layer species. It would be worthwhile to experimentally test this by the creation of microsites to follow actual coloni-

zation as might be predicted based on the dispersal and aggregation data.

*Viola selkirkii* and *Dryopteris intermedia* occurred significantly more often than expected on decayed logs, while maple seedlings occurred significantly less often than expected. Most of the *D. intermedia* individuals on logs were quite small (pre-reproductive), suggesting that this microsite may not be valuable in augmenting its population, but several of the violets were noted flowering (T. F. Miller, *personal observation*). The clubmoss (*Lycopodium lucidulum*), yellow birch, and eastern hemlock also occurred more frequently on logs than expected, although it was not possible to test these distributions due to small sample sizes. Many other ground-layer species have been reported to grow on logs in the eastern United States (Bratton 1976, Thompson 1980). The negative relationship between maple seedlings and logs suggests that logs may be a favorable microsite for several ground-layer species because of reduced competition with maple seedlings. This could be tested by planting the seeds of maple and various ground-layer species on decayed logs.

### Understory communities in relation to sapling density and soils

Our hypothesis that the overstory structure will determine the understory plant community was supported by our finding that the evenness of the stands was negatively associated with sapling density. This is a result of many species having lower frequencies in stands with high sapling density than in stands with low sapling density. It is unclear whether these infrequent species will continue to occur at low frequencies until the sapling layer self-thins, or whether they will be extirpated from these stands, and later recolonize.

If we consider only the 20 species that occurred in two stands, 75% of these occurred exclusively on one soil type. This distribution is highly unlikely ($\chi^2$ $P <$ 0.001) to be a chance result. This fidelity suggests that soil texture, related to moisture and nutrient status, may explain patterns of species occurrences at the resolution of kilometers (the distance between stands in this study). Soil characteristics may also influence plant communities; stands on similar soil types were the most similar in relation to species composition and frequency (Table 5). This is consistent with the widely acknowledged generality of the relationship between plant distributions and soils (e.g., Beals and Cope 1964, Foster 1998). Soil texture appeared more important than overstory structure as a determinant of community composition (Miller 1999).

### Sampling strategy and spatial analysis

In some instances, the correlograms detected autocorrelation beyond the extent of a single patch. It appears that autocorrelation over larger distances coincides with the distance between patches (Radeloff et al. 2000, Scheller 2000, Scheller and Mladenoff 2002).

The cyclic sampling strategy that we employed yields much more spatial information over a broader range of extents for the same effort, than does the typical, complete, contiguous sampling, because a greater range of lags can be sampled with a given number of quadrats. This strategy should prove extremely useful to ecologists who seek to understand the role that spatial patterns have in ecological relationships.

### Management implications

In our small-sized study areas, plant species in the forest understory grow more sparsely in unfavorable environments, as reflected by the reduced distances over which they are autocorrelated. In these northern hardwood forests, light is often limiting in the understory, and is patchily distributed at a range of process areas. Consequently, it may be possible to use autocorrelation analysis to study the effects of different forest management regimes on these species.

Coarse woody debris and treefall mounds appear to contribute to plant species diversity by providing microsite heterogeneity with reduced competitive pressure from sugar maple seedlings and saplings. In unmanaged forests, these microsites are continually replenished by treefalls. Consequently, harvesting regimes that leave a percentage of large trees would appear useful in enhancing native plant diversity in these forests.

Most species in this study were restricted to one soil type, even within a single general forest community type. Soil diversity may contribute to regional plant species diversity, and should be considered when deciding the management intensity of an area. Although only anecdotal, there was no reduction in species richness in the stands with sandy soil due to the dominance of saplings, but in the stands with loamy soils, there were considerably fewer species in the stand dominated by sugar maple saplings (Table 2). This suggests that managing stands by small group selection may have less impact on the native plant diversity of sandy sites than on mesic sites. Individual tree selection on mesic sites will more closely mimic the natural disturbance regime of one to multiple treefall gaps. This is consistent with the conclusion of Bratton et al. (1994) that mesic forests and floodplains are probably more vulnerable to species loss than xeric forest types.

Several researchers (e.g., Matlack 1994, Meier et al. 1995) assert that the continued existence of species with low migration rates (e.g., ant-dispersed species and species without adaptations for dispersal) is threatened in increasingly fragmented second-growth landscapes. This assertion is supported by the inverse relationship between autocorrelation of dispersal guilds in this study and their migration rates in Matlack's (1994) study. It is further supported by our findings that many species were autocorrelated in optimal environments and appeared to establish poorly in suboptimal environments. Indeed, in Europe many species

are more prevalent in older, less intensively managed forests, and may be declining even in these due to lack of recolonization from the surrounding areas (Peterken and Game 1984, Wittig et al. 1985, Brunet and von Oheimb 1998).

Metapopulation biology assumes recolonization. At the regional level, if we wish to retain species that migrate slowly while still utilizing our forests for production, we will need to maintain a contiguous forest landscape so that recolonization can occur. Alternatively, in landscapes that are highly fragmented, we must afford these species more protection, when locally rare, to avert their becoming rare over larger areas. For example, national forests currently alter their timber harvests only if a stand is found to contain a species deemed rare ($\leq100$ occurrences) at the state or federal level. Thus, it is possible that other species lacking adaptations for long-distance dispersal could be extirpated from the national forest, if the forest is isolated from the nearest population of the plant by a relatively short distance. Forest managers can help maintain biological diversity by giving preferential treatment to all species that are rare at the extent of their jurisdiction, that once locally extirpated have poor dispersal and recolonization ability.

### Future research

One of the conclusions of this study is that the sapling layer may be a strong determinant of the spatial patterns of understory vegetation in old-growth northern hardwood forests, and this appears to vary with soil types. A long-term study would provide information about the temporal variation in these patterns, and the time it takes ground-layer species to recover from competition with saplings, after self-thinning of the sapling layer. A long-term study of the spatial patterns of understory vegetation in old-growth forests can also serve as a baseline to compare the spatial patterns of understory vegetation in managed forests. A comparison of the spatial patterns of understory vegetation in old-growth and managed forests, and over larger within-stand scales (hundreds of meters to 0.5 km extent; 4.0-$m^2$ grain or resolution), has recently been completed (Scheller 2000, Scheller and Mladenoff 2002).

An alternative to a long-term study is a chronosequence. A chronosequence of gap dynamics can reveal trends in the spatial patterns in the understory, but a larger sample size is necessary to overcome the variation among stands that is independent of the gap dynamics. An experimental approach that uses various intensities and extents of canopy harvesting may reveal sapling densities that are adequate to regenerate the canopy, but that only minimally impact the ground layer.

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