

Study of spatial components of forest cover using partial Mantel tests and path analysis

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Abstract. Plant species distributions are generally thought to be chiefly under environmental control, although they may be affected by disturbance events or dispersion properties of the species. The relative importance of these different factors is not easy to evaluate because they often share common spatial patterns, such that an inextricable network of relationships occurs between plant distributions, environmental conditions, disturbance events and endogenous factors such as propagule dispersion. In this paper we propose a method for untangling the common spatial component from the relationship between environmental conditions and the distribution of tree species. Using partial Mantel tests and path analysis, we test models of relationships between these data sets.

Results show that in our study area, spatial patterns of species associated with hydric conditions remain largely correlated with environmental conditions. However, mesic sites show more complex forest covers, in which a significant spatial component persists when environmental variation is statistically controlled for. This remaining spatial variability suggests that other factors possessing spatial structure partly explain species distributions.

Keywords: Distance matrix; Environmental control; Northern hardwood forest; Partial correlation.

Introduction

Traditionally, vegetation scientists have considered environmental conditions to be the major determinant of patterns in plant distributions (e.g., Curtis & McIntosh 1951; Whittaker 1956; Bray & Curtis 1957). This perspective is complemented by studies of disturbance dynamics (White 1979; West, Shugart & Botkin 1981; Pickett & White 1985). In such studies, fire (Heinselman 1973), wind (Canham & Loucks 1984; Foster 1988), episodic infestations by pathogenic organisms (Schowalter 1985), as well as gap dynamics (Runkle 1982) have been recognized to be important factors that

can override environmental conditions as determinants of plant species distributions.

In man-dominated landscapes, intense and variable land use can be viewed as adding to the disturbance of vegetation cover. The types of land use (Boerner 1985; Brisson, Bergeron & Bouchard 1988), the size of the disturbances (Oliver & Stephens 1977), neighboring plant communities (Hughes & Fahey 1988) and early successional environments (Finegan 1984), are factors that can influence species composition in disturbed areas (Grubb 1977; Canham & Marks 1985). Combinations of these spatially autocorrelated factors may further weaken the correspondence between plant distributions and environmental conditions.

Spatial variation in forest cover may also be related to factors other than environmental or disturbance heterogeneity. The effect of propagule dispersal, which is typically represented by a negative exponential function (Okubo & Levin 1989), can lead to clumping of species in what is called by Shmida & Ellner (1984) a spatial mass effect. These factors, combined with natural disturbance events, may interact in space, leading to a cumulative effect on canopy cover (Harmon, Bratton & White 1983; Denslow 1985).

Evaluation of the relative importance of environmental conditions versus other factors that may induce spatial patterns in plant species densities can thus be viewed as a problem of spatial covariation. One way to deal with this problem is to consider the spatial location of the sampling sites as a variable upon which statistical analyses are to be performed. Taking this approach, relationships between plants and their environment are not only viewed in terms of co-distribution (without reference to spatial location), but also in terms of their spatial covariation.

In this paper we investigate the importance of environmental conditions to the spatial distribution of tree species in a disturbed northern hardwood forest near the

Adirondack piedmont, in Québec. For a sample of 198 quadrats occurring along a moisture gradient from mesic to hydric conditions, we measure the covariation between the spatial patterns of the environmental conditions and the spatial patterns of the tree species distributions. Relationships are sought at the community and the species level through the use of the partial Mantel test, a correlative method that allows us to incorporate spatial locations as a variable within the statistical framework. We also develop paths of relationships between groups of factors such as space, environment, tree and sapling compositions, using path analyses based upon Mantel statistics.

Materials and Methods

Study area

Data were gathered in a privately owned forested zone of 50 ha located near the Adirondack piedmont, in southwestern Québec. The area is part of an undulating landscape dominated by glacial till deposits where small kettles facilitate the accumulation of organic material. Deposits lie on Beekmantown dolomite, a calcareous sedimentary rock (Globensky 1981). Soils are mostly composed of humo-ferric podzols (Clayton et al. 1977; Rowe 1972). Located in the meridional bioclimatic zone of Québec, this region annually receives about 3250 degree-days of solar energy (Rousseau 1974). On average, 140 days are frost-free. The average minimum temperature is -10°C in January and the average maximum is 20.8°C in July. Precipitation averages 960 mm, 250 of which are in the form of snow.

The forest belongs to the Great Lakes Saint Lawrence forest region. In this region, the Haut-Saint-Laurent section is characterized by hardwood forest on deep calcareous soils and conifers on thin acidic or eroded materials (Rowe 1972). The adjacent territory in the United States is classified as part of the northern-hardwood forest, whose mature composition is dominated by *Acer saccharum* Marsh. (sugar maple), *Fagus grandifolia* Ehrh. (beech), *Tsuga canadensis* (L.) Carr. (hemlock), *Betula alleghaniensis* Britton (yellow birch), and *Pinus strobus* L. (white pine) (Braun 1950).

European colonization of the area began around 1820 (Sellar 1888). The region is presently devoted to agriculture, 65 to 70% of the territory being used for agriculture-related activities. Initially, forests were exploited for lumber and for the fertilizer industry (mostly potash: see Sellar 1888). After the valuable pines and oaks had been selectively lumbered at the start of 19th century, hemlock, spruce, maple, yellow birch and beech were lumbered in a second wave of forest exploitation

culminating during the late 1800's (Bouchard et al. 1989). At that time, agriculture became more important. Presently, soils that are considered unsuitable for agriculture are generally wooded. These forests belong to private farmers who use them as pasture for cattle or as sources of firewood.

Sampling design and data collection

The data analyzed in this paper were gathered during a multidisciplinary ecological study that involved an inventory of the geomorphology, soils, vegetation, and land uses found in the Haut-Saint-Laurent region of southern Québec (Bouchard et al. 1985). A systematic sampling design (Cochran 1977) was used to locate 198 vegetation quadrats, each 10 m by 20 m in size, in an area of approximately 0.5 km^2 . The quadrats were positioned at 50-m intervals along staggered rows separated also by 50 m. In each quadrat, trees larger than 10 cm in diameter at breast height (dbh) and saplings (5 to 10 cm dbh) were counted and identified to species. The description of the physical conditions of each quadrat includes exposure, slope and topography. In each quadrat, soil variables were obtained after digging a 1 m-deep trench. These variables include thickness of the A and B horizons, texture and stoniness of the B horizon and depth to the water table. Occurrence of marbling and color of mineral horizon were used to determine drainage index. These variables were noted using the Canadian system of soil classification (Anon. 1978). Texture was determined manually with the help of a field key developed in the laboratory. Finally, photo-interpretation allowed us to describe the geomorphology of each quadrat's surroundings.

Data analyses

In this study, interpolated maps were obtained by trend surface analysis (Student 1914). Maps were not part of the modeling process, but they played an important role in allowing us to visualize distribution patterns and to check the validity of the relationships uncovered by modeling.

The inclusion of 'space' in statistical analyses is no simple task since we are dealing with a surface rather than a single transect. On the one hand, spatial relationships among sampling localities are difficult to handle as simple variables; they are best represented in the form of a distance matrix among localities. Such matrices cannot readily be analyzed by classical statistical methods and packages designed to handle simple variables. On the other hand, a 'space' variable is not in and of itself an explanation of the spatial distribution of a biological phenomenon; correlating phenomena with

'space' is useful only insofar as this correlation may indicate the existence of some underlying biological or physical process having a spatial component. Because most of the components analyzed in vegetation science, such as plants, soil, disturbances, propagule dispersion and so on, possess spatial properties of diffusion or aggregation, they are said to be autocorrelated. Introducing 'space' as a variable in analyses is a way of looking for relationships between the components while taking into account their spatial properties. For instance, one can study the plant-soil relationship while taking into account the diffusion (autocorrelation) properties of each of the components. Controlling for the effect of environmental conditions when we analyze the relationship between plant species and space, two questions can be addressed: how much of the plant spatial distribution can be accounted for by the spatial distribution of the environmental conditions, and how much of the plant spatial structure still remains to be explained by other factors, such as contagious growth and propagule dispersal.

What the questions posed above have in common is that they imply sets of variables instead of single variables. This is the case for the set of environmental variables, and also for the spatial coordinates of the sampling locations. To establish the relationships between our sets of variables (trees, saplings, environment and space) we use the standardized Mantel (1967) test, also known as the 'Quadratic Assignment Procedure' in the psychometric literature (Hubert & Schultz 1976). This technique allows the computation of a correlation coefficient between distance matrices. A distance matrix contains all pairwise distances between the quadrats of a sample set. For instance, in our study, each distance matrix contains 19 503 pairwise distances. Consequently, an important analytical step using the Mantel tests is to represent data sets in a distance matrix form.

The 'space' variable is naturally represented in the form of a distance matrix. However, the matrix of geographic distances among sampling locations must be customized in order to reflect the spatial properties of the material under investigation. What we mean is that although plant spatial distributions exhibit a contagious behavior (Greig-Smith 1979), that effect becomes quite attenuated with distance. From the results of a multivariate Mantel correlogram and of clustering with a spatial contiguity constraint, Legendre & Fortin (1989) have shown that, in the area under study here, the average tree assemblage patch diameter is 230 to 240 m. Borrowing the terminology of variogram analysis, 240 m is the *range* of the phenomenon; farther away than 240 m from any point, on the average, the variance of the phenomenon is stable. In order for the geographic distance matrix to reflect this characteristic of plants, it

was truncated and all distances larger than this average patch diameter (240 m) were grouped in a single distance class following the assumption that ecological differences are linearly related to distances, up to the range.

The soil variables were chosen to represent environmental factors likely to influence the distribution of tree species. The six variables were: quality of drainage (7 semi-quantitative classes); stoniness of the soil in percentage (5 semi-quantitative classes); thickness (cm) of the organic horizons (A and O); texture of the mineral B horizon (6 unordered qualitative classes); and geomorphology (6 unordered qualitative classes). Although data about slope, relief and exposure had been collected during the survey, we excluded them from the analysis because these factors showed very little variation in the study area. Soil variables were used to compute an Estabrook-Rogers similarity coefficient among quadrats (Estabrook & Rogers 1966; Legendre & Legendre 1983, 1984). The Estabrook-Rogers similarity coefficient makes it possible to assemble a mixture of quantitative, semi-quantitative and qualitative data into an overall measure of similarity. Following this computation, a cluster analysis was performed, using the flexible clustering method of Lance & Williams (1966, 1967) with parameter $\beta = -0.25$. The results (groups of sample plots) were mapped, and the validity of this cartography of soil conditions was compared with an independent geomorphological photo-interpretation of the survey area, in order to confirm our environmental matrix. Finally, similarities were converted into dissimilarities ($D = 1 - \text{similarity}$) and were used as the soil distance matrix in the Mantel and partial Mantel tests.

Vegetation distance matrices among stands were obtained in two different ways. At the community level, Odum's (1950) percentage difference coefficient (also called the Bray and Curtis coefficient; Legendre & Legendre 1983, 1984) allowed us to compare stands on the basis of their respective species abundance data. At the single-species level, abundance values were transformed into classes. This transformation permits a more meaningful comparison of differences between abundance values. For instance, a difference of 30 saplings resulting from a comparison of sites showing respectively zero and 30 saplings cannot be interpreted in the same way as one that results from sites with 100 and 130 saplings. When using abundance classes, differences between sites are expressed in terms of class numbers. So, in our example, sites showing 100 and 130 saplings do not differ and have a distance value of zero because they belong to the same class, whereas a comparison between sites with no saplings and 30 saplings can lead to a distance of one. For each species, classes were obtained by dividing the distribution of absolute abun-

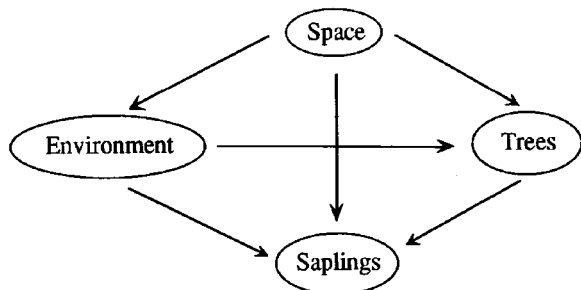


Fig. 1. Path diagram of the relationships linking the sets of variables under study.

dance values into equal frequency classes. Distance matrices for single-species data were computed using the Euclidian distance based on 3 to 5 classes, depending on the extent of the distribution of abundance values.

Because the environment possesses a spatial structure, the evaluation of the relative importance of environment and space on the distribution of trees and saplings poses the problem of collinearity between predictor variables. In such a case, partial correlations and path analysis can help to untangle the independent effect of each predictor variable (Sokal & Rohlf 1981). Correlations among our distance matrices were computed using the Mantel statistic and were used in the path analysis procedure to calculate path coefficients, which are standard partial regression coefficients. However, because of the lack of independence of spatially autocorrelated data, correlations and path coefficients cannot be tested for significance in the usual way, even when they are computed from ordinary variables instead of distance matrices (Cliff & Ord 1981; Legendre & Fortin 1989). Statistical significance of the path coefficients was thus assessed through the partial association test developed by Smouse, Sokal & Rohlf (1986), which operates on distance matrices and is an extension of the Mantel (1967) test of matrix association. In short, the Smouse, Sokal & Rohlf (1986) statistic is a partial correlation computed between the values of two distance matrices, controlling for the effect of the values in a third distance matrix. As in the Mantel test, significance is assessed either by repeated permutations that provide a reference distribution for the computed statistic, or, as we have done, by using the normal approximation developed by Mantel (1967). Levels of significance were corrected to take multiple testing into account (Bonferroni correction: Cooper 1968; Miller 1977). Partial matrix association tests have been interpreted in a causal framework by Legendre & Troussellier (1988). The network of correlations (and path coefficients) that can be computed among our four sets of variables is

Table 1. Mode of the substrate descriptors for each soil type obtained by cluster analysis. Coding for drainage is: (1) very rapid, (2) rapid, (3) well, (4) moderate, (5) imperfect, (6) poor, (7) very poor; for soil texture: (S) sand, (L-S) loamy sand, (S-L) sandy loam, (L) loam, (Si-L) silty loam, (O. G.) organic material; and for geomorphology: (1) kettle, (2) Champlain sea deposits, (3) relict channel, (4) reworked marine moraine, (5) stratified till, (6) moraine ridge.

Soil types:	1	2	3	4	5	6	7	8	9
Descriptors									
Drainage	6-7	6-7	5-6	5-6	4-5	4-5	3-4	3-4	1-2
Stoniness (%)	0	1-5	1-5	25-50	1-5	>25	6-25	>25	1-5
Thickness of Oh horizon (cm)	>40	15-40	0	0	0	0	0	0	0
Thickness of Ah horizon (cm)	0	0-20	10-20	5-30	5-30	>30	5-30	5-30	5-30
Texture of B horizon	-	L-S	L-S	L-S	L-S	L-S	L-S	L-S	L-S
Geomorphology	1	1	2	2-3	2,4	4	4-5	5	6

illustrated by a path diagram (Fig. 1). We test this path diagram, which includes six specific relationships (arrows), for all tree species in turn. All programs allowing these computations are available from P. Legendre for Macintosh microcomputers (see Legendre & Fortin 1989).

Results

Spatial pattern of soil conditions

Clustering performed on the matrix of soil data (198 stands by six descriptors, Estabrook & Rogers similarity index) produced nine soil types. Their characteristics are summarized in Table 1. Types range from poorly drained and weakly stony organic soil, observed in kettles, to well-drained loamy sand, found on moraine ridges. The mapped results (assignment of a soil type to each sample site) reveal a spatial aggregation of soil conditions (Fig. 2). We found a good agreement between this map of soil conditions and the geomorphological units that were identified by photo-interpretation of the study area in conjunction with field studies.

Spatial pattern of species distributions

All species under study present a patchy distribution, with a patch size usually around 100 to 200 m in diameter (some are larger); these patches are supported by spatial correlogram analyses and can be seen in the

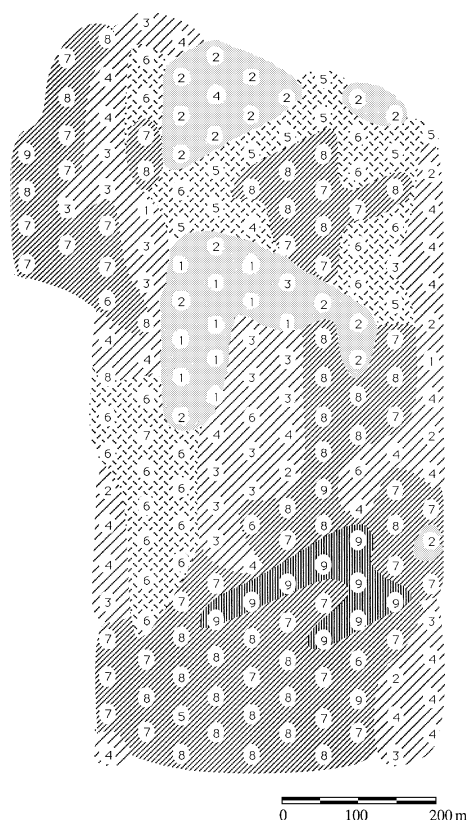


Fig. 2. Map of soil conditions. Each sampling plot is localized and identified by its soil type number, as determined by cluster analysis. Soil types are grouped in four broad categories (shading patterns follow the mesic-hydric gradient).

maps in Figs. 3 and 4. Sugar-maple (*Acer saccharum*) and red maple (*Acer rubrum*) are the most abundant species, with relative frequencies (r.f.) of 66% and 77% respectively and patches of 400 to 500 m in diameter. Hemlock (*Tsuga canadensis*; r.f. = 51%) and yellow birch (*Betula alleghaniensis*; r.f. = 41%) are second in abundance. A third group contains basswood (*Tilia americana*), American elm (*Ulmus americana*), old-field birch (*Betula populifolia*) and white cedar (*Thuja occidentalis*). These species have a lower relative frequency (r.f. = 28 - 34%) and, with the exception of the American elm, form smaller patches. Finally, white pine (*Pinus strobus*), American beech (*Fagus grandifolia*), black ash (*Fraxinus nigra*) and aspen (*Populus tremuloides*) have the lowest relative frequencies (r.f. = 19 - 24%) and are found in very small groves. Distribution maps in Figs. 3 and 4 make it easier to see the range of space-occupation patterns found among these species, in the area under study. In summary, some of the species are widespread and either form a few large or several smaller patches; other species have more restricted spatial distributions and are found in only a few small patches.

Partial Mantel tests and path coefficients

At the community level, partial Mantel tests performed on the species assemblages (Odum distance matrices separately calculated on all tree and on all sapling abundances) show significant partial associa-

Table 2. Path coefficients for all the paths that connect sets of variables (see path diagram, Fig. 1). Significance is assessed from partial Mantel tests. The matrix partialled out follows the slash bar (/). The Mantel statistic between environment and space is 0.084, which is significant ($p < 0.0005$).

	Trees by Space /Env. (*)	Saplings by Space /Env. (*) and Trees (†)	Trees by Environment /Space (*)	Saplings by Environment /Space (*) and Trees (†)	Saplings by Trees /Space (*) and Env. (†)
Community level	0.128*	0.115*†	0.156*	0.063*†	0.370*†
Basswood	0.087*	0.066*†	0.034	0.000	0.424*†
Sugar-maple	0.063*	0.051*†	0.015	-0.013	0.330*†
Red-maple	0.053*	0.039*†	0.000	-0.050	0.165*†
White pine	0.032*	0.048*†	-0.005	-0.060	0.457*†
Hemlock	0.031*	0.055*†	-0.019	0.050	0.223*†
Beech	0.025	0.046*†	-0.043	-0.059	0.501*†
Old-field birch	0.048*	0.000	-0.072	0.067	0.300*†
Trembling aspen	0.000	0.000	0.120*	0.000	0.413*†
American elm	0.009	0.011†	0.075	0.205*†	0.315*†
White cedar	0.026*	0.014†	0.092	0.148*†	0.468*†
Yellow birch	0.013	0.009†	0.101*	0.239*†	0.159*†
Black ash	0.014	0.000	0.253*	0.270*†	0.545*†

* † Mantel test is significant at the Bonferroni-corrected probability level of (0.05/96 = 0.00052) for an overall significance level of 0.05 over 96 simultaneous tests.

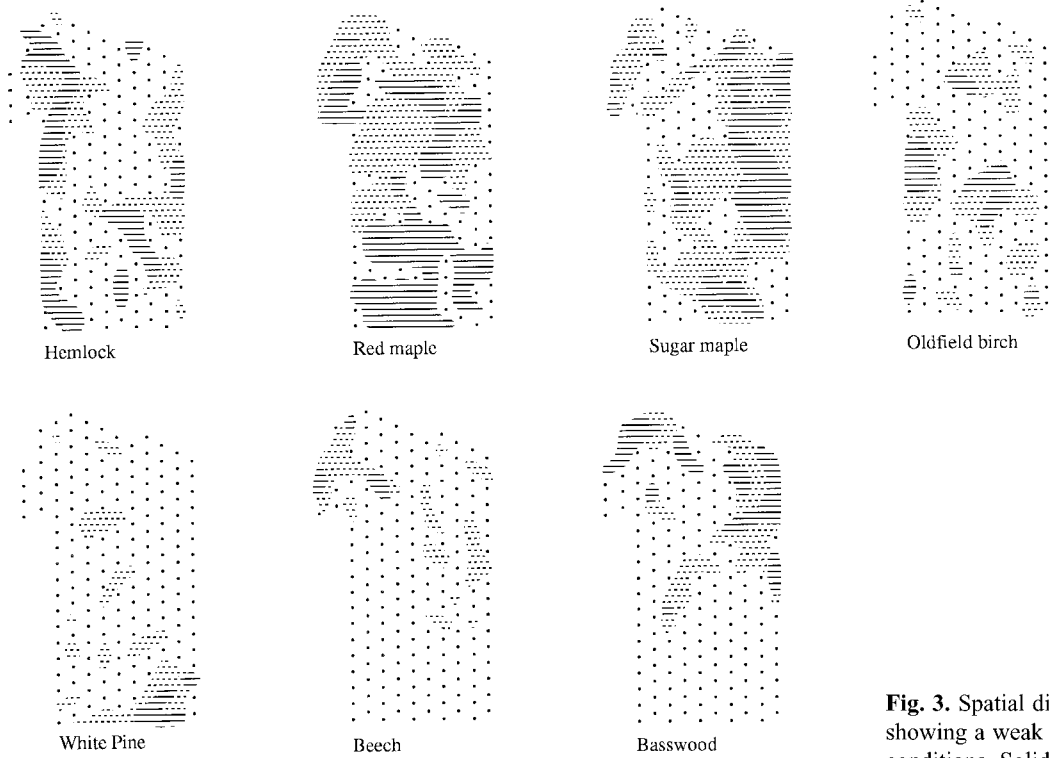


Fig. 3. Spatial distributions of species showing a weak relationship with soil conditions. Solid bars show the zones of high abundance whereas dotted lines represent zones of lower abundance.

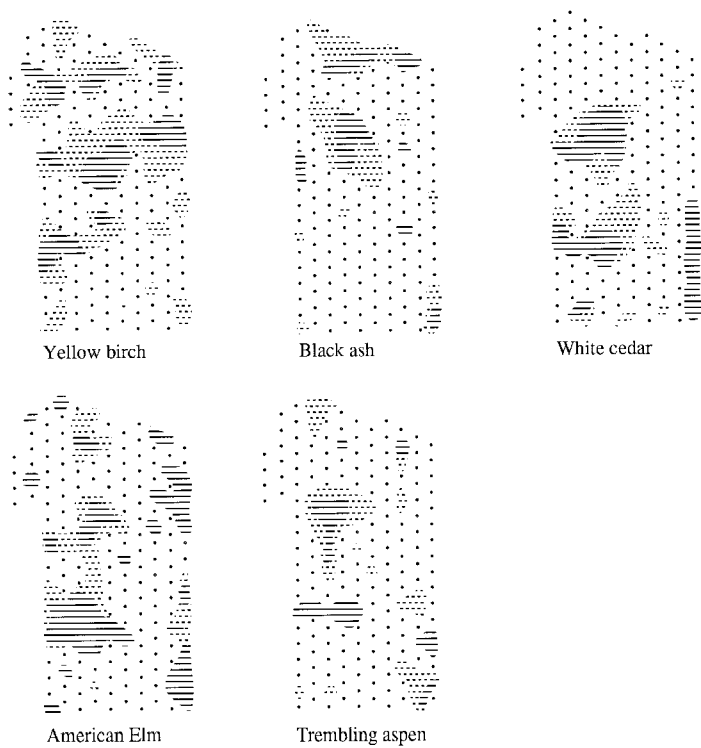


Fig. 4. Spatial distributions of species showing a strong relationship with soil conditions. Solid bars show the zones of high abundance whereas dotted lines represent zones of lower abundance.

tions of both the trees and the saplings with the environmental data matrix, when controlling for geographic distance (Table 2). However, even when environmental variation is controlled for, a significant geographic component remains in the model of forest cover variations (tests of trees and of saplings against space, controlling for the environmental matrix).

At the species level, results (Table 2) are schematically represented in the form of path diagrams (Fig. 5) from which non-significant arrows have been excluded. Among the four models derived from the partial Mantel tests, two major trends are found. The first group of models (a, b) strongly relates tree and sapling distributions to the effect of space with no effect of the environmental matrix on the distribution of species. Tree and sapling distributions of sugar-maple, red-maple, white pine, basswood, beech and hemlock (model a) are linked to space only (Table 2). Although beech trees cannot be significantly related to the spatial matrix, their overall relationships fit model a. Oldfield birch (model b) shows a significant effect of space only on trees, not on saplings. This group of species includes several types of spatial distributions, with varying degrees of extent in our study area (Figs. 3 and 4).

The second group (models c and d, Fig. 5) is characterized by a single relationship between the environment and the distribution of species. The spatial pattern, as observed in species of this group (black ash, white cedar, American elm, yellow birch and aspen, Fig. 4), is mainly due to the autocorrelated (i.e. spatialized) structure of the environmental characteristics. Environmental control appears stronger on saplings than on trees. The exception is the aspen (model d) that shows environmental control only on trees. Tree distributions of the American elm and white cedar are too weakly related to the environmental matrix to show significance at the conservative Bonferroni-corrected level $p < 0.00052$. Most of these five species have a restricted distribution (Fig. 4), being linked to hydric sites (Fig. 2). Like the species described by models a and b, this group includes both early and late successional species.

All models derived from the partial Mantel tests (Table 2, Fig. 5) show a significant association between the distributions of tree and sapling densities. However, these two categories respond individually to the spatial and environmental components. Among the 12 species analysed, only two, the oldfield birch and the aspen, show a sapling distribution that is solely under the control of the tree distribution.

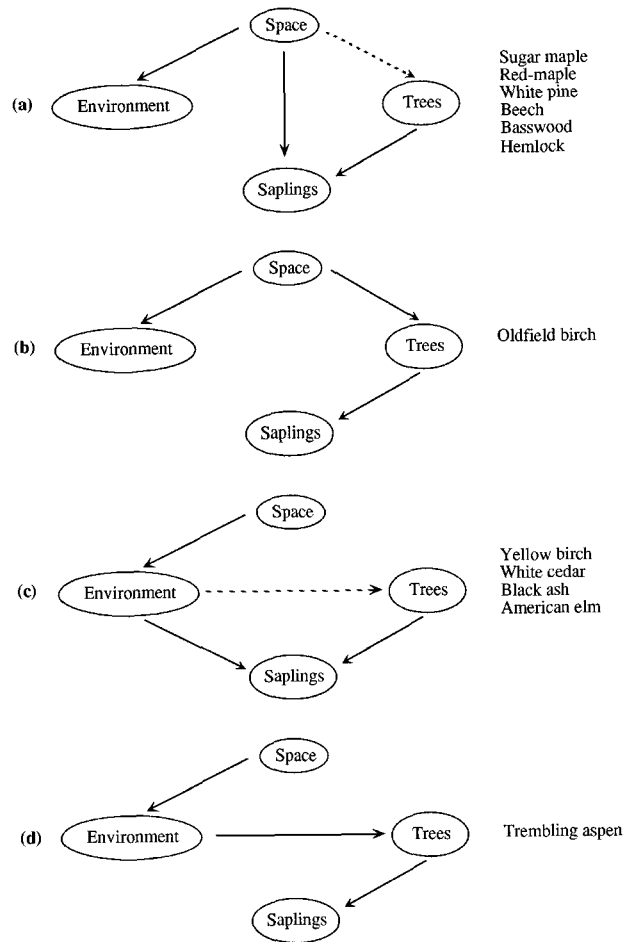


Fig. 5. Models of relationships derived from partial Mantel tests performed on four distance matrices (tree abundance, sapling abundance, environmental conditions and space) for each species. Species responses are grouped in four distinct models (a to d). In models a and c, the dotted line indicates an inconsistent response of some species attributed to the group (see text).

Discussion

Although environmental conditions are usually invoked as the prime factor to explain species distributions (Harper 1977), they are not the only factors responsible for spatial variations in the forest cover under study here. While the measured environmental conditions can adequately predict a significant part of the variation in vegetation cover at the community level, predictability remains weak for many species (Table 2). At the community level, the multifactorial character of

species assemblages spreads the dependent community variable broadly across the environmental gradient whereas single species abundances are often confined to a limited portion of the environmental gradient. Consequently, community composition is likely to show a stronger correlation with environmental gradients than single species abundance data.

Species that appear only related to spatial components

Among the 12 species analysed here, seven show, for their trees, a spatial distribution that does not track the measured environmental variations. This lack of relationship between species distributions and abiotic conditions may be regarded as counter-intuitive. It could be attributed, however to limitations of our research design. For instance, the set of abiotic variables used to construct our environmental model-matrix may be incomplete or/and inaccurately measured. This lack of relationship can also be related to methodological limitations; Mantel tests assume linearity of relationships between distance matrices while ecological distance matrices can show non-linear relationships (Faith, Minchin & Belbin 1987).

Several aspects of our data appear to mitigate these problems. First, the spatial distribution of soil types that results from the analysis of the environmental matrix is consistent with the major geomorphological units identified during an independent study of the glacial deposits of the region (Delage in prep.). Second, the abiotic variables used in this study have proved to be among the most efficient environmental factors in the explanation of the vegetation gradient of our region, when compared with soil chemical components (St-Jacques & Gagnon 1988). Finally, and notwithstanding the limit of our environmental data matrix, we observe nevertheless that half of our species are related to the environmental conditions modeled in this matrix.

We have verified the linearity of the relationships among our distance matrices by comparing measures of rank correlations (Kendall's τ) to Pearson correlations. For all pairwise comparisons between distance matrix values, the linear Pearson correlation has a higher value than the Kendall correlation. We can thus conclude that the transformations performed on our distance matrices (see methods) have linearized the relationships.

If we admit that our environmental model can adequately describe the environmental gradient in our study area, then the significant spatial variability remaining after considering environment suggests that there are other factors imposing spatial pattern on our species distributions.

Environmentally-dependent species

Non-environmental factors do not always obscure the correspondence of environmental conditions with species distributions. For species such as the yellow birch, white cedar, black ash, American elm and trembling aspen, spatial distributions are related to environmental factors (Fig. 5, c and d). In our study area these five species are found on hydric sites characterized by poor drainage, thick organic soil horizon and high water table. This relationship shared by hydric species contrasts with the lack of response of species occurring in mesic conditions. This result suggests that the severity of hydric conditions may limit the effect of non-environmental factors on the spatial patterns of species distribution.

Conclusion

Spatial components are inherent to plant distributions. Although soil conditions are the prime factor usually invoked to explain them, it is possible for species, particularly at the local scale, to exhibit a weak relationship with soil variation. Disturbance events such as lumbering or wind-falls, followed by opportunistic reinvasion of the space by the closest species, may produce such effects. In this paper, we propose a method to separate the spatial and environmental factors in the analysis of species distributions. The method is designed to reveal how much of the spatial structure still remains after considering the environmental factors in plant-species spatial pattern. Residual spatial structure is not in and of itself an explanation of the spatial distribution of a biological phenomenon, but knowledge of its presence can facilitate the formulation of more specific hypotheses. For instance, our results show that spatial covariance between species abundances and environmental conditions is observed only among species occurring on hydric sites, whereas mesic sites show more complex patterns of species distributions. These results suggest that different forest cover dynamics may operate in these two major types of abiotic conditions, although the underlying processes or mechanisms responsible for such patterns will require further research.

Analytical procedures such as the partial Mantel tests, and path analysis based upon Mantel matrix correlations, lead to better discrimination of the factors that could be invoked in the explanation of species distributions. These analyses provide flexibility in terms of data distributions (no normality assumption), they open the way to at least a limited form of inferential modeling, they work directly on distance matrices and they provide an evaluation of the contribution of the site factors

(e.g., soil conditions) to the explanation of spatial structure in vegetation.

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