PARTITIONING THE FACTORS OF SPATIAL VARIATION IN REGENERATION DENSITY OF SHADE-TOLERANT TREE SPECIES

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Abstract. Understanding coexistence of highly shade-tolerant tree species is a long-standing challenge for forest ecologists. A conceptual model for the coexistence of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) has been proposed, based on a low-light survival/high-light growth trade-off, which interacts with soil fertility and small-scale spatiotemporal variation in the environment. In this study, we first tested whether the spatial distribution of seedlings and saplings can be predicted by the spatiotemporal variability of light availability and soil fertility, and second, the manner in which the process of environmental filtering changes with regeneration size. We evaluate the support for this hypothesis relative to the one for a neutral model, i.e., for seed rain density predicted from the distribution of adult trees. To do so, we performed intensive sampling over 86 quadrats (5 × 5 m) in a 0.24-ha plot in a mature maple–beech community in Quebec, Canada. Maple and beech abundance, soil characteristics, light availability, and growth history (used as a proxy for spatiotemporal variation in light availability) were finely measured to model variation in sapling composition across different size classes. Results indicate that the variables selected to model species distribution do effectively change with size, but not as predicted by the conceptual model. Our results show that variability in the environment is not sufficient to differentiate these species' distributions in space. Although species differ in their spatial distribution in the small size classes, they tend to correlate at the larger size class in which recruitment occurs. Overall, the results are not supportive of a model of coexistence based on small-scale variations in the environment. We propose that, at the scale of a local stand, the lack of fit of the model could result from the high similarity of species in the range of environmental conditions encountered, and we suggest that coexistence would be stable only at larger spatial scales at which variability in the environment is greater.

Key words: Acer saccharum; *American beech; coexistence; environmental heterogeneity;* Fagus grandifolia; *Quebec, Canada; sapling dynamics; spatial structure; sugar maple.*

INTRODUCTION

Understanding coexistence of highly shade-tolerant tree species is a long-standing challenge for forest ecologists. While pioneer species clearly exhibit differentiated life-history traits, shade-tolerant species tend to share common attributes, such as low mortality and growth rates, limited response to increase of light availability, and low dispersal rates (Rees et al. 2001). Some theoretical evidence (Chesson 2000a) suggests that only a limited amount of niche differentiation would be necessary to compensate for small competitive inequalities among shade-tolerant trees. There is a long list of life-history strategies allowing such differentiation, including negative density dependence (the Janzen-Connell effect; see a review by Wright [2002]), the regeneration niche (Grubb 1977), the presence of a

differentiated response to canopy gaps (Pacala et al. 1996), and the competition–colonization trade-off (Tilman 1994). Others would argue that when species are so similar in their life-history strategies, demographic stochasticity would dominate the dynamics (Hubbell 2001) and that the slow turnover rate of forest communities would favor transient coexistence (Woods 2007).

The dynamics of sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) communities is a simple and well-studied system that can be useful in improving our understanding of coexistence in highly shade-tolerant species (e.g., Forcier 1975, Woods 1979, Poulson and Platt 1996). The dynamics of this community type are similar to those observed in other systems around the world (e.g., Yamamoto 1989, Lertzman 1992, Lusk and Smith 1998, Russo et al. 2005). A conceptual model of coexistence for these two species was proposed by Forcier (1975) and further developed by Canham (1989), Poulson and Platt (1996), and Arii and Lechowicz (2002). The model predicts that species relative abundance will vary along the micro-succession initiated by a canopy gap (Forcier 1975), as

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well as with canopy gap history (Poulson and Platt 1996).

Sugar maple and American beech can both survive long periods of suppressed growth (Canham 1990). American beech, however, is slightly more tolerant of shade because of higher survival and growth under low-light conditions (Canham 1989, Kobe 1996). Sugar maple is usually thought to grow faster than beech in high-light conditions (Canham 1989, 1990, Poulson and Platt 1996, McClure et al. 2000), but there is evidence to the contrary (Pacala et al. 1994, Beaudet and Messier 1998, Beaudet et al. 2007a). Variation in species relative abundance is thought to be affected further by an interaction between survival and soil properties (Arii and Lechowicz 2002, Kobe et al. 2002). Soil fertility influences the shade tolerance of maple and beech; the former species has lower survival on soils with low calcium availability (Kobe 1996), while the survival of the latter is more greatly affected by low soil moisture (Caspersen and Kobe 2001). Spatial heterogeneity in soil characteristics, arising from both natural variability in mineral content (van Breemen et al. 1997) and soil–plant interactions (Dijkstra et al. 2001), is believed to further contribute to the coexistence of these species by allowing them to differentiate in space (Finzi et al. 1998, Arii and Lechowicz 2002).

The conceptual model of coexistence described here needs to be validated. Significant statistical differentiation between species in the response to the environment supports the idea of niche differentiation, but it is not evidence that it promotes their coexistence. One approach to testing the model is to assess how small-scale variations in the environment contribute to the variability in species distribution. It is particularly important to conduct such an analysis at the local scale (e.g., ~25–40 m^2, the approximate area covered by the crown of a mature tree), with the corresponding range of environmental conditions, to determine whether such a range of variation is sufficient to allow coexistence of the species in a forest community. Numerous observational studies have been conducted at larger spatial scales (e.g., Woods 2000, Arii and Lechowicz 2002; D. Gravel, M. Beaudet, and C. Messier, *unpublished manuscript*), where environmental gradients could be strong, but these scales do not match the one at which competitive interactions occur.

The objective of this study is to test whether environmental characteristics (light and soil properties) are good predictors of small-scale spatial variation in the relative abundance of sugar maple and beech seedlings and saplings in a forest community, as suggested by the aforementioned coexistence model. If this is so, it would confirm the necessary factors needed for the spatial storage effect (Chesson 2000b) to apply in this community. A first prediction of the model is that, globally, the spatial distribution of seedlings and saplings can be predicted by small-scale variation in light availability and soil fertility. The null hypothesis is that of a neutral model (Hubbell 2001) in which seedling and sapling spatial distribution is the result of dispersal limitations only (Gotelli and McGill 2006). However, since the impact of environmental limitation on spatial distribution is expected to increase over time, a second prediction is that new-year seedling distribution will be mostly neutral (dispersal limited), while the relationship between the spatial distribution of the species and the environment will increase in strength with plant size. In order to test these predictions, we performed a detailed sampling over a grid of 25 m^2 quadrats in a 0.24-ha plot representative of a mature sugar maple–beech community. We measured soil characteristics and current light levels, used the radial growth history of understory saplings to estimate the light conditions that prevailed in the recent decades, and modeled the expected seed rain from the spatial distribution of adult trees. These variables were used to model the seedling and sapling spatial distribution in different size classes.

METHODOLOGY

Study site

The study site is located at the Duchesnay forest station (46°70′–47°00′ N, 71°35′–71°45′ W), 50 km northwest of Quebec City, Quebec, Canada. The vegetation is dominated by mature deciduous forest with patches of mixed and coniferous forests. Mean annual temperature is 3.4°C, and mean annual precipitation is 1300 mm (Houle et al. 1997). A mature forest stand was selected as being representative of conditions under which sugar maple–beech communities are found in the region. The stand is located at mid-slope on a thick glacial till deposit that is well- to moderately well-drained. The location of the sampling plot was arbitrarily chosen to provide sufficient within-plot heterogeneity in microtopography to assure spatial variation in soil properties. The canopy (trees >9 cm at dbh, measured at 1.3 m above the ground surface) is dominated by sugar maple (56% of basal area), American beech (27%), and *Betula alleghaniensis* Britton (16%), with the presence of *Acer rubrum* L., *A. pensylvanicum* L., *Tsuga canadensis* (L.) Carr., *Abies balsamea* (L.) Mill., and *Picea rubens* Sarg. in the stand surrounding the plot.

Vegetation and physicochemical properties characterizing the plot have been summarized in Table 1. Among these properties, sugar maple and beech overstory basal areas were the most variable, while soil pH and base saturation were the least variable (as indicated by their respective coefficients of variation; Table 1). Although not reported in Table 1, total basal area across the plot was 24.9 m^2/ha, and the largest dbh that we recorded was 71.1 cm. The most common herbaceous and shrub species were *Lycopodium lucidulum* Michx., *Dryopteris spinulosa* (O. F. Mueller) Watt, *Streptopus roseus* Michx., *Trillium erectum* L., *Oxalis montana* L., *Clintonia borealis* Aiton (Raf.), and *Taxus canadensis* Marsh. Signs of beech bark disease were present, but at

TABLE 1. Summary information for the study site located at the Duchesnay forest station, 50 km northwest of Quebec City, Quebec, Canada.

Variable	Mean	CV (%)	Minimum	Maximum
Sapling (1.1–9.0 cm dbh) density (stems/ha)				
Sugar maple (*Acer saccharum*)	1990.7	113.71	0	10 400
Beech (*Fagus grandifolia*)	5107.0	45.49	800	13 200
Overstory basal area (m²/ha)				
Sugar maple	15.5	168.82	0	117.6
Beech	7.5	257.50	0	89.6
Sapling radial growth (mm/yr)				
1980–1984	0.48	47.56	0.10	1.49
1985–1989	0.66	50.78	0.08	1.64
1990–1994	0.84	57.73	0.09	2.16
1995–1999	1.04	54.93	0.02	2.87
2000–2004	0.98	55.42	0.08	2.50
Light availability (% PPFD)				
1 m height	1.7	77.56	0.3	7.6
4 m height	4.2	68.96	0.5	14.5
Soil properties				
pH	3.34	5.97	2.91	3.73
Exchangeable acidity (cmol⁺/kg)	3.00	31.43	1.29	5.60
Calcium (cmol⁺/kg)	0.41	51.38	0.08	1.25
Potassium (cmol⁺/kg)	0.15	73.05	0.04	0.93
Magnesium (cmol⁺/kg)	0.12	44.67	0.04	0.45
Cation exchange capacity (cmol⁺/kg)	3.72	30.78	1.63	6.73
Base cation saturation (%)	19.27	26.74	7.06	37.84

Notes: Data are from the 30 × 80 m subplot containing 86 5 × 5 m quadrats. "PPFD" stands for photosynthetic photon flux density.

the time of the study the disease appeared to have had no visible effect on the survival of beech in this forest. The stand might have been subjected to partial harvest prior to the 1950s, as were most stands in the region, but there was no evidence of more recent disturbance on the site. Furthermore, understory saplings of maple and beech between 100 and 200 years old were found at this site (D. Gravel, *personal observation*).

Field sampling

Spatial coordinates, dbh, and species identity were recorded for every tree with dbh > 4 cm in a 75 × 125 m plot. A more intensive sampling was conducted in a 30 × 80 m subplot (0.24 ha) centered on the main plot, which was further divided into a grid of 5 × 5 m quadrats. In each quadrat, we recorded every sapling of sugar maple and beech between 1 m height and 4.0 cm dbh. The density of new-year seedlings (with cotyledons) was determined in a 1-m² subplot at the center of each quadrat. The density of seedlings up to 1 m height was measured in a 2 m radius (12.57 m²) subplot centered on the quadrat. Light availability was determined at the center of each quadrat, at 1 and 4 m above the ground by measuring the photosynthetic photon flux density (PPFD) with a light sensor (LI-190SA point quantum sensor, LI-COR, Lincoln, Nebraska, USA); these data were expressed as the percentage of PPFD measured simultaneously with a sensor located in a open area <250 m from the study site. Measurements were taken under cloudy sky conditions, following the method of

Parent and Messier (1996). Sapling radial growth history was used as a rough proxy for past light availability. This approach has been used successfully for these species at the regional scale (D. Gravel, M. Beaudet, and C. Messier, *unpublished manuscript*). A stem disk of a sapling between 2 and 4 cm at dbh was sampled at 20 cm above the forest floor on one sapling per quadrat. Beech saplings were preferred because their rings are easier to read and have fewer ring anomalies; otherwise, we used sugar maple. The selected sapling was the closest to the center of the quadrat. One soil sample was taken at the center of each quadrat and combined with three other samples taken at 1 m from the center of the quadrat. Soil was sampled in the first 5 cm of the B horizon because this horizon is less sensitive to the composition of the litter and better reflects long-term properties of soil fertility (Brady and Weil 2002).

Laboratory analysis

Sapling stem disks were air-dried and sanded. Annual growth over the last 25 years was measured to a precision of 0.001 mm under 40× magnification with an electronic micrometer (Velmex, Bloomfield, New York, USA) coupled with a digital meter (Acurite III, Jamestown, New York, USA). Annual increments were measured along one radius per disk, located at 30° from the longest radius. Visual examination of the disks was done prior to measurements on at least two additional radii in which annual rings were clearly readable to identify partial and false rings.

The soil samples were air-dried and sieved (2-mm mesh) prior to analysis. Soil pH was measured electrometrically (10 g soil in 20 mL 0.01 mol/L $CaCl_2$). Exchangeable cations were extracted from 10 g soil with unbuffered (100 mL) aqueous 0.1 mol/L $BaCl_2$ + 0.1 mol/L NH_4Cl (Amacher et al. 1990). Cations were measured by inductively coupled plasma emission spectroscopy.

Statistical analysis

The abundance of sugar maple and beech seedlings and saplings in the quadrats was modeled as a function of environmental characteristics (light and soil properties) and dispersal limitations, the latter by taking into account the spatial distribution of adult trees as potential seed sources. The partitioning of the variance between the "environmental" and "dispersal limitations" groups of variables allowed us to assess their relative contributions to the spatial distribution of the regeneration instead of a formal test of hypotheses opposing the niche and neutral perspectives (Gravel et al. 2006). The residuals of this model were then analyzed to determine whether some important, spatially structured environmental variables might have been missing from our analysis.

Species abundance per size class was modeled with redundancy analysis (RDA), the multivariate extension of multiple regression analysis (Legendre and Legendre 1998). Redundancy analysis is a constrained ordination method that models the structure of the community while accounting for a set of explanatory variables. It first models each species distribution with respect to the explanatory variables and then performs the ordination for all species in the community with respect to the modeled relationships with the environment. Size classes were: A, new-year seedlings; B, 0–30 cm in height; C, 31–100 cm height; D, height > 1 m and dbh < 4 cm; and E, 4 cm < dbh < 9 cm. Abundance data (number of stems per quadrat) were first square-root transformed and then standardized per species/size class to assure equal weights between classes and species. The matrix of explanatory variables consisted of cation availability (Ca, Mg, Na, H, Al, K), pH, PPFD at 1 and 4 m, the mean radial growth per five-year period from 1980 to 2004, and the predicted seed rain. Variables describing microtopography (slope on x and y axes of the plot, elevation in meters relative to the lowest point of the 30 × 80 m subplot) were also included in the matrix of predictors (even if they are not variables that played a role in the conceptual model) to account for potential impacts of variation in local drainage and, therefore, to reduce residual error. Analysis was conducted first by selecting variables in a forward procedure using an alpha level of 0.1, while the test of significance for the whole-model analysis was performed with an alpha level of 0.05. Statistical significance was assessed by comparison of the initial F statistic to the distribution of F values obtained after 9999 permutations of the abundance matrix. We also performed a non-constrained ordination (principal component analysis [PCA]) of the species/size classes to compare with the results obtained with the RDA ordination. This comparison was done to understand the manner in which the environmental variables included in the analysis contributed to the resulting patterns observed in the ordination with the RDA.

A common approach to account for the presence of spatial structure in either the modeled or the explanatory variables is to use partial RDA, treating space as a covariate (Borcard et al. 1992). However, this technique commonly results in a large fraction of the variance being explained by both the environmental and spatial variables. This is likely to happen when the environmental variables are themselves strongly spatially structured. Moreover, this technique complicates the interpretation of space as an explanatory variable since space in itself does not relate to any biological hypothesis. Instead, dispersal limitation was quantified in RDA using the predicted seed rain, obtained from the dispersal kernel and parameters in Ribbens et al. (1994). We did not expect this variable would have a good fit with the distribution of larger saplings because the latter established many years prior to sampling and the actual distribution and dbh of adult trees at the time of sampling might not be representative of the ones at the time of sapling establishment. The predicted seed rain was nevertheless necessary to take into account to model the seedling distribution in relation to environmental variables. The seed rain in each quadrat was thus predicted using the spatial distribution and dbh of all sugar maple and beech trees >9.1 cm dbh in the 75 × 125 m plot. A Weibull dispersal kernel with $\theta = 2$ was used, and the mean dispersal distances for sugar maple and beech were, respectively, 8 and 6 m, based on Ribbens et al. (1994). Results were not sensitive to variation in mean dispersal distance from 5 to 10 m. The predicted seed rains were scale-transformed between 0 and 1 to provide unitless variables reflecting the degree of dispersal limitations in the plot (0, maximal dispersal limitation; 1, minimal dispersal limitation). We did not control for the seedbed type in the model since sugar maple and beech are large-seeded species with low substrate limitations (Caspersen and Saprunoff 2005). The origin of beech seedlings and saplings (seed vs. root sprouts) was not determined because root sprouts were rare at the site (D. Gravel, *personal observation*). Residuals of the RDAs were finally analyzed with the principal coordinates of neighbor matrices (PCNM) method (Borcard and Legendre 2002). The PCNM analysis describes the spatial structure in a manner similar to that of spectral analysis, by quantifying the variability in community composition at all spatial scales. It first creates a set of explanatory variables that correspond to the different spatial scales of the sampling design and then analyzes how the data respond to these.

TABLE 2. Summary of redundancy analysis (RDA) in which variation in the abundance of sugar maple and American beech in various size classes was modeled as a function of a suite of environmental variables.

	Analysis with environmental variables and predicted seed rain				Analysis with PCNM variables applied to the residuals			
Size class	R^2	Adjusted R^2	P	N variables	R^2	Adjusted R^2	P	N variables
All	0.349	0.262	<0.001	10	0.233	0.143	<0.001	8
A, new-year seedlings	0.479	0.409	<0.001	10	0.318	0.226	<0.001	10
B, height 0–30 cm	0.443	0.416	<0.001	4	0.241	0.173	<0.001	7
C, height 31–100 cm	0.327	0.285	<0.001	5	0.341	0.272	<0.001	8
D, height > 1 m and dbh < 4.0 cm	0.191	0.151	<0.001	4	0.683	0.579	<0.001	22
E, 4.0 cm < dbh < 9.0 cm	0.181	0.151	<0.001	3	0.489	0.397	<0.001	14

Notes: See Table 3 for a list of the selected variables. The principal coordinates of neighbor matrices (PCNM) variables quantify the amount of spatial variability in the residuals.

The PCNM variables were also selected by a forward procedure at $\alpha = 0.1$.

Results

When all size classes were included in the RDA model, 26.2% of the variance (adjusted R^2, $P < 0.001$) was explained by 10 variables (Tables 2 and 3). The locations of quadrats (points) were well dispersed across the ordination space produced by RDA (Fig. 1); there were no apparent groups of quadrats or outliers driving the model. Sugar maple in size classes B–D and beech in class B were positively correlated. Their abundance was positively related to light availability at 1 m and to the seed rain of beech, but negatively related to soil pH, sapling growth during the 1990–1994 interval, and sugar maple seed rain. This group of species/size classes was orthonormal (uncorrelated) to a second group composed of beech in size classes A, C, and D. The PCA was also conducted for the standardized abundance data for the larger plot with the full description of the vegetation (200 quadrats). The results (not shown) were the same as for the RDA, with the small size classes orthonormal between species and the largest class strongly correlated between species. The abundance of beech in size classes A, C, and D was positively related to elevation and exchangeable acidity, but negatively related to growth

during the 2000–2004 interval and soil pH. The relationship of density with the predicted seed rain was weak for both species in all size classes, including the smallest. Finally, stems of both species in the largest size class (E) were found together in the ordination space and their abundance was positively related to growth during the 1990–1994 interval, seed rain of sugar maple, and soil pH. These species/size classes were also negatively related to the group that included sugar maple of size classes B–D and beech in size class B.

Overall, the relationship between each species/size class abundance and the selected environmental variables was weak for most variables (see Fig. 2 for an example with size class C). In some cases (e.g., Fig. 2D), the relationship could be related to a skewed data frequency distribution. In other cases, the relationship that was observed was opposite to that predicted (e.g., sugar maple abundance was negatively related to predicted seed rain in Fig. 2C). This suggests the presence of some spurious correlations. An example of such a case was the selection of previous year's growth as a predictor of the abundance of newly germinated seedlings (Table 3).

The fraction of variance explained by the model decreased with increasing size class (Table 2). There was no relationship between size class and the residual

TABLE 3. Environmental variables selected by the forward procedure in the redundancy analysis (RDA; at $P < 0.1$), sorted by P values that entered into the model.

Order of entry in the model	Size class					
	All	A	B	C	D	E
1	Seeds SM	Seeds SM	PPFD 1 m	Seeds SM	Growth 1990	Growth 1990
2	Growth 1990	Growth 2000	Seeds SM	PPFD 4 m	Exch. H + Al	Seeds SM
3	PPFD 1 m	Slope y	Growth 1990	Elevation	pH	Growth 1985
4	Exch. H + Al	Growth 1995	Seeds AB	Growth 1990	PPFD 1 m	
5	Seeds AB	BS		PPFD 1 m		
6	Slope y	Exch. Na				
7	Growth 2000	Seeds AB				
8	Exch. Mg	PPFD 4 m				
9	Elevation	pH				
10	pH	Exch. K				

Notes: Key to variables: Growth, mean radial growth over the 5-year period starting at the year indicated; Seeds, the predicted seed rain of sugar maple (SM) or American beech (AB); PPFD, percentage of photon flux density measured at 1 or 4 m aboveground; Exch., exchangeable cations; BS, base cation saturation.
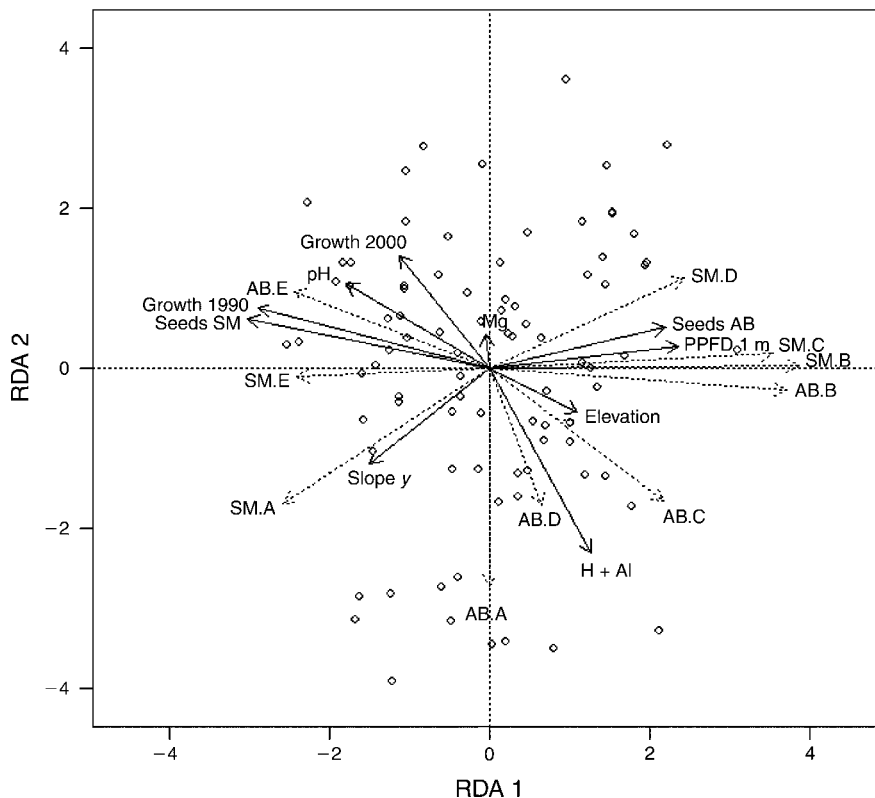
Fig. 1. Biplot of the redundancy analysis (RDA) on sugar maple (SM, *Acer saccharum*) and American beech (AB, *Fagus grandifolia*) regeneration density after forward selection of the environmental variables at $P < 0.1$. Abundance data were standardized prior to analysis. The solid arrows represent environmental vectors, and dotted arrows represent species positions. The letter following the species abbreviation indicates the size class: A, new-year seedlings; B, 0–30 cm in height; C, 30–100 cm height; D, height > 1 m and dbh < 4 cm; E, 4 cm < dbh < 9 cm. For an explanation of other variable abbreviations, see Table 3.

fraction explained by the spatial variables derived from PCNM. The residuals of the model for size class E were highly spatially structured. For that size class, the proportion of the residuals explained by the PCNM variables was 0.489 (adjusted R^2). The selected predictor variables differed among size classes (Table 3), yet there was no clear or emergent pattern in the change of selected variables with increasing size.

DISCUSSION

The conceptual model of coexistence that we initially described predicts that the relative abundance of sugar maple and beech will vary spatially with light availability (current and past) and soil properties, once we have accounted for dispersal limitations. Although this prediction had been tested at the regional (D. Gravel, M. Beaudet, and C. Messier, *unpublished manuscript*) and landscape scale (Arii and Lechowicz 2002), we are not aware of any study that has tested this prediction at the scale of a local community. The results obtained in our study, which was performed at such a local scale, do not support the hypothesis. Species composition and abundance were significantly related to the measured environmental characteristics, but the fraction of explained variation was relatively small. The relationships

between species abundance and the predictor variables were in some cases consistent with the model (e.g., beech in classes C–D was positively correlated with exchangeable acidity, and sugar maple in classes B–C was positively correlated with light availability at 1 m), but in other cases they were not (e.g., sugar maple in classes B–D was negatively related to soil pH).

The ordination of species abundance per size class suggests that sugar maple and beech are differentiated in space in the smallest size classes. The relationships between the abundance of sugar maple and beech were uncorrelated for regeneration in size classes between 30 cm tall and 4 cm dbh. However, sapling abundances in the larger size classes were positively correlated between species. This positive correlation between the abundance of sugar maple and beech larger saplings might result from previous gaps that may have promoted the recruitment of both species at the same locations. Indeed, the abundance of the two species in the largest size class was positively related to the average radial growth recorded during the 1985–1989 and 1990–1994 intervals. The abundance of sugar maple in the smaller size classes was negatively related to conspecific abundances in the larger size classes, suggesting strong intraspecific competition. The appearance of a canopy
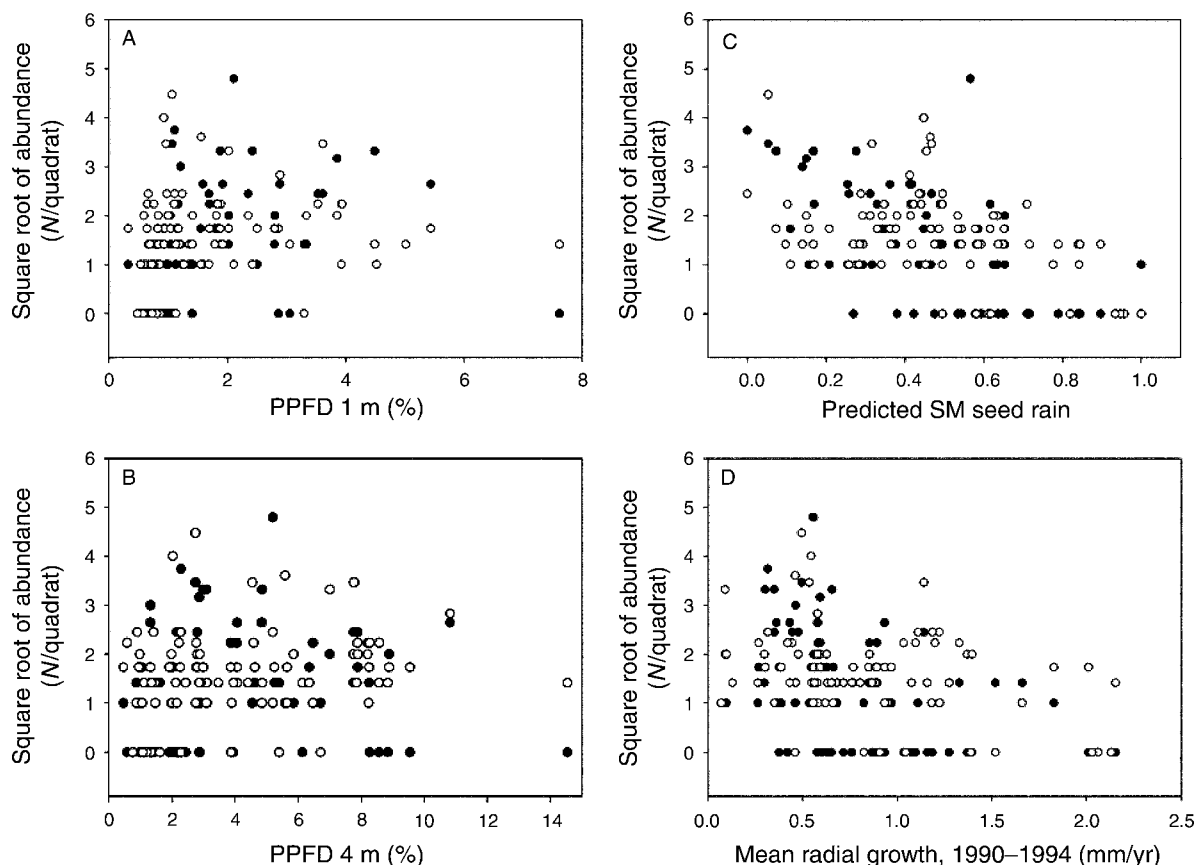
FIG. 2. Abundance per quadrat for the size class C (30–100 cm height) as a function of the environmental variables selected in the forward procedure. Solid circles are for sugar maple, and open circles are for American beech. (A) Photosynthetic photon flux density (PPFD; %) at 1 m, (B) PPFD (%) at 4 m, (C) sugar maple (SM) scale-transformed predicted seed rain (unitless variable, ranging from 0 [minimum seedling density] to 1 [maximum seedling density]), and (D) mean radial growth between 1990 and 1994.

opening is usually followed by a massive recruitment of seedlings to the sapling stage for both species, which will increase in size and eventually cast a deep shade that may prevent further establishment (Beaudet et al. 2007a). However, our results do not fit the conceptual model since the abundance of larger saplings, the most likely candidates for recruitment, varied in the same manner for both species. Spatiotemporal variation in regeneration density promotes species coexistence only if it lasts to the recruitment stage (Chesson 2000a). Variation in seedling density through time and space tends to be buffered by long periods of suppression that the regeneration has to suffer prior to final recruitment and by the positive response of both species to canopy gaps. This result suggests that the potential for species differentiation in the smaller size classes to promote coexistence might be canceled by the co-occurrence of species on the same microsites prior to recruitment.

We also tested whether the variables selected as predictors of species distribution would change with increasing size due to an increase in environmental filtering. We hypothesized that the distribution of parent trees would best predict the distribution of the new-year germinants (since the latter would be mostly dispersal-limited), while past growth history and soil fertility would be the best predictors for the distribution of larger saplings. The selected variables did change with size, but not as predicted. Moreover, the fraction of variance explained by the model decreased with increasing size. The emerging pattern, in terms of selected variables as a function of size class, rather confirms that some variables were selected by chance alone. The analysis performed here, by partitioning size classes, thus illustrates the importance of a detailed interpretation of the output of a multivariate analysis such as RDA before inferring processes from patterns. Based on the analysis performed on all size classes, it would have been reasonable to conclude, as Woods (2000) and Arii and Lechowicz (2002) have concluded, that the distribution of light and soil conditions differentiate species; the analysis performed by size class sheds new light on this conclusion. Our results also emphasize the importance of studying the distribution of regeneration across all size classes, rather than limit study to newly germinated seedlings (Caspersen and Saprunoff 2005, Messaoud and Houle 2006, Norden et al. 2007).

It is admittedly difficult to convincingly demonstrate that the spatial distribution of a species is not related to environmental conditions, since a lack of correlation could always be attributed to inadequate sampling of the environment, which could either be due to a wrong choice of environmental variables or due to insufficient sampling intensity (Hardin 1960, Clark et al. 2007). In our study, the characterization of the environment was focused on the environmental variables that were hypothesized to limit and structure maple and beech distribution (i.e., present and past light conditions and soil properties related to calcium availability). We did not sample other environmental variables, such as water or nitrogen availability, because these have not been found to be limiting at our study site (Finzi and Canham 2000, Ricard et al. 2003). Nevertheless, the presence of spatial structure in the residuals suggests that some environmental variables (other than the ones we accounted for in our study) must have structured the distribution of the regeneration.

Despite the presence of such residual spatial structure, some of our results clearly do not support the conceptual model of coexistence for maple and beech based on niche differentiation with respect to light and soil properties. For example, we performed a distinct ordination of the species/size classes that did not account for the environment variables (PCA, results not shown) to validate the ordination obtained with RDA and to test whether the environment had been adequately characterized. If the pattern shown by ordination with RDA (which accounts for environmental variables, by definition) had emerged due to the influence of some irrelevant explanatory variables, it should have disappeared with an unconstrained ordination (PCA). Yet this was not the case, since the spatial convergence of species with increasing size, which had been observed with RDA, was still clearly apparent in the PCA. Moreover, to verify whether the sampling intensity was sufficient, the latter analysis was conducted on abundance data for a larger plot of 100×50 m (200 quadrats). The ordination results were exactly the same: the small classes were still orthonormal and the largest class strongly correlated between species. This indicates that even if some environmental variables may have promoted spatial segregation of the species at the seedling stage, the subsequent occurrence of canopy gaps tended to cluster the species in the same locations, thereby reducing the likelihood of spatial niche differentiation.

An alternative hypothesis for the coexistence of maple and beech could be either a competition/colonization trade-off (Tilman 1994) or strong dispersal limitations (Clark et al. 1998, Gilbert and Lechowicz 2004). This hypothesis was tested indirectly in this study by investigating the relationship between the spatial distribution of seedlings and dispersal limitations. If beech had been more dispersal-limited than maple, the spatial distribution of beech seedlings would have been better predicted by the spatial distribution of the parents than in the case of maple. The expected seed rain (based on the distribution of adult trees) was selected to model the distribution of both species, but the ordination showed the relations were opposite to the predictions, in that observed seedling densities were negatively correlated to the predicted distribution. The abundance of adult trees in this community was most likely sufficiently elevated to prevent dispersal limitations for both species.

The conceptual model of coexistence for these two shade-tolerant species could actually be correct, but not at a scale of a few individual adult trees. The mean and the range of environmental conditions found in a community are important factors that affect the strength of niche differentiation relative to neutral dynamics (Gravel et al. 2006). Within species, high variability among individuals in terms of the expression of life-history traits can also promote neutral dynamics if species are not sufficiently differentiated (Gravel 2007). Such high levels of variability have been frequently reported in the literature. For instance, regarding the relationship between light availability and sapling growth, Kobe (1996) reported regression coefficients that ranged from 0.17 to 0.79, while Bigelow and Canham (2002) reported coefficients around 0.25 (even with the inclusion of soil fertility as a second explanatory variable).

The range of environmental conditions necessary for sugar maple and beech differentiation might also be wider than the range of conditions encountered in a single community. At our study site, when extensively measured over 200 quadrats, light availability at 1 m height varied between 0.3% and 16.9% PPFD. The average light availability was only 1.9%, with 75% of the microsites below 2.1%. Furthermore, the frequency distribution of light availability was similar to that found by Beaudet et al. (2007b) in an old-growth forest prior to an ice storm. Immediately following this catastrophic ice storm, these authors found that light availability increased to nearly 20% on average (from 2.8% prior to the storm). However, even such a marked increase in light levels was insufficient to lead to a significant change in the species growth hierarchy (Beaudet et al. 2007a). At the regional scale, however, it has been shown that variation in the frequency of growth release episodes was the main factor that explained site-to-site variation in sapling composition (D. Gravel, M. Beaudet, and C. Messier, *unpublished manuscript*). Regarding soil conditions, pH values were found to vary, at our study site, from 2.9 to 3.7, a much narrower range than that reported in other studies, which compared different sites across a region. For instance, Kobe (1996) studied sites with a soil pH ranging from 3.3 to 8.0 (note that it was not specified from which horizon). Finzi et al. (1998) studied sites with a range of pH between 3.5 and 5.0, while Arii and Lechowicz (2002) reported pH values ranging from 3.6 to 6.6. As was the case for light, the range of soil

conditions encountered at the local scale at our site might have been insufficient to allow niche differentiation. Consequently, we suggest that coexistence might be stable only at the regional scale at which environmental variability might be sufficient for spatial segregation based on niche differentiation to occur, thereby allowing stable coexistence (Chesson 2000a). At the local stand scale, we suggest that variability in environmental conditions might not be sufficient to permit stable coexistence. However, local coexistence of shade-tolerant species in forest communities can still be observed, due either to a transient phenomenon caused by the slow turnover rate of trees (Woods 2007) or to neutrality because of high species similarity and elevated demographic stochasticity (Gravel et al. 2006).

CONCLUSION

The results presented in this study showed that environmental characteristics are not good predictors of small-scale variation in sugar maple and beech seedling and sapling abundances and that the response of these two shade-tolerant species to small-scale environmental variability is not sufficient to allow their differentiation in space. This suggests that the conceptual model of coexistence described in the introduction might not be adequate for predicting dynamics at the local scale. We propose this might be due to the high level of similarity between the two species in terms of their response under the relatively limited range of environmental conditions that are typically encountered in a single stand. We suggest that, when combined with demographic stochasticity, the dynamics would rather be highly variable and coexistence transient at this scale. Consequently, any past historical factor that preferentially affected one species over the other, such as past logging episodes or windstorms, could still be influencing the species' relative abundance.

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