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Determinants of fine-scale plant species richness in a deciduous forest of northeastern North America

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Abstract

Question: What are the determinants of fine-scale plant species richness (SR)?

Location: Île-aux-Grues, Québec, Canada.

Methods: Elevation, soil organic matter, soil pH, irradiance, tree basal area (BA) and plant SR (herbs, shrubs, and trees) were determined in 100 contiguous 25 m^2 quadrats in a deciduous forest. Each variable was analysed for spatial autocorrelation using Moran's *I*. Path analysis was used to determine the effects of different variables on tree, shrub and herb SR in a hierarchical modelling approach.

Results: Most of the variables, except tree BA, PPFD (photosynthetic photon flux density) and shrub SR, were positively autocorrelated at a scale of ca. 20 m or less. The path analyses explained ca. 11%-40% of the variance in plant SR; however, the model for shrub SR was not significant. Tree SR was positively associated, but herb SR was negatively associated with tree BA. Tree SR had a positive influence on shrub SR, but herb SR remained unaffected by tree or shrub SR.

Conclusion: The positive association of tree BA and tree SR suggests that the data from the study site correspond to the left (ascending) portion of the SR-biomass relationship (undersaturated SR). The negative effect of tree BA on herb SR is direct and not mediated through reduced PPFD. High tree BA might cause high resource use, induce high litter production and affect soil properties, all of which might significantly affect herb SR. Several factors not considered here might influence fine-scale SR, such as interspecific interactions, fine-scale disturbances and heterogeneity (both spatial and temporal) in resources and abiotic conditions. Within-site variations of SR might be difficult to model with precision because of the relative importance of stochastic vs deterministic processes at this spatial scale.

Keywords: Biodiversity; Moran's *I*; Path analysis; Soil fertility; Spatial autocorrelation.

Abbreviations: BA = Basal area; CV = coefficient of variation; GFI = goodness of fit index; OM = Organic matter; PPFD = photosynthetic photon flux density; RMSEA = root mean square error of approximation; SR = species richness.

Introduction

Species richness (SR) is spatially variable at scales from local to regional, continental and global (Levin 2000; Whittaker et al. 2001). While we expect local processes to influence local SR (Huston 1999; Pausas & Austin 2001), several studies have tried to explain how more coarse scale processes might affect local SR (Pärtel 2002) and how local processes might influence more coarse scale SR (Huston 1999). However, no consensus has been reached on these aspects and more research is needed to fully understand how environmental factors might scale up or scale down to explain SR (Currie et al. 1999; Levin 2000; Crawley & Harral 2001; Willis & Whittaker 2002; Weiher & Howe 2003; Graae et al. 2004; Stevens 2006).

Fine-scale heterogeneity of SR is an important component of community structure that ecologists have been trying to model for quite some time now, with variable results. In a widely cited review on factors explaining local-scale plant (mostly herbaceous) SR, Grace (1999) reported that ca. 57% (range: 23%-89%) of the variance of SR could be explained by various environmental factors, mostly plant biomass, resources, abiotic conditions and disturbances, but also plant morphology, plant density and soil microbial effects (see also Wohlgemuth 1998: 21%-94% of explained variance, in his literature review). The use of sophisticated regression techniques or structural equation modelling (including path analysis) has increased over the last few years, allowing for the test of more 'mechanistic' models on the factors that control SR (Grace & Pugesek 1997; Grace 1999; Weiher 2003; Kubota et al. 2004; Désilets & Houle 2005; Houle 2005). While most studies have either lumped all plant species together (tree, shrub and herb species) or analysed only a specific subset of species (tree, shrub or herb species), few studies have tested the influence of environmental variables (resources and abiotic conditions) on tree, shrub and herb species richness in a hierarchical model (tree SR → shrub SR → herb SR). Such an approach makes biological sense, as one should expect taller and larger species (such as tree species) to have 'preferential' access to resources, both above- and below-ground (light, nutrients and water), over smaller ones (such as herb species).

In the present study, I used path analysis to estimate the influence of resources and abiotic conditions on tree SR, then consider how resources, abiotic conditions and tree SR might affect shrub SR and, in a final model, look at how resources, abiotic conditions, tree SR and shrub SR can be associated to determine herb SR, in a cold, deciduous forest of northeastern North America. This hierarchical approach allows me to estimate the separate influence of several environmental variables on the different components of plant SR (Pausas & Austin 2001; Le Brocque & Buckney 2003). I also study the spatial autocorrelation of each variable to determine if, and how, resources, abiotic conditions and SR are spatially structured.

Study site

The study site occupies the western section of Île-aux-Grues (47°02'N, 70°33'W), an island of the Montmagny archipelago in the St. Lawrence River, ca. 70 km east of Quebec City (Québec, Canada). The island has been cleared for agriculture on most of its surface, except for its western tip. At the study site, the forest (ca. 75 ha) is composed primarily of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*) and ironwood (*Ostrya virginiana*).

Mean annual temperature is 4.4°C at the nearby Montmagny weather station and annual precipitation totals 1087 mm, of which 23% falls as snow (Anon. 1993). The frost-free period lasts ca. 146 days and there are 1685 degree days above 5°C (Anon. 1982).

Methods

A 50 m × 50 m area (0.25 ha) was delimited at the study site and subdivided into 100 5 m × 5 m contiguous quadrats. This set up had been used in previous studies of tree seedling recruitment by our research team (García & Houle 2005; Messaoud & Houle 2006). In the summer of 1999, the geographic position of all the trees with a DBH ≥ 5 cm was determined and their DBH was recorded. Elevation was measured at 121 points regularly distributed over the 0.25 ha study area with a Pentax AL-M5C level and later standardized so that the lowest point corresponded to 0 m. In 2003 and 2004, repeated surveys of the vascular flora (herbs and shrubs, including understorey trees, i.e. those with a DBH < 5 cm) were carried out in each 5 m × 5 m quadrat. By doing so, I presumed that all plant species could be surveyed and accurately identified (three surveys per year, for each of two years).

In early July 2004, three soil samples (12.6 cm^2 × 10 cm; H and top of A horizons) were collected from each quadrat and pooled for further analysis in the laboratory. On the same day (a clear, sunny day), between 1100 hr and 1300hr, one 15 second scan was made over a 1 m^2 surface in the centre of each 5 m × 5 m quadrat (at 1 m from the ground) with a LiCor 250 light meter (LiCor, Lincoln, Nebraska, USA) to determine photosynthetic photon flux density (PPFD). One PPFD measurement was also made in the open, near the study stand, immediately before 1100hr and immediately after 1300hr to express PPFD in terms of percent of open field conditions.

In the laboratory, the soil samples were passed through a 2 mm mesh sieve to remove coarse debris and then dried in a forced air oven at 60°C for 48 hr. Percent organic matter was determined by mass loss on ignition (500°C, for 4 hr) and pH was measured in a 1:1 soil:water solution with a pH-meter (IQ Scientific Instruments, San Diego, California, USA).

Statistical analyses

Moran's *I* served as an index of spatial autocorrelation for the different variables: elevation, soil organic matter, soil pH, tree basal area (BA), PPFD, species richness (SR) of herbs, SR of shrubs and SR of trees. Moran's *I* typically varies between –1 (repulsion) and +1 (contagion). The expected value of Moran's *I* in the absence of spatial autocorrelation (randomness) approaches 0 (Legendre & Fortin 1989). Twelve distance classes of 5.3 m each were used in the analyses (the geographical coordinates of each data point represented the quadrat centroid). Before concluding on the significance of individual values of Moran's *I*, a correlogram has to be globally significant (Bonferroni criterion; Legendre & Fortin 1989), meaning that at least one value has to be significant at $P \leq 0.05/k$, with *k* representing the number of distance classes (here, 12).

The Pearson coefficient of correlation was calculated as an estimate of the intensity of the association between the different variables. This analysis is presented here as an overall description of the correlation patterns of the data.

With path analysis, the influence of several variables was tested on each of the three plant diversity components (herb, shrub and tree SR). In a first model, tree SR was the focus variable with tree BA, PPFD, soil organic matter and pH (important indicators of soil fertility: Fu et al. 2004; Härdtle et al. 2004) and elevation as causal variables. In a second model, the focus variable was shrub SR with the above mentioned causal variables in addition to tree SR. In a third model, the focus variable was herb SR and the causal variables were as in the second model in addition to shrub SR. In these models, BA and elevation were associated to the focus variable directly but also indirectly through PPFD (for BA) and soil organic matter and pH (for elevation). In the second model, BA was indirectly associated to the focus variable shrub SR through tree SR. In the third model, BA was indirectly associated to the focus variable herb SR through tree SR and shrub SR. These models depict *a priori* defined links between the variables and are based on demonstrated ecological interactions (e.g. Désilets & Houle 2005; Marchand & Houle 2006; Messaoud & Houle 2006): for instance, tree BA might influence PPFD, which in turn might be associated with SR; tree SR might influence shrub and herb SR and shrub SR might influence herb SR; soil organic matter is associated with soil pH, and both might be associated with elevation; in turn, soil organic matter, soil pH and elevation might influence SR. All three models were tested with the minimum fit function chi-square (to test for an *exact* fit between the model and the data; a P-value > 0.05 indicates that the model cannot be rejected and, thus, that there is an *exact* fit), the root mean square error of approximation (RMSEA; to test for a *close* fit between the model and the data; a P-value > 0.05 indicates that the model cannot be rejected and, thus, that there is a *close* fit) and the goodness of fit index (GFI; to test for an *acceptable* fit between the model and the data; a GFI-value > 0.9 indicates an *acceptable* fit). These tests can be interpreted as hierarchically nested tests of fit between the model and the data.

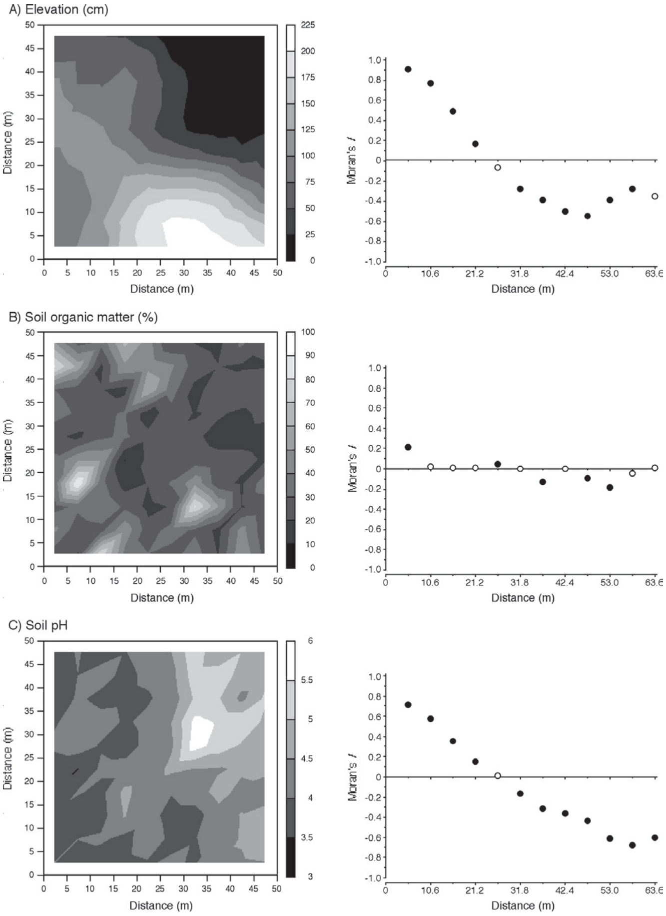

Fig. 1. Left: Spatial pattern of elevation (cm), soil organic matter (%) and soil pH at the study site (values increase from darker to lighter shades). Right: Matching spatial correlograms (significant Moran's I values are represented by black dots on globally significant correlogram, $P \leq 0.004$; Bonferroni criterion).

Analyses were carried out with R 4.0 of Casgrain et al. (2004), SAS 9.1 (SAS Institute, Cary, North Carolina, USA) and LISREL 8.71 (Scientific Software International, Lincolnwood, Illinois, USA) for spatial autocorrelation, Pearson correlation, and structural equation modelling (path analysis), respectively. For the path analyses, most of the variables were transformed for normality assumptions as follows: shrub SR and PPFD: log (variable); tree SR and BA: square root (variable + 1); elevation: square-root (variable); organic matter: 1/square root (variable); pH: 1/variable.

Results

The maximum difference in elevation at the site was 2.13 m and topographical heterogeneity (coefficient of variation, CV) was 72.4% (Fig. 1). Elevation was spatially structured at the scale studied with significant positive values of Moran's I up to 21.2 m and significant negative values between 31.8 m and 58.3 m. The interpolation map (Fig. 1a) shows a peak in elevation in the lower right corner of the study area with progressively smaller values radiating from that point, suggesting a more or less continuous gradient. Mean soil organic matter was 30.6% ± 1.5 % (± s.e.), with a CV of 50.2%. This variable was also spatially structured, with significant values of Moran's I at 5.3 m and 26.5 m (positive) and at 37.1 m and 47.7-53.0 m (negative). The interpolation map of soil organic matter (Fig. 1b) shows several small patches of high values, in the lower and left sections of the study area. Mean soil pH was 4.3 ± 0.1, with a CV of 11.7%. Spatial autocorrelation was also evident for this variable with positive values of Moran's I up to 21.2 m and negative values from 31.8 m to 63.6 m (Fig. 1c). The interpolation map of soil pH shows a clear gradient with higher values in the centre right section of the study area and lower values in the left section.

Mean tree BA was 904 ± 89 cm^2 25 m^{-2} (or 36.2 ± 3.6 m^2 ha^{-1}). Although quite heterogeneous (CV = 98.6%), this variable was not spatially structured, as the correlogram did not reveal global significance (after Bonferroni correction at $P \leq 0.05/12$, i.e. $P \leq 0.004$; Fig. 2a). Mean

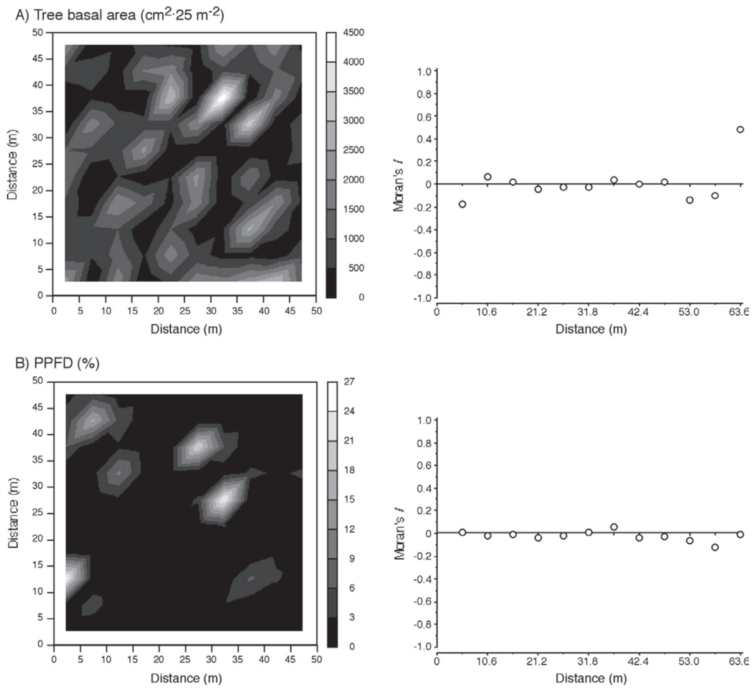

Fig. 2. Left: Spatial pattern of tree basal area (cm^2 25 m^{-2}) and photosynthetic photon flux density (PPFD: %) at the study site (values increase from darker to lighter shades). Right: Matching spatial correlograms (neither correlegram is globally significant at $P \leq 0.004$; Bonferroni criterion).

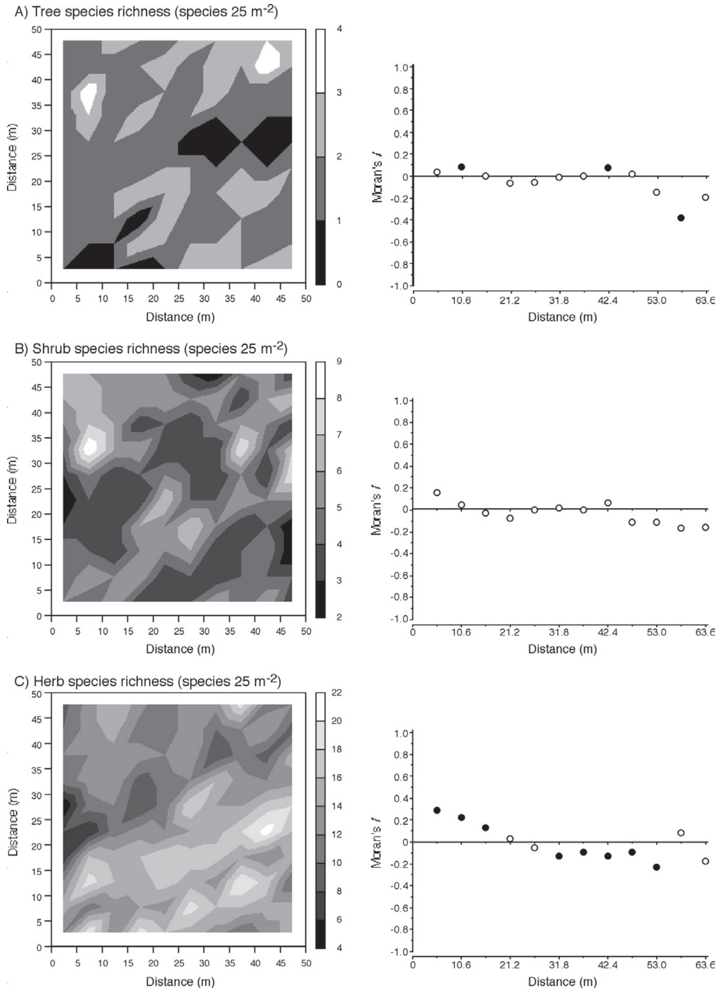

Fig. 3. Left: Spatial pattern of tree species richness (25 m^{-2}), shrub species richness (25 m^{-2}), and herb species richness (25 m^{-2}) at the study site (values increase from darker to lighter shades). Right: Matching spatial correlograms (significant Moran's I values are represented by black dots on globally significant correlogram, $P \leq 0.004$; Bonferroni criterion).

Table 1. Correlation table (Pearson coefficient of correlation, *r*) between the different variables, at Île-aux-Grues, Québec, Canada ($n = 100$). Significant coefficients ($P < 0.05$) are indicated in bold.

	Tree BA[1]	Elevation	PPFD	Tree SR	Shrub SR	Herb SR	Soil OM	Soil pH
Tree BA	-	-	-	-	-	-	-	-
Elevation	0.0787	-	-	-	-	-	-	-
PPFD	–0.0473	-0.1338	-	-	-	-	-	-
Tree SR	**0.4321**	0.0530	**–0.2199**	-	-	-	-	-
Shrub SR	**0.2029**	-0.1390	0.0297	**0.2686**	-	-	-	-
Herb SR	**–0.2371**	0.1707	–0.0128	–0.1094	–0.0371	-	-	-
Soil OM	0.0739	0.1909	0.0138	–0.0330	0.0431	–0.1069	-	-
Soil pH	0.0555	**–0.4936**	0.0624	0.0600	–0.0002	0.0749	**–0.4353**	-

[1] Tree BA: tree basal area; PPFD: photosynthetic photon flux density; Tree SR, Shrub SR, and Herb SR: species richness (25 m^{-2}) for trees, shrubs, and herbs, respectively; Soil OM: soil organic matter.

PPFD was low, 2.3 ± 0.4%. Despite high heterogeneity (CV = 185.4%), as for tree BA, PPFD was not spatially structured (correlogram not globally significant; Fig. 2b).

Overall, there were 12 tree species on the study area, with a mean SR of 1.66 ± 0.09 species 25 m^{-2} (CV = 53.6%). Tree SR was spatially structured, with significant values of Moran's *I* at 10.6 m and 42.4 m (positive) and

Table 2. Direct (DE) and total (TE) effects of the independent variables on the dependent variables in the three structural equations models, at Île-aux-Grues, Québec, Canada ($n = 100$). Significant effects ($P < 0.05$) are indicated in bold.

Model 1 (focus variable: tree species richness)

Independent variables	Dependent variables							
	PPFD		Tree SR		Soil OM		Soil pH	
	DE	TE	DE	TE	DE	TE	DE	TE
Tree BA[1]	-0.024	-0.024	**0.608**	**0.610**	-	-	-	-
Elevation	-	-	0.032	-0.047	**-0.220**	**-0.220**	**0.486**	**0.462**
PPFD	-	-	-0.097	-0.097	-	-	-	-
Soil OM	-	-	0.072	0.057	-	-	0.107	0.107
Soil pH	-	-	-0.137	-0.137	-	-	-	-

Model 2 (focus variable: shrub-understorey tree species richness)

Independent variables	Dependent variables									
	PPFD		Tree SR		Shrub SR		Soil OM		Soil pH	
	DE	TE	DE	TE	DE	TE	DE	TE	DE	TE
Tree BA	-0.024	-0.024	**0.603**	**0.603**	0.076	**0.210**	-	-	-	-
Elevation	-	-	-	-	-0.136	-0.097	**-0.220**	**-0.220**	**0.486**	**0.462**
PPFD	-	-	-	-	0.148	0.148	-	-	-	-
Tree SR	-	-	-	-	**0.230**	**0.230**	-	-	-	-
Soil OM	-	-	-	-	-0.014	-0.006	-	-	0.107	0.107
Soil pH	-	-	-	-	0.077	0.077	-	-	-	-

Model 3 (focus variable: herb species richness)

Independent variables	Dependent variables											
	PPFD		Tree SR		Shrub SR		Herb SR		Soil OM		Soil pH	
	DE	TE	DE	TE	DE	TE	DE	TE	DE	TE	DE	TE
Tree BA	-0.024	-0.024	**0.603**	**0.603**	-	**0.147**	**-0.287**	**-0.282**	-	-	-	-
Elevation	-	-	-	-	-	-	**0.308**	0.177	**-0.220**	**-0.220**	**0.486**	**0.462**
PPFD	-	-	-	-	-	-	0.028	0.028	-	-	-	-
Tree SR	-	-	-	-	**0.245**	**0.245**	-0.008	0.011	-	-	-	-
Shrub SR	-	-	-	-	-	-	0.075	0.075	-	-	-	-
Soil OM	-	-	-	-	-	-	0.140	0.117	-	-	0.107	0.107
Soil pH	-	-	-	-	-	-	**-0.217**	**-0.217**	-	-	-	

[1] Tree BA = tree basal area; PPFD = photosynthetic photon flux density; Tree SR, Shrub SR and Herb SR: species richness (25 m^{-2}) for trees, shrubs and herbs, respectively; Soil OM = soil organic matter.

at 58.3 m (negative). The interpolation map (Fig. 3a) indicates two peaks in tree SR (separated by ca. 40 m) towards the upper left and the upper right corners of the study area. Seventeen species were represented in the shrub layer, with a mean SR of 4.61 ± 0.15 species 25 m^{-2} (CV = 32.8%). Shrub SR was not spatially structured, as suggested by the lack of global significance for the correlogram (Fig. 3b). Herbs comprised 62 species, overall, with a mean SR of 13.44 ± 0.32 species 25 m^{-2} (CV = 24.0%). Herb species richness was spatially structured, with significant values of Moran's I from 5.3 m to 15.9 m (positive) and from 31.8 m to 53.0 m (negative; Fig. 3c). The interpolation map for this variable reveals several small patches of high values in the lower half section of the study area, and lower values in the centre left area.

Of the 28 correlation coefficients calculated between the variables, seven were significant at $P < 0.05$: those between tree BA and tree SR (positive), shrub SR (positive) and herb SR (negative); that between elevation and soil pH (negative); that between PPFD and tree SR (negative); that between tree SR and shrub SR (positive) and that between soil organic matter and soil pH (negative).

All together, the causal variables explained 39.5% of the variance in tree SR ($P < 0.001$). Tree BA was the only variable significantly associated with the focus variable ($\rho = 0.608$, $P < 0.001$; Fig. 4, model 1). This direct effect of tree BA on tree SR was slightly enhanced by indirect paths through PPFD (total effect = 0.610; Table 2 and Fig. 4). Elevation was significantly associated with soil organic matter ($\rho = -0.220$, $P < 0.05$) and soil pH ($\rho = 0.486$, $P < 0.001$). There was an *exact* fit between the data and the proposed model (minimum fit function chi-square = 2.908, df = 5, $P = 0.714$; RMSEA < 0.001, $P_{\text{RMSEA} < 0.05} = 0.808$; GFI = 0.990).

The path model for shrub SR explained only 10.9% of the variance of the focus variable ($P > 0.05$; Fig. 4, model 2). Only one of the path coefficients leading to the focus variable was significant: that from tree SR ($\rho = 0.230$, $P < 0.05$). Although the direct effect of tree BA on shrub SR was not significant, the total effect (direct plus indirect paths through tree SR) was significant (total effect = 0.210, $P < 0.05$; Table 2). As in the first model, elevation was significantly associated with soil organic matter and soil pH, and tree SR was significantly associated with tree BA (Fig. 4). There was an *exact* fit between the data and this second model (minimum fit function chi-square = 8.023, df = 9, $P = 0.532$; RMSEA < 0.001, $P_{\text{RMSEA} < 0.05} = 0.669$; GFI = 0.976).

The third path model explained 15.5% of the variance in herb SR ($P < 0.05$; Fig. 4, model 3). Of the paths leading to the focus variable those from tree BA, elevation and soil pH were significant ($\rho = -0.287$, $P < 0.05$; $\rho = 0.308$, $P < 0.01$; and $\rho = -0.217$, $P < 0.05$, respectively). However, the total effect of elevation on herb SR (direct

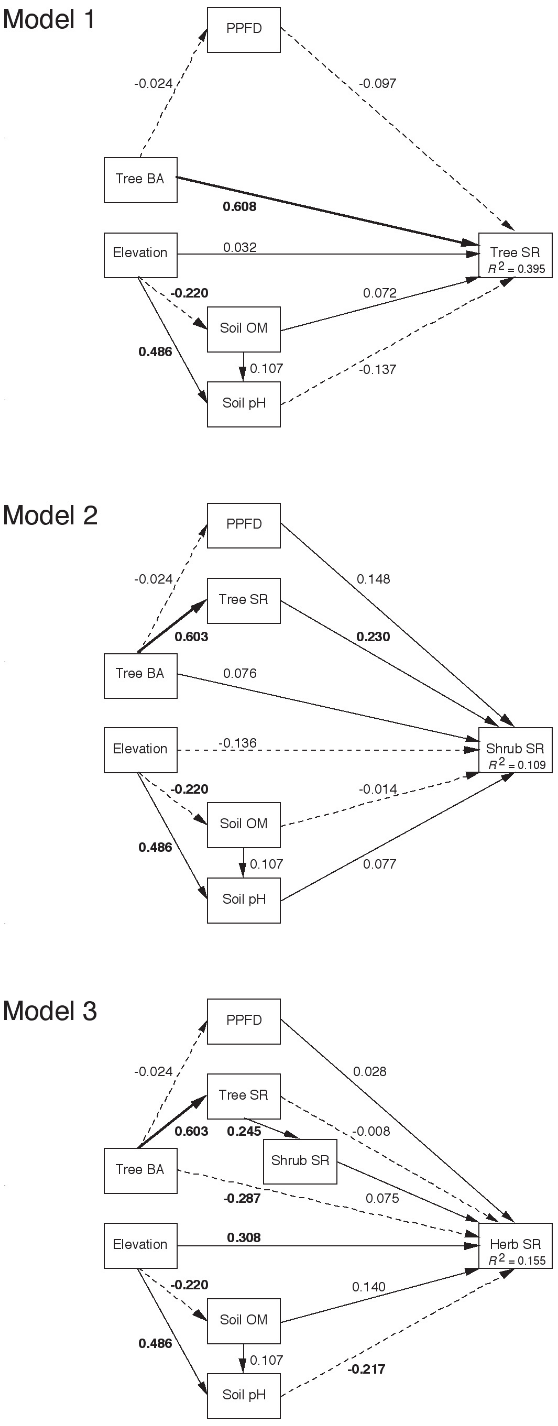

Fig. 4. Path diagram for tree species richness (model 1), shrub species richness (model 2), and herb species richness (model 3). Continuous lines: positive paths; broken lines: negative paths. Significant path coefficients (ρ, standardized partial regression coefficients) are presented next to each path. R^2 represents the total variance of species richness explained by the model. PPFD = photosynthetic photon flux density; soil OM = soil organic matter; SR = species richness; tree BA = tree basal area.

plus indirect paths through soil organic matter and soil pH) was not significant (total effect = 0.177, $P > 0.05$; Table 2). As in the previous two models, BA was associated with tree SR, and elevation was associated with soil organic matter and soil pH. There was an *exact* fit between the data and this model (minimum fit function chi-square = 12.719, df = 14, $P = 0.549$; RMSEA < 0.001, $P_{\mathrm{RMSEA} < 0.05} = 0.695$; GFI = 0.967).

Discussion

Spatial autocorrelation of abiotic variables

Spatial autocorrelation was significant for elevation (gradient), soil organic matter (patches) and soil pH (gradient), but not for irradiance, despite high spatial heterogeneity ($\mathrm{CV}_{\mathrm{irradiance}} = 185\%$). Patch size for soil organic matter was 5.3 m, with inter-patch distances of 15.9 m. Such fine-scale (even finer scale) spatial structure is typical of several environmental variables in forest ecosystems (Lechowicz & Bell 1991; Farley & Fitter 1999a; Ferrari 1999; Guo et al. 2004). Indeed, although local disturbances have the potential to create fine-scale spatial structure for both abiotic conditions and resources in forest ecosystems (Hutnik 1952), tree species identity might also influence soil or light properties (soil: through species specific or even individual specific litter effects; Pelletier et al. 1999; Iason et al. 2005; light: through species specific leafing out or transmittance effects; Grimmond et al. 2000; Kato & Komiyama 2002). In turn, fine-scale spatial structure of both abiotic conditions and resources might affect plant establishment, growth and survival, with direct effects on SR (Farley & Fitter 1999b; Moody & Meentemeyer 2001; Beckage & Clark 2003; Hutchings et al. 2003; Wijesinghe et al. 2005).

Spatial autocorrelation of biotic variables

Spatial autocorrelation was significant for tree SR (patches) and herb SR (gradient), but not for tree BA (despite high spatial heterogeneity, CV = 99%) or for shrub SR. Patch size for tree SR was 10.6 m, with inter-patch distances of 26.5 m. Fine-scale spatial structure in tree SR and in herb SR has been reported previously for northern deciduous forests (Miller et al. 2002; Scheller & Mladenoff 2002; Marchand & Houle 2006; Messaoud & Houle 2006). Spatial heterogeneity in microsite suitability for germination, emergence, growth and survival has been invoked as a major determinant of spatial patterns of SR in both observational and experimental studies (Grime 1973; Houle 1994; Nakashizuka 2001; Hutchings et al. 2003). Surprisingly, SR was more heterogeneous for trees ($\mathrm{CV}_{\mathrm{tree\ SR}} = 54\%$) than for herbs ($\mathrm{CV}_{\mathrm{herb\ SR}} = 24\%$): this most likely represents an artefact of the uniform grain size (25 m^2 quadrat), which tended to inflate the spatial heterogeneity of SR for the larger plants (i.e. trees) and reduce that for the smaller plants (i.e. herbs).

Path model for tree species richness

Tree SR was significantly determined by the path model ($R^2 = 0.395$), but of the five explanatory variables included in the analysis, only tree BA was significantly associated with tree SR ($\rho = 0.608$): indeed, as BA increased, so did tree SR. This result supports the findings of several studies which have shown plant biomass and SR to be significantly associated. Grace (1999) in his review of the factors controlling SR in (mostly) herbaceous communities reported between 0% and 64% of the variability in SR explained by some estimate of biomass (although the relationship has been typically described more as unimodal than monotonic; Grime 1973; Tilman & Pacala 1993; Abrams 1995; Grace 1999; Waide et al. 1999; Gross et al. 2000; Mackey & Currie 2001; Mittelbach et al. 2001; Huston 2002; Weiher 2003). If one accepts tree BA as an appropriate estimate of tree biomass, the model presented here shows that biomass directly, not through a significant effect on light, affects SR (Weiher 2003; but see Grace & Pugesek 1997; Grace 1999, 2001): as BA increases, so does tree SR. Assuming a unimodal relationship between SR and biomass, these results suggest that the data presented here are located to the left of the potential peak of SR, where SR is undersaturated (Grime 1973; Tilman & Pacala 1993).

Elevation had a positive influence on soil organic matter ($\rho = -0.220$, after an inverse transformation of soil organic matter), but a negative effect on soil pH ($\rho = 0.486$, after an inverse transformation of soil pH); however, none of these factors had a significant effect on tree SR.

Path model for shrub species richness

Shrub SR was not significantly determined by the second path model ($R^2 = 0.109$). Only one of the explanatory variables, i.e. tree SR, had a significant direct association (positive) with the focus variable. This result might be explained by the fact that the shrub category included both *true* shrubs and sub-canopy trees (those with a DBH < 5 cm). Species richness would seem to covary in the canopy and the sub-canopy, a result consistent with preferential recruitment close to parent trees (Hubbell 1980; Houle 1994). Nevertheless, the total effect of tree BA on the focus variable (direct plus indirect paths through tree SR) was significant and positive ($P < 0.05$; Table 2 and Fig. 4).

Path model for herb species richness

Herb SR was significantly determined by the explanatory variables, although the amount of variance explained by the model was relatively low ($R^2 = 0.155$). While elevation (ρ = 0.308) and soil pH (ρ = –0.217, after an inverse transformation for soil pH) had a significant positive effect on herb SR, tree BA had a significant negative influence on the focus variable (ρ = –0.287). This latter result cannot be explained by indirect paths through PPFD, the two path coefficients (from tree BA to PPFD and from PPFD to herb SR) being small and non significant. It cannot be explained by a direct or an indirect effect of tree SR either. Most likely, high soil resource use in quadrats of high tree BA restricts herb SR. The indirect effect of elevation on herb SR (through soil organic matter and soil pH) counter-balanced its direct effect, such that the total effect was not significant (Table 2 and Fig. 4).

Synthesis

From 10% to 40% of the variance of SR were explained by the models presented here. These values are in the lower part of the range (from 23%-89%) reported by Grace (1999) for multi-variable models of SR (see also: Keith & Myerscough 1993: 80%; Wohlgemuth 1998: 49%; Lobo et al. 2001: 65%; Le Brocque & Buckney 2003: from 24%-67%; Kubota et al. 2004: 74%; Désilets & Houle 2005: 73%). Several factors not considered here might affect fine-scale SR, such as interspecific interactions, fine-scale disturbances and temporal heterogeneity in resources and abiotic conditions (Dupré et al. 2002; Le Brocque & Buckney 2003; Lundholm & Larson 2003; Désilets & Houle 2005; Houle 2005). The hierarchical approach used here suggests that shrub SR is positively associated with tree SR, but that herb SR is not associated with either shrub SR or tree SR. Tree BA positively affects tree SR, but has a negative influence on herb SR: however, this latter effect is direct and not mediated through reduced PPFD. High tree BA might cause high resource use, induce high litter production and affect soil properties, all of which might significantly affect herb SR (Crozier & Boerner 1984; Graae et al. 2004). Within-site variations of SR might be difficult to model because of the relative importance of stochastic vs deterministic processes at this spatial scale (Levin 2000; Schuster & Diekmann 2005). The positive association of tree BA and tree SR suggests that the data from the study site correspond to the left (ascending) portion of the SR-biomass relationship (undersaturated SR), assuming an overall unimodal relationship.

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