

Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest

Etienne Laliberté · Alain Paquette · Pierre Legendre ·
André Bouchard

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Abstract Niche processes and other spatial processes, such as dispersal, may simultaneously control beta diversity, yet their relative importance may shift across spatial and temporal scales. Although disentangling the relative importance of these processes has been a continuing methodological challenge, recent developments in multi-scale spatial and temporal modeling can now help ecologists estimate their scale-specific contributions. Here we present a statistical approach to (1) detect the presence of a space–time interaction on community composition and (2) estimate the scale-specific importance of environmental and spatial factors on beta diversity. To illustrate the applicability of this approach, we use a case study from a temperate forest understory where tree seedling abundances were monitored during a 9-year period at 40 permanent plots.

We found no significant space–time interaction on tree seedling composition, which means that the spatial abundance patterns did not vary over the study period. However, for a given year the relative importance of niche processes and other spatial processes was found to be scale-specific. Tree seedling abundances were primarily controlled by a broad-scale environmental gradient, but within the confines of this gradient the finer scale patchiness was largely due to other spatial processes. This case study illustrates that these two sets of processes are not mutually exclusive and can affect abundance patterns in a scale-dependent manner. More importantly, the use of our methodology for future empirical studies should help in the merging of niche and neutral perspectives on beta diversity, an obvious next step for community ecology.

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E. Laliberté · A. Paquette · A. Bouchard
Institut de recherche en biologie végétale (IRBV),
Université de Montréal, 4101 Sherbrooke Est,
Montréal, QC H1X 2B2, Canada

P. Legendre
Département de sciences biologiques,
Université de Montréal, C.P. 6128,
Succursale Centre-ville, Montréal,
QC H3C 3J7, Canada

Present Address:
E. Laliberté (✉)
School of Forestry, University of Canterbury,
Private Bag 4800, Christchurch 8140, New Zealand
e-mail: etiennelaliberte@gmail.com

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Introduction

Disentangling the overall importance of deterministic processes relative to stochastic processes on community patterns has been a continuing challenge for ecologists (Barot and Gignoux 2004; Ricklefs and Schluter 1993). For example, environmental heterogeneity and dispersal have been frequently cited as important deterministic and stochastic processes controlling plant beta diversity, respectively, and the corresponding views have been referred to as niche assembly and dispersal assembly (Hubbell 2001). One approach to estimate the relative importance of these processes on beta diversity has been to partition the variation of community composition between environmental and a posteriori-selected spatial factors (Gilbert and Lechowicz

2004; Jones et al. 2008; Karst et al. 2005; Legendre et al. 2005).

Both deterministic and stochastic processes readily give rise to spatial patterns in community composition within a given region (Soininen et al. 2007), and assessing which of these two sets of processes exerts stronger control over beta diversity can be difficult, particularly at local scales. Part of this difficulty is due to the fact that both sets of processes can lead to very similar patterns (Bell et al. 2006; Borcard et al. 1992; Currie 2007) since the environment is typically spatially structured (Bell et al. 1993; Legendre 1993). Tree beta diversity, for example, has recently been found to be associated with soil nutrient patterns on Barro Colorado Island (John et al. 2007), yet in this same forest, stochastic recruitment limitation had earlier been suggested as the main driver of tree beta diversity (Hubbell et al. 1999).

Holyoak and Loreau (2006) have recently argued that a key issue is to understand at which spatial scales may fitness equalization through demographic stochasticity overcome niche differences, and that doing so may help to reconcile empirical ecology with neutral community models. Although the importance of scale in ecological patterns has gained considerable interest in the last two decades (Levin 1992; Wiens et al. 1986), only recently have methods been developed to dissect the spatial variability of community data at multiple scales (Borcard and Legendre 2002; Borcard et al. 2004). Used in a variation partitioning context, such methods allow for the testing of predictions related to the origin and maintenance of beta diversity (Legendre et al. 2005).

Here we show how existing methods (e.g. principal coordinate of neighbor matrices, canonical redundancy analysis) can be combined to assess the scale-specific importance of niche processes and other spatial processes on beta diversity, using empirical data from standard community surveys. To illustrate the applicability of our methodological approach, we present a case study from a temperate forest understory where tree seedling abundances were monitored during a 9-year period at 40 permanent plots (Paquette et al. 2007). Specifically, our aim was to answer the following questions:

1. Do the spatial patterns of tree seedling abundance vary through time during the 9-year-study period, i.e. is the space–time interaction significant?
2. What is the relative importance of niche processes and other spatial processes on tree seedling beta diversity across different spatial scales for a given year?

Rationale of the statistical approach

Ecologists frequently gather community (e.g. species abundances) and environmental data from sampling sites along

transects or across surfaces, and they do so for various purposes. Yet, the underlying motivation for many of these surveys is to unravel the processes that drive variation in community composition across a given area (beta diversity). When such sites have been surveyed repeatedly, one first needs to examine whether the spatial patterns displayed by the composition of the community significantly have varied through time since this would mean that the underlying processes varied as well. This can be achieved by testing the space–time interaction on community composition (P. Legendre et al., submitted), as shown in Fig. 1a. A significant space–time interaction should lead to separate analyses for each sampling period in order to detect potential temporal shifts in the relative importance of niche processes and other spatial processes that drive beta diversity (Fig. 1b–d). Conversely, if the space–time interaction is not significant, restricting the analyses to a particular sampling period is sufficient because the results obtained from different periods should be qualitatively similar.

One way to estimate the relative contribution of niche processes and other spatial processes on beta diversity is to partition the variation of community composition between environmental and spatial factors (Borcard et al. 1992; Legendre et al. 2005), as shown in Fig. 1b–d. Provided that the environment has been accurately quantified (with relevant variables), the variation due to environmental factors (spatially structured or not) can be attributed to niche processes, while the residual spatial variation can be attributed to other spatial processes (e.g. dispersal). However, it should be noted that part of the “environment–space” fraction could be due to other spatial processes that show fortuitous correlations with the environment (Bell et al. 2006) and that the “pure space” fraction may hide the effect of some unmeasured spatially structured environmental variables (Borcard and Legendre 1994; Jones et al. 2008).

The main interest of our methodological approach lies in the fact that prior to variation partitioning, we propose to dissect the spatial structures of species abundances into additive scale-specific models through principal coordinates of neighbor matrices (PCNM) analysis (Fig. 1b; Borcard and Legendre 2002; Borcard et al. 2004; Dray et al. 2006). Traditionally, a popular way of modeling spatial processes has been trend surface polynomial regression, but this method can only model global structures, such as a gradient, a single wave or a saddle (Legendre and Legendre 1998). On the other hand, PCNM analysis is much better at modeling fine-scale spatial structures than trend surface polynomial regression, and it can model spatial structures over a wide range of scales (Borcard and Legendre 2002). Moreover, because the resulting PCNM variables are orthogonal to each other, they can be combined into additive scale-specific models (Borcard and Legendre 2002; Borcard et al. 2004). PCNM analysis is one of two types of

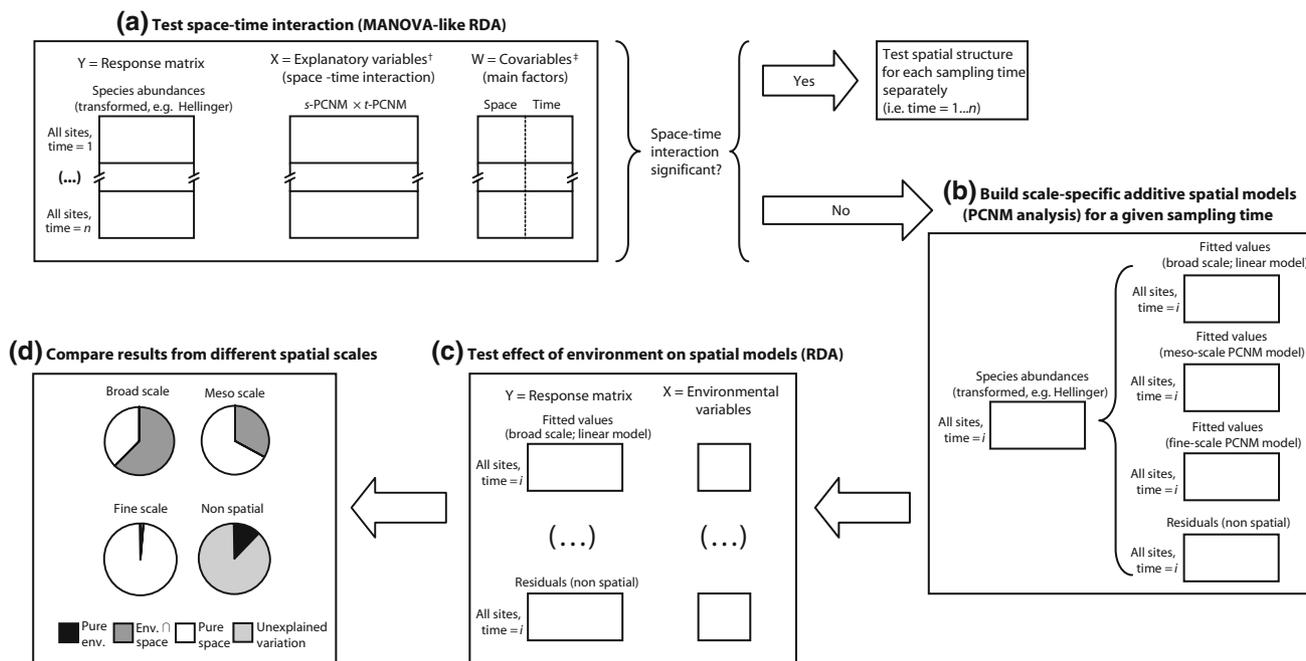


Fig. 1 Diagram showing the step-by-step statistical methodology. [†] This matrix is composed of variables which are the product of the first $s/2$ and $t/2$ spatial and temporal principal coordinates of neighbor matrices (PCNM) variables, respectively (where s is the number of

sites and t the number of sampling times). [‡] The main factors, space and time, are coded using orthogonal dummy variables. *RDA* Redundancy analysis

recently developed spatial modeling methods that are based on the eigenfunctions of spatial configuration (i.e. connectivity) matrices, both of which aim to create spatial predictors that can be directly integrated into regression models (Griffith and Peres-Neto 2006). A detailed description of the PCNM procedure (along with freely available code to easily perform the analysis) is given by Dray et al. (2006), but it essentially consists in the following three steps:

1. Calculate a geographical (i.e. Euclidean) distance matrix ($\mathbf{D} = [d_{ij}]$) between the sampling sites.
2. Build a truncated connectivity matrix ($\mathbf{W} = [w_{ij}]$) so that $w_{ij} = 0$ (i.e. pairs of sites are not connected) when $d_{ij} > t$ (where t , the truncation distance, is a value decided by the user which is larger than or equal to c , which itself is the minimum distance which keeps all sites connected, based on a minimum spanning tree algorithm), while $w_{ij} = [1 - (d_{ij}/4t)^2]$ when $d_{ij} \leq t$.
3. Compute the eigenvalues and eigenvectors of the centered matrix \mathbf{W} .

The resulting eigenvectors with positive eigenvalues (which we refer to as “PCNM variables”) can be used in regression to model spatial structures at all spatial scales; the eigenvectors with large eigenvalues describe global structures, whereas the ones with small eigenvalues describe local structures (Borcard and Legendre 2002). Assessing the contribution of the environment on each scale-specific spatial model through canonical redundancy

analysis (RDA, Legendre and Legendre 1998) can provide new insights into the relative importance of niche processes and other spatial processes on beta diversity (Fig. 1b–d), as will be shown from our temperate forest case study.

Materials and methods

Study area

The study site is located within the Station de biologie des Laurentides of Université de Montréal (SBL), Saint-Hippolyte, Québec, Canada (45°59’N, 73°59’W). Both the study site and study area have been described elsewhere in more detail (Paquette et al. 2007; Savage 2001). The bedrock is primarily composed of Precambrian anorthosite, and soils are ferro-humic podzols which formed in sandy loams derived from glacial till. The 30-year average annual precipitation is 1100 mm, 30% of which falls as snow, and the mean annual temperature is 3.6°C. Forest tree cover is primarily composed of *Acer saccharum* Marsh., *A. rubrum* L. and *Betula alleghaniensis* Britt., but pioneer species, such as *Populus grandidentata* Michx. and *B. papyrifera* Marsh., are also common. *Acer pensylvanicum* L. is an important sub-canopy tree. The disturbance regime has been characterized mostly by logging activities in the 19th and early 20th centuries as well as a major fire which occurred in the mid-1920s.

Vegetation sampling

Tree seedling abundances were measured from five permanent transects at the north-eastern tip of Lac Croche, separated by approximately 50 m (Paquette et al. 2007). Transects started at the edge of the lake and followed an elevation gradient. Along each of the five transects, seven to ten permanent 20 × 20-m (400 m²) plots were established approximately every 50 m. These plots are located within an area of approximately 9 ha. Within each plot, all mature trees [diameter at breast height (DBH) >10 cm] were identified and measured in 2005. For tree seedlings (DBH < 1 cm), ten 1-m² quadrats were established every 2 m in a row in the center of the plot, and all tree seedlings were counted by species every year (with the exception of 1999 and 2002). Data from those ten sub-quadrats were then pooled.

Environmental variables

A number of environmental variables were measured in each plot (Paquette et al. 2007). Slope (%) was measured with a clinometer. Slope microtopography was judged on a qualitative scale (concave, convex or flat). Percentage cover of surface rockiness (i.e. exposed bedrock and boulders) was evaluated on a semi-quantitative cover scale (1 ≤ 1%; 2 = 1–5%; 3 = 5–15%; 4 = 15–25%; 5 = 25–50%; 6 = 50–75%; 7 ≥ 75%). We measured the following soil variables: thickness of the organic (O) horizon, thickness of the upper layer of soil, nearest the surface (horizon A), presence of eluviation (E horizon) (Soil Survey Division Staff 1993) and maximum root depth. Canopy openness was estimated in August 2000 from hemispherical photographs taken in the middle of each plot at 1 m above the ground (Englund et al. 2000), which were analyzed with the Gap Light Analyzer (GLA) software (Frazer et al. 2000). The age of the largest tree in each plot was evaluated from cores taken in 1998 in order to have a general measure of the successional status of each plot and integrate potential historical effects (i.e. time since last major canopy disturbance) on the underlying environment. Finally, we measured the geographic coordinates and elevation of each plot with a differential global positioning system (GPS; Trimble Navigation, Sunnyvale, CA; estimated accuracy of 2 m).

Variations in soil chemistry at the watershed scale at SBL can be largely attributed to topography and drainage for the mineral horizons (F. Courchesne, personal communication), whereas for the organic horizons it is primarily controlled by historical events (e.g. fire, logging) and tree composition (Bélanger et al. 2004). Although soil chemistry was not measured, earlier pedological studies at SBL have shown that soil chemistry varied relatively little at the scale of our study (i.e. a few hectares). For instance, the

mean percentage coefficient of variation of physical and chemical properties of soil litter, organic and mineral horizons calculated from plots located in highly contrasted areas of the 5-ha Hermine watershed (1 km from our study site) was only 16.5% (Courchesne and Hendershot 1988; Courchesne et al. 2005). Despite this, we acknowledge that the absence of soil chemistry data is a limitation of the dataset.

Statistical analyses

Space–time interaction

In order to test the space–time interaction, we used canonical RDA as a form of multivariate analysis of variance (ANOVA) to test the relationship between a response matrix (species abundance data) and two crossed factors (Legendre and Anderson 1999). In this special case, space and time were the two factors. When coding for two crossed factors in a regression context, orthogonal dummy variables (Draper and Smith 1981), also called Helmert contrasts (Venables and Ripley 2002), can be used. Although it is possible to test the effect of space or time separately with this approach, the space–time interaction, in the no-replication case, cannot be tested in classical two-way ANOVA because no degrees of freedom are left for the denominator of the *F* statistic (P. Legendre et al., submitted). To circumvent this problem, an alternative is to use spatial and temporal PCNM variables (Borcard and Legendre 2002; Dray et al. 2006) to code for the space–time interaction (P. Legendre et al., submitted). With this approach, the main factors, space and time, are coded using Helmert contrasts, but the space–time interaction is modeled (although under-fitted) using variables that are the product of the first *s*/2 and *t*/2 spatial and temporal PCNM variables, respectively (where *s* is the number of sites and *t* the number of sampling times). Empirical simulations have shown that this model had correct Type I error and that its power was equal or greater than other possible ANOVA models (P. Legendre et al., submitted).

Our response matrix contained tree seedling abundances from 1998 to 2006 (except for 1999 and 2002, during which years tree seedlings were not sampled) from 40 permanent plots. Seedlings of 16 tree species were present in the plots, but only three species (*A. pensylvanicum*, *A. rubrum* and *A. saccharum*), which together accounted for more than 97% of total seedling abundance, were considered in our analyses. Seedling abundances were Hellinger-transformed so that the Hellinger distance—and not the Euclidean distance—was preserved in RDA (Legendre and Gallagher 2001). The use of the Hellinger distance effectively deals with the “species abundance paradox” associated with the Euclidean distance, where the distance

between two sites sharing no species can be smaller than that between two sites that share species (Legendre and Legendre 1998). Although no theoretical criteria exist for selecting a particular data transformation for a given situation, the Hellinger transformation is well-suited for canonical partitioning and multivariate (M)ANOVA-like RDA of species abundance data (Legendre and Gallagher 2001).

We used a mixed model in which space was considered to be a random factor and time fixed, and both factors and interaction were tested accordingly using RDA (Legendre and Anderson 1999). Space was considered random because we had no a priori reason for establishing transects at these specific locations, while time was considered fixed because we were interested in this specific time period, during which no major canopy disturbance occurred. When testing for the interaction, the main factors, space and time, were used together as covariables in the analysis. If the interaction is not significant, space and time can be tested by the usual test without replication. When the *P* value of the interaction test is close to 0.05, indicating a possible lack of power, it is recommended that the test of the main factors be duplicated using the interaction term as a covariable (P. Legendre et al., submitted). If the interaction is significant, the spatial structure should be modeled for each time period separately. Since there was a significant spatial linear trend in the data, two series of analyses were conducted: the first one on the original seedling abundances; the second on the detrended abundances.

Multi-scale spatial modeling

Spatial PCNM analyses were conducted to dissect the multi-scale spatial structures of tree seedling abundances. To generate the PCNM variables, we first calculated a geographical (i.e. Euclidean) distance matrix between plots. The truncation value *t* was the largest value in the minimum spanning tree linking the sites (Legendre and Legendre 1998), and the truncated connectivity matrix **W** was constructed following the procedure described in the [Rationale of the statistical approach](#) section (see also Dray et al. 2006). Twenty-six PCNM variables were obtained, which corresponded to the number of eigenvectors with positive eigenvalues (Borcard et al. 2004).

Seedling abundances were detrended because a significant linear trend was present, which indicated a spatial structure at a broader scale than the sampling extent (Borcard et al. 2004). This step is important because a large number of PCNM variables would be required to model a linear trend, which may obscure finer-scale spatial structures that are present in the data (Borcard et al. 2004). Forward selection ($\alpha = 0.10$) of all 26 spatial PCNM was then conducted. Fitted values were kept to model the spatial structures at multiple scales: broad scale (linear trend),

meso scale (selected from PCNM 1–12 for the 2005 data: PCNM 2, 5–9) and fine scale (selected from PCNM 13–26 for the 2005 data: PCNM 13–15, 22, 24, 25). It is important to note that our use of the terms “broad”, “meso” or “fine” scales have no absolute meaning, but are instead relative to the particular sampling design under study and constrained by its grain (i.e. resolution) and spatial extent (i.e. surface covered). To help visualize how these three spatial scales relate to each other in our study, we show the scale-specific spatial models of *A. rubrum*, the most abundant tree seedling species on our study site, in Fig. 2. Non-spatial variation was estimated from the residuals of the RDA involving forward-selected PCNM variables from detrended abundances. We also conducted spatial PCNM analyses on single-species abundances (*A. pensylvanicum*, *A. rubrum* and *A. saccharum*). In that case, abundances were first log-transformed to make their distributions more symmetrical.

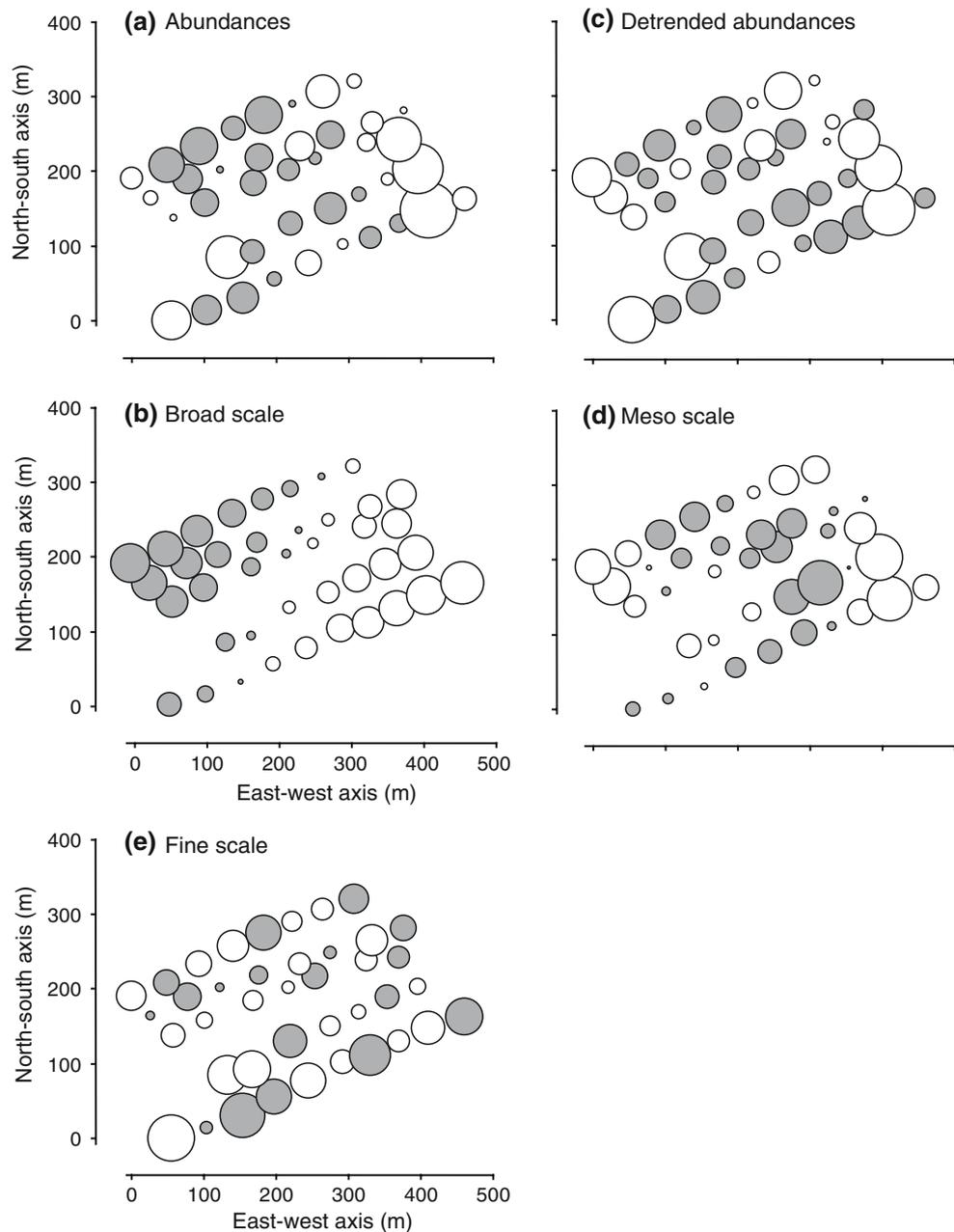
Variation partitioning

We assessed the relative weight of niche processes versus other spatial processes on multi-scale spatial patterns through partial RDA. We used the same set of environmental variables in all analyses, which were chosen by forward selection ($\alpha = 0.10$; only the variables that were selected for 2 years or more were retained). Eight out of ten environmental variables were selected (canopy openness; elevation; age of largest tree; surface rockiness; slope; slope microtopography; thickness of soil litter and humic layer; thickness of horizon A).

First, partial RDAs involving the three seedling species was used to partition the variation due to environment and space (geographic coordinates and the set of forward-selected PCNM variables, e.g. 12 PCNM variables for the 2005 data). The relative weight of each independent fraction was estimated following the methodology described by Peres-Neto et al. (2006). We then tested the effect of the environmental factors on four spatial models: the broad scale (linear trend), “finer scales” (PCNM model) and the meso-scale and fine-scale models (dissected from the “finer scales” model). The fitted values of each spatial model were used in these analyses. Finally, the effect of the environmental factors on the residual non-spatial variation was also tested.

Second, we conducted analyses on individual tree seedling species in which we incorporated the basal area of mature parent trees of the same species (DBH > 10 cm) as an additional explanatory variable in order to assess the potential influence of seed rain input on seedling abundance patterns, since dispersal limitation has often been identified as a key stochastic process. Seed rain was not directly measured in this study, but we assumed that a higher abundance of parent trees in a particular plot would lead to a higher seed rain in that plot. We partitioned the variation of

Fig. 2 Spatial patterns of *Acer rubrum* seedling abundances at different scales. Data from the 2005 census ($n = 40$) are shown and are centered on their mean. *Filled circles* positive values, *empty circles* negative values, *larger circles* larger absolute values. **a** Log-transformed seedling abundances, **b** “detrended abundances” corresponding to the residual variation after regression on geographic coordinates of the sites, **c** “broad scale” corresponding to a linear trend in seedling abundances. Other spatial models are calculated from detrended abundances, using different sets of PCNM variables: **d** meso (PCNM 2, 6, 7, 11), **e** fine (PCNM 17, 18, 21, 22, 24)



individual *Acer* seedling species spatial patterns (linear trend, meso scale and fine scale) between environmental variables and basal area of *Acer* trees. Again, the relative weight of each independent fraction was estimated (Peres-Neto et al. 2006).

The analyses were performed in the R-language environment (R Development Core Team 2007) using the packages “vegan” (Oksanen et al. 2007) for RDA, variation partitioning and Hellinger transformation of species abundances, “spacemaker” (Dray et al. 2006) for the construction of PCNM variables and “packfor” (Dray 2005) for the forward selection of explanatory variables in RDA. The

tests of the interaction of the main factors in the presence of the interaction were conducted using the R-language function “manovRDa”, which is provided as [Electronic Supplementary Material S1](#). This function allows one to test the effect of space, time and their interaction in one single step, with the choice of time and space being considered as fixed or random factors. The test of space and time without replication was conducted using the “rda” function of the “vegan” package. In all tests of significance, 9999 permutations were used. Following Anderson and Legendre (1999), permutation of the raw data is adequate for ANOVA since there are no outlier values in the factors.

Table 1 Effects of space, time and their interaction on tree seedling abundances

	Seedling abundances			Spatially detrended abundances		
	R^2	F^a	P	R^2	F^a	P
Source						
Space × time	–	1.2247	0.094	–	1.2248	0.0549
Interaction excluded in model						
Space	0.767	0.2832	0.0001*	0.449	0.0702	0.0001*
Time	0.025	0.0593	0.0001*	0.058	0.0593	0.0001*
Interaction included in model						
Space	0.767	23.7889	0.0001*	0.449	5.8930	0.0001*
Time	0.025	4.0635	0.0001*	0.058	4.0636	0.0001*

* Values are significant at $P \leq 0.05$

All tests were performed using 9999 permutations of the raw data

^a Pseudo- F

Results

The space–time interaction on trees seedling abundances was not significant ($P = 0.094$; Table 1). Even after controlling for the strong spatial linear trend in seedling abundances, the space–time interaction was still not significant ($P = 0.055$; Table 1), although it was very close to the usual $\alpha = 0.05$ level. We thus considered that the spatial patterns of abundance were stable though time and that the temporal variation was common to all sites. Tests of the main factors space and time showed that tree seedling abundances in this forest were strongly spatially structured ($P \leq 0.0001$) and also significantly varied in time ($P \leq 0.0001$; Table 1); this was true irrespective of the exclusion or inclusion of the interaction as covariable in the models (Table 1).

We then assessed the relative importance of niche processes and other spatial processes on the data for 2005 using variation partitioning (Fig. 3). Since spatial patterns were similar through time during the period 1998–2006, analyses performed on other years yielded highly similar results to the ones presented here. In the global analysis (Fig. 3, top pie chart), the proportion of variation in seedling abundances explained through space alone (“pure spatial” fraction) was 42%, sevenfold higher than the variation attributed to environment alone. The covariation between space and environment explained an additional 42% of the variation of tree seedling abundances. Unexplained residual variation accounted for only 10% of the variation of seedling abundances.

Spatial variation, either alone or in conjunction with the environment, accounted for 84% of the total variation of tree seedling abundances (Fig. 3, top pie chart). This spatial structure was primarily due to a highly significant ($P \leq 0.0001$) linear trend which explained 68% of the total variation in seedling abundances (Fig. 3, middle left pie chart). Even after removing the linear trend in seedling abundances, there remained a highly significant spatial structure in the detrended data (adjusted- R^2 , or $R_a^2 = 0.49$, $P \leq 0.0001$), which explained 16% of the total variation of

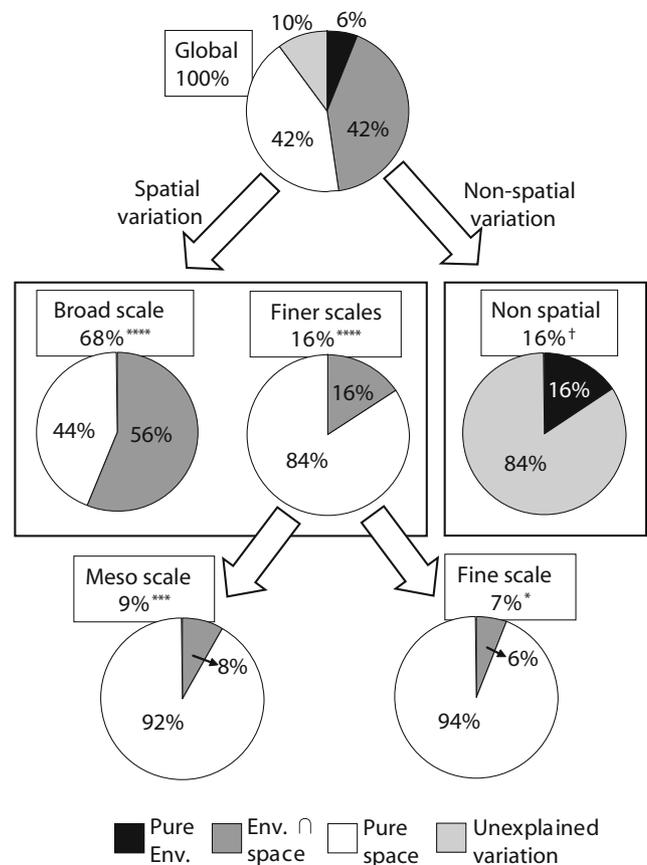


Fig. 3 Relative influence of environment (*Env.*) and space on tree seedling abundances at different scales, using the data from 2005. The importance of each spatial model is indicated by the percentage (calculated using R_a^2) above each chart (in boxes). The importance of each spatial (or non-spatial) model is given in boxes. The percentage variation corresponding to each fraction (R_a^2) is included in the pie charts. * $P \leq 0.05$, *** $P \leq 0.001$, **** $P \leq 0.0001$. † Cannot be tested

seedling abundances [calculated by multiplying the residual variation of the RDA after extracting the linear trend in seedling abundances with the R_a^2 of the RDA of the PCNM variables on the detrended abundances, i.e. $(1 - 0.68) \times 0.49 = 0.16$]. This spatial model corresponds to the “finer

scales” model found in the middle pie chart of the middle row in Fig. 3. This model was further dissected into two spatial models, meso (PCNM 2, 5–9) and fine scale (PCNM 13–15, 22, 24, 25), which respectively explained 9 and 7% of the total variation of seedling abundances (Fig. 3, bottom pie charts). Each of these scale-specific spatial models was significant ($P \leq 0.05$).

The analyses showed that the influence of spatially structured environmental variation on tree seedling beta diversity decreased from broad- to fine-spatial scales (Fig. 3). More than half ($R_a^2 = 0.56$, $P \leq 0.0001$) of the broad-scale spatial structure of seedling abundances was explained by the environment, whereas the PCNM spatial model (“finer scales” model, Fig. 3) was weakly, but significantly, influenced by the environment ($R_a^2 = 0.16$, $P = 0.0228$). Once this PCNM spatial model was further dissected, we found that the influence of the spatially structured environmental variation further decreased from the meso scale (8%) to the fine scale (6%) (Fig. 3).

A highly significant ($P \leq 0.0001$) RDA environmental model which explained 48% of the total variation of seedling abundances (corresponding to 42% spatially structured environmental variation + 6% non-spatial environmental variation in Fig. 3, top pie chart) showed that *A. pensylvanicum* and *A. saccharum* were more abundant at higher elevations and under denser canopies, while *A. rubrum* was more abundant at lower elevations and under sparser canopies (results not presented). Moreover, *A. pensylvanicum* and *A. saccharum* occurred in sites where deeper rooting was observed, and there was a trend for *A. pensylvanicum* to be more abundant in deeper soils with less surface stoniness. The broad-scale spatial model (i.e. linear gradient), which explained 68% of the total variation in seedling abundances (Fig. 3), was primarily explained by elevation, and secondarily by canopy openness and the age of the largest tree.

Analyses conducted on individual species showed that mature tree basal area (variable Tree in Fig. 4) was a poor predictor of seedling abundance patterns at all scales, except for *A. saccharum* at the broadest scale. The environmental variables explained a greater portion of the variation of the broad-scale spatial patterns than tree basal area for *A. pensylvanicum* and *A. rubrum* (Fig. 4). However, the covariation between environmental factors and parent tree basal area explained a large fraction of the *A. saccharum* spatial patterns at the broadest scale (Fig. 4) and, consequently, it was not possible to distinguish between the relative influences of mature trees and the environment in that case because of confounding. At finer spatial scales, both the environment and tree basal area weakly explained seedling spatial patterns (Fig. 4).

In addition, analyses conducted on individual species showed a similar scale-dependent influence of niche processes versus other spatial processes to what we had previ-

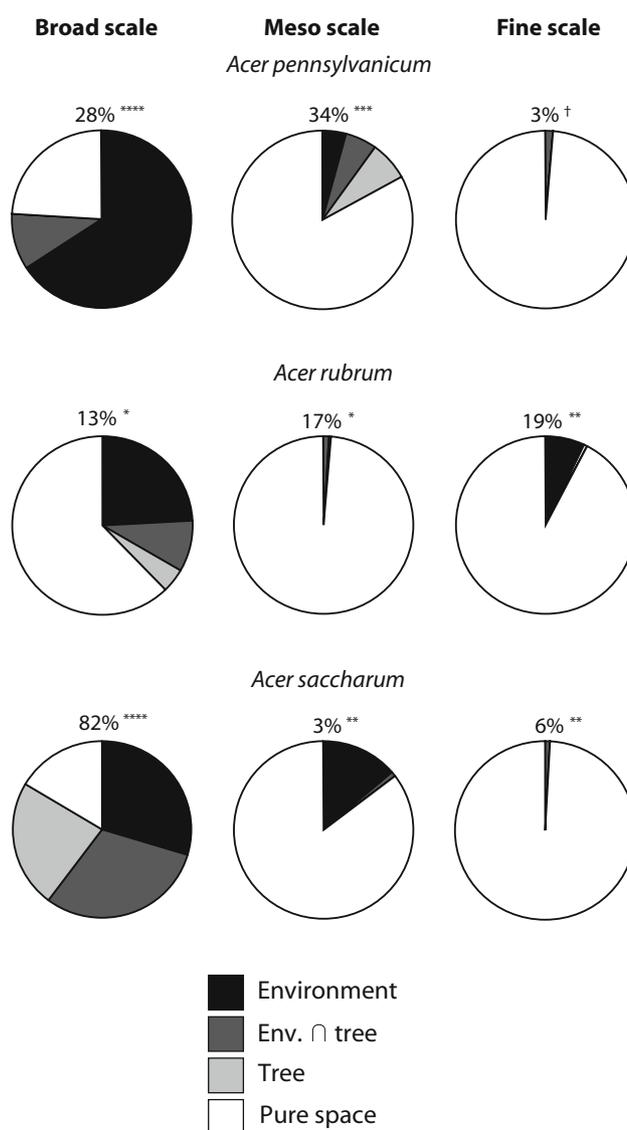


Fig. 4 Relative influence of environment (*Env.*) and tree (diameter at breast height > 10 cm) basal area (*Tree*) on spatial patterns of tree seedling abundance at different scales, using the data from 2005. Non-spatial variation is not shown. The importance of each spatial model (calculated using R_a^2) is given above each pie chart. † $P \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, **** $P \leq 0.0001$

ously shown (Fig. 4). They further indicated that this influence was species-specific (Fig. 4). For example, at the broadest scale, environmental factors strongly explained the *A. pensylvanicum* seedling spatial patterns, while they had a weaker effect on the *A. rubrum* seedling patterns (Fig. 4). Not all species showed similar spatial patterns, even though all were strongly spatially structured (40–92%). *Acer rubrum* showed a weaker spatial structure at the broadest scale than the other two species, but it was more strongly spatially structured at finer scales (Figs. 2, 4). Despite those differences, the progressively smaller influence of the environment from the broader to finer scales as

well as the increasing dominance of other spatial processes at finer scales were consistent across species.

Discussion

Because of the dominant contribution of a primarily environmentally controlled broad-scale spatial structure (mostly due to elevation), our results suggest that niche partitioning is the main process influencing tree seedling abundances in this temperate forest. While this general conclusion about the dominance of niche processes is consistent with those drawn from previous studies (Gilbert and Lechowicz 2004; Jones et al. 2006; Karst et al. 2005; Tuomisto et al. 2003), dissecting the spatial structure of community composition at different scales allowed us to see that environmental control could not account for the finer-scale spatial patterns of tree seedling abundances, which can be attributed to other spatial processes (e.g. dispersal).

We attribute the fine-scale spatial patterns of tree seedling abundances to other spatial processes because these spatial patterns showed little covariation with the underlying environment; however, the possibility that these fine-scale patterns may be partly due to unmeasured spatially structured environmental variables cannot be excluded. For example, the coexistence of *A. rubrum* and *A. saccharum* within a given area has been explained through spatial variation in soil chemistry, with *A. saccharum* outcompeting *A. rubrum* on more nutrient-rich and less acidic soils, and vice versa (Host et al. 1987; Nowacki et al. 1990). Unfortunately, soil chemistry data were not available for the dataset used here. While several of the environmental variables measured likely acted as surrogates for variation in soil chemistry within the study site at the broadest scale (i.e. linear trend), it is unclear whether those same environmental variables adequately represented variation in soil chemistry at the finest spatial scales. Consequently, we cannot disregard the possibility that our analyses may have underestimated the importance of niches in explaining the fine-scale spatial structures of tree seedling composition and abundance. This illustrates that the strength of the results obtained from our methodological approach greatly depends on the quality and relevance of the environmental variables used in the analyses and that conclusions must be weighted accordingly (see Jones et al. 2008 for more details).

Despite this limitation, our results support the hypothesis that environmental heterogeneity should be more important at broader scales, whereas the influence of other spatial processes, such as dispersal, should become increasingly stronger at finer spatial scales (e.g. Gilbert and Lechowicz 2004; Jones et al. 2006). However, the niche model has so far received stronger empirical support at various spatial scales

ranging from global to local (Gilbert and Lechowicz 2004; Jones et al. 2006; Karst et al. 2005; Tuomisto et al. 2003; Van der Gucht et al. 2007). The strategy used to compare the relative strength of niche processes and other spatial processes (often strictly referred to as “dispersal”) at different scales has simply been to compare the results from different sampling schemes (either from the same system or from different systems) conducted at distinct spatial scales (Cottenie 2005; Freestone and Inouye 2006; Jones et al. 2006; Karst et al. 2005; Van der Gucht et al. 2007). On the other hand, our statistical approach allowed us to dissect the spatial structure of a single region at multiple scales and assess the contributions of niche processes and other spatial processes at each of the identified scales, thereby opening new possibilities. Importantly, while several earlier studies have used trend surface polynomial regression to model space (Cottenie 2005; Gilbert and Lechowicz 2004; Karst et al. 2005; Van der Gucht et al. 2007), our approach is based on PCNM analysis, which is much more powerful for modeling the fine-scale spatial structures (Borcard and Legendre 2002) where dispersal and other biotic spatial processes are expected to become important.

Analyses conducted on individual species also revealed a progressively decreasing influence of the environment from broader to finer spatial scales. A good relationship between tree seedling and parent tree abundances may have been expected given that dispersal limitation has often been proposed as an important stochastic mechanism that influences community patterns (Chave and Leigh 2002), but our results showed that the abundance of parent trees was a rather poor predictor of tree seedling patterns at all scales. The fact that all three species are wind-dispersed (Burns and Honkala 1990) may have decreased the likelihood of finding strong covariation between the abundance of mature trees (which were generally around 15–20 m high) and tree seedling abundances over the 20 m × 20-m plot. Strong spatial uncoupling between seed rain and seedling recruitment patterns has often been observed in temperate forests for wind-dispersed species (e.g. *Acer* sp.) and is generally attributed to stochastic post-dispersal events (Houle 1992). Moreover, the lack of a relationship between the basal area of parent trees and seedling abundances likely arose from the fact that there is very high intraspecific variability in fecundity and dispersal in temperate tree species (Clark et al. 2004).

Still, there appeared to be relationships between spatial patterns and seed dispersal strategy. *Acer saccharum* and *A. pensylvanicum* both disperse their seeds after leaf shed in the fall when forest foliage density is at its lowest (Hibbs and Fischer 1979; Houle 1999), whereas *A. rubrum* disperses them in early summer when foliage density is high (Burns and Honkala 1990; Houle 1994). Low foliage density greatly increases dispersal efficiency and the likelihood

of long-distance dispersal events (Nathan and Katul 2005), which may explain why *A. saccharum* and *A. pensylvanicum* were structured at broader spatial scales than *A. rubrum*. Similar relationships between tree or sapling spatial patterns and dispersal mode have previously been shown for trees in temperate (Schwarz et al. 2003) and tropical forests (Seidler and Plotkin 2006).

Our results on species–environment relationships were consistent with earlier findings on the autecology of the tree species. For example, Hibbs et al. (1980) found that *A. pensylvanicum* increased in density with elevation in Massachusetts forests, something which we also observed. In addition, the strong dichotomy between *A. rubrum* and *A. saccharum* seedling abundances appeared to be linked to canopy openness and to the presence of large trees of the early-successional *P. grandidentata* in lower elevation sites (indicating past disturbances), where more *A. rubrum* seedlings were found. Indeed, *A. rubrum* is somewhat less tolerant to shade than *A. saccharum* (Ashton et al. 1999) and can be favored by forest disturbances (Abrams 1998).

We found that seedling abundances varied little through time, although this variation was significant. On the other hand, by using our methodology to test for the space–time interaction, we found that this temporal variation did not vary through space (i.e. non-significant space–time interaction). Given that *A. rubrum* and *A. saccharum* do not maintain permanent seed banks in the soil, that seedlings readily germinate after seed fall, but that the majority of these do not survive throughout the first season (Houle 1991; Houle 1994), the observed temporal variation of seedling abundances may be primarily linked to yearly variations in seed rain, which lead to brief increases in the 1-year-old transient seedling bank. However, because tree seedlings in the dataset were defined by size and not age, we cannot directly test this hypothesis.

We also found that tree seedling abundances were strongly spatially structured, but that about half of this spatial structure occurred in conjunction with environmental variables. Although this finding was not surprising given that the natural physical environment is typically spatially structured (Bell et al. 1993), this highlights a drawback of variation partitioning for such tests—i.e. that the strong covariation between environment and space found in nature makes it difficult to decisively discriminate between niche processes and other spatial processes (Bell et al. 2006; Gilbert and Lechowicz 2004). At meso to very broad scales, it is possible to reduce this covariation through a study design that decouples environmental and geographical distances (e.g. Gilbert and Lechowicz 2004), but at more local scales (e.g. less than a few hectares), such an approach is not feasible because of the inherently strong spatial autocorrelation of the physical environment (Karst et al. 2005).

Consequently, the strength of our methodological approach was to dissect the spatial structure of species abundances into additive scale-specific models with PCNM analysis and to test the influence of the environment at each of these scales. This brought new insights on the relative importance of niche processes and other spatial processes that control tree seedling beta diversity in this forest, allowing us to go beyond the simple observation of a strong environment-to-space correlation in variation partitioning analyses. While an evenly distributed contribution of the environment across spatial scales would have brought no further information, the strong uneven cross-scale contribution of the environment suggested that the relative weight of niche processes and other spatial processes may be scale-dependent. The results obtained from our case study suggested that tree seedling abundances were primarily controlled by a broad-scale environmental gradient (largely due to elevation), but that within the confines of this gradient the finer scale patchiness could be due to other spatial processes (e.g. tree fecundity, dispersal, herbivory). It must be noted that, as with all types of spatial analyses, our results are constrained by the grain (i.e. resolution) of the sampling design since no spatial structures at scales finer than the grain size can possibly be modeled.

Our use of PCNM analysis yields new perspectives to disentangle the importance of niche processes and other spatial processes that control beta diversity. Because they are orthogonal to each other, PCNM variables can be used instead of dummy variables to model for the space–time interaction in MANOVA-like RDA (Legendre and Anderson 1999; P. Legendre et al., submitted). A significant space–time interaction indicates that spatial patterns varied through time and suggests that the importance of the underlying processes may have varied as well, thus prompting further analyses conducted at different times. In a given ecosystem, it is possible that spatial patterns would be primarily structured by the environment during some time intervals, while other spatial processes would be dominant in others. All of these predictions can be tested with the combined use of canonical variation partitioning and PCNM analysis. Importantly, PCNM analysis brings new insight into the scale-specific influence of niche processes and other spatial processes on beta diversity by looking at the cross-scale distribution of the influence of environmental variables on community composition.

Because our methodological approach relies on PCNM analysis, it is best suited to sampling designs where the spatial and temporal coverage of the geographical surface and time period sampled, respectively, is not too irregular (Borcard and Legendre 2002). While somewhat irregularly sampled data can still be analyzed with our approach (as shown in our tree seedling case study, where the spatial coverage

is not perfectly regular, and where some years were missing), strongly irregular data would yield individual PCNM variables which would show spatial (or temporal) structures at several scales, thus complicating interpretation (Borcard and Legendre 2002). In addition, large gaps in the spatial coverage of the geographical surface would yield fewer fine-scale PCNM variables, thus limiting the strength of our approach.

In conclusion, dissecting the spatial structure of tree seedling abundance at different spatial scales allowed us to find that tree diversity in this forest may be primarily maintained through niche partitioning at broader spatial scales, while other spatial processes may allow the coexistence of functionally similar species at finer scales. Because the environmental variables used in our case study were somewhat limited, the value of our study primarily lies in illustrating how our method can be used and the type of results it can yield—and not necessarily in the nature of the results obtained per se. Despite this limitation, our results support the view that niche processes and other spatial processes are not mutually exclusive but, rather, contribute differently depending on spatial scales. More importantly, our study provides researchers with an appropriate statistical methodology to estimate the scale-specific importance of environmental and spatial factors on beta diversity. Given the fundamental nature of this question, our methodological approach should be of great practical value for future tests. Such future tests will be crucial for the merging of niche and neutral perspectives, an obvious next step for community ecology.

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References

- Abrams MD (1998) The red maple paradox: what explains the widespread expansion of red maple in eastern forests? *BioScience* 48:355–364
- Anderson MJ, Legendre P (1999) An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *J Stat Comput Simul* 62:271–303
- Ashton PMS, Yoon H, Rajesh T, Berlyn GP (1999) Seedling leaf structure of New England maples (*Acer*) in relation to light environment. *For Sci* 45:512–519
- Barot S, Gignoux J (2004) Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos* 106:185–192
- Bélanger N, Côté B, Fyles JW, Courchesne F, Hendershot WH (2004) Forest regrowth as the controlling factor of soil nutrient availability 75 years after fire in a deciduous forest of Southern Quebec. *Plant Soil* 262:363–372
- Bell G, Lechowicz MJ, Appenzeller A, Chandler M, Deblois B, Jackson L, Mackenzie B, Preziosi R, Schallenberg M, Tinker N (1993) The spatial structure of the physical environment. *Oecologia* 96:114–121
- Bell G, Lechowicz MJ, Waterway MJ (2006) The comparative evidence relating to functional and neutral interpretations of biological communities. *Ecology* 87:1378–1386
- Borcard D, Legendre P (1994) Environmental control and spatial structure in ecological communities: an example using Oribatid mites (*Acari*, *Oribatei*). *Environ Ecol Stat* 1:37–61
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Modell* 153:51–68
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Burns RM, Honkala BH (1990) *Silvics of North America*, vol 2: hardwoods. USDA Agricultural Handbook No. 654. U.S. Department of Agriculture, Washington DC
- Chave J, Leigh EG (2002) A spatially explicit neutral model of beta-diversity in tropical forests. *Theor Popul Biol* 62:153–168
- Clark JS, LaDeau S, Ibanez I (2004) Fecundity of trees and the colonization-competition hypothesis. *Ecol Monogr* 74:415–442
- Cottenie K (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett* 8:1175–1182
- Courchesne F, Côté B, Fyles JW, Hendershot WH, Biron PM, Roy AG, Turmelet M-C (2005) Recent changes in soil chemistry in a forested ecosystem of southern Québec, Canada. *Soil Sci Soc Am J* 69:1298–1313
- Courchesne F, Hendershot WH (1988) Cycle annuel des éléments nutritifs dans un bassin-versant forestier: contribution de la litière fraîche. *Can J For Res* 18:930–936
- Currie DJ (2007) Disentangling the roles of environment and space in ecology. *J Biogeogr* 34:2009–2011
- Draper NR, Smith H (1981) *Applied regression analysis*. Wiley, New York
- Dray S (2005) packfor: forward selection with multivariate Y by permutation under reduced model. Laboratoire Biométrie et Biologie Évolutive, Lyon. Available at: <http://biomserv.univ-lyon1.fr/~dray/software.php>
- Dray S, Legendre P, Peres-Neto P (2006) Spatial modeling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). *Ecol Modell* 196:483–493
- Englund SR, O'Brien JJ, Clark DB (2000) Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Can J For Res* 30:1999–2005
- Frazer GW, Canham CD, Lerstanz KP (2000) Gap light analyzer version 2.0. *Bull Ecol Soc Am* 81:191–197
- Freestone AL, Inouye BD (2006) Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology* 87:2425–2432
- Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. *Proc Natl Acad Sci USA* 101:7651–7656
- Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87:2603–2613

- Hibbs DE, Fischer BC (1979) Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). *Bull Torrey Bot Club* 106:222–227
- Hibbs DE, Wilson BF, Fischer BC (1980) Habitat requirements and growth of striped maple (*Acer pensylvanicum* L.). *Ecology* 61:490–496
- Holyoak M, Loreau M (2006) Reconciling empirical ecology with neutral community models. *Ecology* 87:1370–1377
- Host GE, Pregitzer KS, Ramm DW, Hart JB, Cleland DT (1987) Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern lower Michigan. *For Sci* 33:445–457
- Houle G (1991) Regenerative traits of tree species in a deciduous forest of northeastern North America. *Holarctic Ecol* 14:142–151
- Houle G (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *J Ecol* 80:99–108
- Houle G (1994) Spatiotemporal patterns in the components of regeneration of four sympatric tree species—*Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. *J Ecol* 82:39–53
- Houle G (1999) Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *J Ecol* 87:413–422
- Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton
- Hubbell SP, Foster RB, O'Brian ST, Harms KE, Condit R et al (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557
- John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF et al (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proc Natl Acad Sci USA* 104:864–869
- Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC (2008) Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. *Oecologia* 155:593–604
- Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of meso-scale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J Ecol* 94:181–195
- Karst J, Gilbert B, Lechowicz MJ (2005) Fern community assembly: the roles of chance and the environment at local and intermediate scales. *Ecology* 86:2473–2486
- Legendre L, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- Legendre P, Borcard D, Peres-Neto P (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450
- Legendre P, Legendre L (1998) *Numerical ecology*, 2nd English edn. Elsevier, Amsterdam
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Nathan R, Katul GG (2005) Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *Proc Natl Acad Sci USA* 102:8251–8256
- Nowacki GJ, Arbams MD, Lorimer CG (1990) Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. *For Sci* 36:276–292
- Oksanen J, Kindt R, Legendre P, O'Hara B (2007) *vegan: community ecology package*, version 1.8-5. Available at: <http://cran.r-project.org/>
- Paquette A, Laliberté E, Bouchard A, de Blois S, Legendre P, Brisson J (2007) Lac Croche understory vegetation data set (1998–2006). *Ecology* 88:3209
- Peres-Neto P, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- R Development Core Team (2007) *R: a language and environment for statistical computing*, version 2.3.1. R Foundation for Statistical Computing, Vienna. Available at: <http://www.r-project.org/>
- Ricklefs RE, Schluter D (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago
- Savage C (2001) *Recolonisation forestière dans les Basses Laurentides au sud du domaine climacique de l'érablière à bouleau jaune*. MSc thesis. Département de sciences biologiques, Université de Montréal, Montréal
- Schwarz PA, Fahey TJ, McCulloch CE (2003) Factors controlling spatial variation of tree species abundance in a forested landscape. *Ecology* 84:1862–1878
- Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol* 4:1–6
- Soil Survey Division Staff (1993) *Soil survey manual*. Soil Conservation Service, United States Department of Agriculture (USDA), Washington DC
- Soininen J, Lennon JJ, Hillebrand H (2007) A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88:2830–2838
- Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* 299:241–244
- Van der Gucht K, Cottenie K, Muylaert K, Vloemans N, Cousin S et al (2007) The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proc Natl Acad Sci USA* 104:20404–20409
- Venables WN, Ripley BD (2002) *Modern applied statistics with S*, 4th edn. Springer, New York
- Wiens JA, Addicott JF, Case TJ, Diamond J (1986) Overview: the importance of spatial and temporal scale in ecological investigations. In: Diamond J, Case TJ (eds) *Community ecology*. Harper & Row, New York, pp 145–153