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# Spatial patterns of plant species richness along a forest edge: What are their determinants?

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#### Abstract

The impact of forest edges on plant species richness is poorly understood. In a sugar maple (*Acer saccharum*) stand in Southern Québec, variations in species richness and spatial pattern were observed as a function of distance to the edge and were associated with different environmental variables. Unexpectedly, light was not higher and soil moisture and organic matter were not lower close to the edge than in the forest interior: edge structure was most likely responsible for these results. At a 2 m<sup>2</sup> scale, richness tended to decrease with distance to the edge, as did fine-scale species turn-over. *Erythronium americanum* patch size increased with distance to the edge, most likely because of differences in clonal growth along the gradient. Cover of newly emerged seedlings of sugar maple decreased with distance to the edge, in association with soil moisture and pH. Path analyses revealed significant links between environmental (micro-elevation, irradiance, soil organic matter, moisture, and pH) and biotic variables (richness, *E. americanum* cover, and *A. saccharum* cover), but only a low proportion of the variance of the biotic variables was explained. At the scale studied, stochastic processes may be more significant than deterministic processes for species richness. (© 2005 Elsevier B.V. All rights reserved.

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# 1. Introduction

Forest edges can be thought of as buffer zones across which environmental conditions progressively change with distance (Matlack, 1993; Jose et al., 1996), with significant impact on forest structure and dynamics (Ries et al., 2004). Indeed, there are indications for both woody and herbaceous plants that changes occur in the forest community from a few meters to a few 10 m from the border (Ranney et al., 1981; Matlack, 1993, 1994; Fraver, 1994; Fox et al., 1997; Gehlhausen et al., 2000; Honnay et al., 2002), depending on edge type and aspect. For example, Brothers and Spingarn (1992) found, in old-growth forests of central Indiana, that increased environmental heterogeneity at forest edges enhanced species richness compared to forest interior. Similar results were obtained by Fox et al. (1997) in Australian rainforests and by Oosterhoorn and Kappelle (2000) in a Costa Rican montane cloud forest. Furthermore, Gehlhausen et al. (2000) showed, at different sites in east-central Illinois, that species richness was correlated to environmental variables such as canopy openness and soil moisture, two variables that often vary with distance to the edge (Cadenasso et al., 1997).

Species productivity can also respond to edges. For instance, Tomimatsu and Ohara (2003) found that the seedling number of Trillium camschatcense, an understory perennial herb, was positively correlated with distance to the edge and negatively correlated with soil and air temperatures, which themselves varied with distance to the edge (see also Jules, 1998, for similar results on Trillium ovatum). It has also been observed that early-successional or disturbance-tolerant species have higher densities at forest edges, while the density of "interior" species, although relatively constant in forest interior, decreases abruptly near edges (Fraver, 1994; Fox et al., 1997; Gehlhausen et al., 2000). Furthermore, Landenberger and Ostergren (2002) found that the flower biomass of white snakeroot (Eupatorium rugosum Houtt.), typically occurring at forest margins but also in the forest interior, was significantly higher at forest edges and could be used to indicate edge depth. While these results were obtained at a relatively fine sampling resolution, it is still largely unknown how small herbaceous species respond at scales more appropriate to describe local demographic processes (ca. 1 m<sup>2</sup>).

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Few studies have characterized the fine-scale spatial pattern of herbaceous forest plants in relation to edges. Miller et al. (2002) demonstrated that the spatial pattern of plant cover in old-growth hardwood forests varied with the species considered and environmental conditions. More specifically, they reported that different species could have different spatial patterns in a given environment and that a given species could have different spatial patterns in different environments, depending on soil type and competition with tree saplings. Bell and Lechowicz (1991) worked on explant trials from a mature maple-beech forest in southern Québec. They found that shoot mass in Hordeum showed well-defined spatial structure within 1 and 100 m<sup>2</sup> quadrats. Their results also indicated that variation in spatial structure was independent of grain, in the sense that inter-plant correlation in shoot mass decreased at the same rate as relative distance increased between quadrats of the same size. It may therefore be possible to predict plant species productivity, or biomass production, over short distances if the spatial structure is known. Unfortunately, edge effects may complicate such predictions if spatial structure effectively depends on environmental conditions. Indeed, edge effects induce micro-environmental conditions different from those of the forest interior (Cadenasso et al., 2003; Ries et al., 2004). These micro-environmental variables (relative humidity, air and soil temperatures, soil moisture, light, soil organic matter, and pH (Matlack, 1993; Jose et al., 1996)), in turn, influence most of the biotic variables.

However, edge influence on micro-environmental forest conditions largely depends upon edge type. Typically, open edges are young and have not yet closed by epicormic branch growth and/or increased growth of tree saplings and shrubs; edge effects penetrate deeply into the forest at open edges. Closed edges are older and present multiple layers of shrubs, tree saplings, and trees, thus reducing edge effects into the forest. Embedded edges are characterized by the horizontal encroachment of trees, tree saplings, and shrubs from the original edge towards the open habitat, thus reducing edge effects into the forest. While closed edges develop 'vertically', embedded edges develop 'horizontally'.

The objective of this study is to determine how edges affect the fine scale pattern of understory plant species. More specifically, we ask the following questions: (1) Does the spatial pattern of understory species richness vary with distance to the edge? and (2) how can major environmental variables explain such variations? A higher species richness is expected near the edge, where a mixture of species typical of field and of understory conditions should be present. Furthermore, two species were chosen to test for edge effects on population characteristics: Erythronium americanum Ker-Gawl. and newly-emerged seedlings of Acer saccharum Marsh. Edge effects should be moderate or absent on E. americanum, given that it is a spring ephemeral species and that most of its aerial growth occurs before canopy development, when there are few differences between field and understory conditions. In contrast, significant negative edge effects are expected for A. saccharum seedlings, given that they persist during the entire growing season and are thus more exposed to field/understory

contrasts. Path analyses were also used to test whether finescale spatial heterogeneity in environmental conditions has more effect on plant species richness than average conditions.

## 2. Study site

The study site is located on the south shore of the St. Lawrence River, at Bécancour near Trois-Rivières, Québec, Canada (46°17′N, 72°29′W). The area falls within the Great lakes—St. Lawrence forest region of Rowe (1972), sub-section Mid St. Lawrence (L-3), characterized mostly by northern hardwoods on thick marine deposits from the Champlain Sea. The annual daily mean temperature for the region is 5.1 °C and annual precipitation totals 931.1 mm, of which 21.5% falls as snow (URL: http://www.climate.weatheroffice.ec.gc.ca/climate\_normals; Nicolet weather station, 30.4 m a.s.l.; 46°12′N, 72°37′W).

The stand, dominated by sugar maple (*Acer saccharum*), is lightly managed and exploited for sap. It ends abruptly into a cornfield. The edge studied, of the closed type, is exposed to the south and is relatively linear. Elevation on the site is uniform and a drainage ditch borders the western and northern sections of the stand, which is part of a "forest tract" of ca. 80 ha.

The understory flora of the forest section studied comprises 24 species and forms, in spring, a dense layer of ephemeral herbaceous species, tree seedlings, and ferns. The forest floor remains relatively dense even after canopy closure, when summer species are more abundant.

# 3. Methods

Matlack (1993) suggested that the responses of microclimate variables, such as air temperature and soil moisture, were driven by light availability at edges. Results from measurements using photosynthetically active radiation (Brothers and Spingarn, 1992), photosensitive blueprint paper (Matlack, 1993), and canopy openness (Gehlhausen et al., 2000) have indicated that the influence of light was not deeper than 40 m from the forest edge. We therefore studied edge effects within this distance. Five 40 m long transects, 4.5 m apart were established perpendicular to the forest border. Five  $1 \text{ m} \times 2 \text{ m}$  quadrats were positioned on each transect at 0, 5, 10, 20, and 40 m from the edge (quadrats straddled the transects, with their longer axis parallel to the edge). However, one quadrat (at position 40 m, on transect 1) could not be established because of the presence of a path. Each quadrat was subdivided into 32 25 cm  $\times$  25 cm sub-quadrats for further analysis of spatial patterns (Legendre and Fortin, 1989). This sampling scale is appropriate to appreciate fine-scale resource heterogeneity (Bell and Lechowicz, 1991; Jackson and Caldwell, 1993; Farley and Fitter, 1999), which may be an important determinant of species diversity (Rajaniemi, 2003).

An inventory of herbaceous plants was carried out on each sub-quadrat three times during the 2003 growing season. This was done to ensure that the entire growing season flora was considered. In addition, the percent cover of two selected species (*Erythronium americanum* and newly-emerged seedlings of *Acer saccharum*) was estimated in each subquadrat. To do so, a grid of 25 5 cm  $\times$  5 cm units was placed over each 625 cm<sup>2</sup> sub-quadrat. Presence/absence was noted for the selected species on every grid. These species were chosen for analysis because of their abundance and distribution over the entire study site.

We extracted a soil core (19.6 cm<sup>2</sup> × 12 cm) in each 625 cm<sup>2</sup> sub-quadrat for measurement of pH, moisture, and organic matter, in mid-summer after a period of at least 3 days without rain. Samples were sieved (2 mm) and dried (80 °C during 24 h). Soil moisture was determined gravimetrically and organic matter (%) was determined by mass loss on ignition (500 °C during 5 h). Soil pH was measured in a 1:1 soil:water solution.

Photosynthetic photon flux density (PPFD) was measured on July 31 between 11:00 and 13:00 on a cloudless day in every  $625 \text{ cm}^2$  sub-quadrat (50 cm from the soil surface) with a LI-250 light meter (LiCor Inc., Lincoln, NE). Soil (at 10 cm depth) and air (at 50 cm from the soil surface) temperatures were measured at the centre of each  $2 \text{ m}^2$  quadrat with a thermistor probe on the same day PPFD measures were taken. Canopy openness was determined from photographs taken at 1.5 m over each quadrat with a 50 mm lens (Minolta SRT-202, Minolta Inc., Tokyo, Japan), providing an approximate view of 80 m<sup>2</sup> at canopy height. Percent canopy openness was estimated with a grid of 100 points superposed onto each photograph. Microelevation was measured within each quadrat (32 measures per quadrat) with a level system. Site topography (relative quadrat elevation) was determined with an optical level (Wild T2, Wild Inc., Heerbrugg, Switzerland) and served to standardize all measures of micro-elevation using the lowest point as reference.

# 4. Statistical analyses

Total richness (over each 1 m  $\times$  2 m quadrat), mean richness (averaged over the 32 values obtained for each 625 cm<sup>2</sup> subquadrat), and *E. americanum* and *A. saccharum* cover (averaged over the 32 values obtained for each 625 cm<sup>2</sup> subquadrat) were analysed for differences with distance from the edge with incomplete bloc design ANOVAs. CV values (measuring heterogeneity) were calculated from the 32 values of each 1 m  $\times$  2 m quadrat for each biotic and abiotic variable and were also analyzed for differences with distance from the edge with incomplete bloc design ANOVAs. Comparisons among distances for these variables were performed using protected LSD. ANOVAS and LSD were performed with SAS 6.12 (SAS Institute Inc., Cary, NC). Considering there was one missing quadrat at distance 40 m (transect 0), all means presented in the Section 5 are least square means (±S.E.).

Autocorrelation (using five distance classes of 38.1 cm to optimize information from the sampling grid pattern) was calculated for the different abiotic variables (PPFD, soil moisture, organic matter, pH, and elevation), richness, and *E. americanum* and *A. saccharum* cover for each quadrat using Moran's *I* (Legendre and Fortin, 1989). For each quadrat, there were 32 sampling points, i.e. the 32 25 cm  $\times$  25 cm sub-quadrats composing the 1 m  $\times$  2 m quadrat. Moran's *I* was calculated

with R 4.0 (Casgrain et al., 2004). Patch-size (positive autocorrelation) was tested for variation with distance from the edge using a *G*-test of independence (Sokal and Rohlf, 1995).

Path analysis was also used to identify the most important variables structuring plant species richness and *E. americanum* and *A. saccharum* cover. Models were constructed from known biological principles. The first series of analyses used data from micro-elevation, soil organic matter, pH, moisture, and light for each 625 cm<sup>2</sup> sub-quadrat (n = 768) and distance to the edge and transect position to explain the focus variables: sub-quadrat richness, *E. americanum* cover, and *A. saccharum* cover (Fig. 3). Another analysis used the mean quadrat value (n = 24) of the same abiotic variables and the information of quadrat position to explain quadrat richness (number of species in 1 m × 2 m quadrats). A final analysis used quadrat position and the CV value of the same abiotic variables to explain quadrat richness (n = 24).

In the models, the variable *Y* indicates the effect of distance to the forest border, while the variable X represents distance parallel to the edge. Soil organic matter (OM) is an index of soil fertility. Soil moisture (SM) is an estimate of water availability for plants and pH is a measure of soil acidity. Both pH and moisture are directly associated with soil organic matter. PPFD is light available at the understory level. OM, SM, pH, and PPFD are associated with Y and X (spatial components) and all of these 'environmental' variables may influence the focus variables. LISREL 8.71 (Scientific Software International Inc., Lincolnwood, IL) was used for the path analyses. Three indices were used to verify how the data fitted the model: the minimum fit function chi-square, which tests for an exact fit between the model and the data (the 'best' fit); the root mean square error of approximation, RMSEA, which tests for a close fit between the model and the data (the second 'best' fit); and the goodness of fit index, GFI, which tests for an acceptable fit between the model and the data (the third 'best' fit).

## 5. Results

#### 5.1. Variables as a function of distance to the edge

Quadrat richness (number of species  $2 \text{ m}^{-2}$ ) tended to decrease with distance, going from  $10.6 \pm 1.3$  to  $8.3 \pm 1.5$ species  $2 \text{ m}^{-2}$  from 0 to 40 m from the edge (Fig. 1). Subquadrat richness (number of species 625 cm<sup>-2</sup>) remained constant along the entire gradient, with values from 2.7  $\pm$  0.2 to  $2.6 \pm 0.3$  species 625 cm<sup>-2</sup>. CV of sub-quadrat richness had marginally significant higher values (P = 0.0997) close to the edge  $(38 \pm 3\%)$  than in the forest interior  $(30 \pm 3\%)$ . Erythronium americanum cover varied from the edge to the forest interior, but no clear pattern emerged from the analyses (Fig. 1). CV of E. americanum cover was much higher at the edge (131  $\pm$  34%) than in the forest interior (51  $\pm$  39%), although not significantly so. Acer saccharum cover varied from  $3.1 \pm 2.8$  to  $14.5 \pm 2.4\%$  (P = 0.0516), with a peak at intermediate distances (5-10 m from the edge). CV of A. saccharum increased with distance to the edge (P = 0.0678), going from  $123 \pm 33\%$  at the edge to  $234 \pm 37\%$  at 40 m. Tree



Fig. 1. Mean value (left) and coefficient of variation (CV; right) for different biotic variables as a function of distance to the edge. *P*-values for differences along the distance gradient (incomplete block design ANOVAs). Different letters represent significant differences among distances for each variable (protected LSD). n = 24.

canopy cover did not vary as a function of distance to the edge (P = 0.3389) and was  $87.6 \pm 2.2$ ,  $91.2 \pm 2.2$ ,  $92.0 \pm 2.2$ ,  $86.6 \pm 2.2$ , and  $91.5 \pm 2.5\%$  at 0, 5, 10, 20, and 40 m, respectively.

Although PPFD varied substantially with distance to the edge, with values from  $16.5 \pm 38.9$  to  $117.0 \pm 44.5 \ \mu \text{mol m}^{-2} \text{ s}^{-1}$ , differences among distances were not significant (Fig. 2). However, CV of PPFD tended to increase with distance (*P* = 0.0899), going from  $38 \pm 22\%$  at the edge to  $99 \pm 25\%$ at 40 m. Soil elevation (micro-elevation) was significantly higher (*P* = 0.0050) and tended to be less heterogeneous at 40 m in the forest than at the edge (Fig. 2). It reached  $74 \pm 6$  cm at 40 m comparatively to  $38 \pm 5$  cm at the edge, and its CV went from  $19 \pm 6\%$  (at the edge) to  $5 \pm 7\%$  at 40 m in the forest. Soil moisture (P = 0.0527) and organic matter (P = 0.0006) decreased with distance, from  $24 \pm 2$  to  $17 \pm 2\%$  and from  $16 \pm 1$  to  $9 \pm 1\%$ , respectively, from the edge to the forest interior (Fig. 2). Heterogeneity in these two variables did not change significantly with distance (Fig. 2; P = 0.0551), but the biological meaning of these subtle variations ( $4.6 \pm 0.1$  at 0 m vs.  $4.4 \pm 0.1$  at 40 m in the forest) is unclear.



Fig. 2. Mean value (left) and coefficient of variation (CV; right) for different abiotic variables as a function of distance to the edge. *P*-values for differences along the distance gradient (incomplete block design ANOVAs). Different letters represent significant differences among distances for each variable (protected LSD). n = 24.

## 5.2. Variations in spatial pattern

Results are presented for patch size as frequency distributions for the largest distance class at which significant autocorrelation was detected (Figs. 3 and 4). Possible autocorrelation may have occurred at a scale smaller than the first class of distance (38.1 cm) but could not be detected.

*Erythronium americanum* patch size increased with distance to the edge (Fig. 3) going from two occurrences in the 38.1 cm class and three non-significant autocorrelations at



Fig. 3. Patch size variations with distance to the edge for some of the biotic variables. Patch size is presented in cm. N.S. indicates that autocorrelation was not significant at any distance class. Distance classes larger than 76.2 cm are not presented since patch size was always smaller. *G*-test indicates whether variations along the distance gradient are significant.

the edge, to two occurrences in the 38.1 cm class and three occurrences in the 76.2 cm class at 40 m in the forest. There were also significant variations in patch size for PPFD: indeed, PPFD was unstructured (random pattern) at 20 m in the forest, while it was patchy at the other distances (Fig. 4). No other variable showed significant variation in patch size with distance to the edge.

#### 5.3. Multivariate analyses

Model 1 (n = 768 data points; Fig. 5) provided an acceptable, although not an exact nor a close fit (minimum fit function chi-square of 43.614, d.f. = 6, P < 0.001; root mean square error of approximation, RMSEA, of 0.0904,  $P_{\text{RMSEA}<0.05} = 0.004$ ; goodness of fit index, GFI = 0.986) for all three focus variables (sub-quadrat richness, cover of E. americanum, and cover of A. saccharum). However, our model explained from only 7 to 20% of the variance of the focus variables (all  $R^2$  significant at P < 0.05). The first path analysis associated sub-quadrat richness negatively with elevation and pH and positively with PPFD. In the second path analysis, E. americanum cover was negatively associated with Y, pH, and soil moisture and positively with X, elevation, and PPFD. *Erythronium americanum* cover had the best fit  $(R^2)$  of all three focus variables. The third path analysis associated A. saccharum cover negatively with Y and soil organic matter and positively with soil moisture and elevation. In model 1, there was a strong positive association between soil organic matter and moisture and a negative association between soil organic matter and pH. By adding a path between PPFD and soil moisture (suggested by LISREL with the subcommand MI), the tested model attained a close, although not an exact fit with an RMSEA = 0.0774 ( $P_{\text{RMSEA} < 0.05} = 0.528$ ).

Models 2 and 3 (Fig. 6) explained 36-37% of the variance of quadrat richness and provided an exact fit to the data (minimum fit function chi-square of 6.130 (P = 0.409) and 3.641 (P = 0.725) with d.f. = 6, respectively) (model 2: RMSEA < 0.001,  $P_{\text{RMSEA}<0.05} = 0.501$  and GFI = 0.942; model 3: RMSEA < 0.001,  $P_{\text{RMSEA}<0.05} = 0.784$  and GFI = 0.965). However, neither one of the two  $R^2$  was significant (P > 0.05): this was most likely the result of a low *n*. In model 2, there was no significant relationship between the focus variable and any of the environmental variables; however, in model 3, there was a significant positive association between CV of soil pH and quadrat richness.

## 6. Discussion

#### 6.1. Edge-forest interior gradient

Sub-quadrat richness ( $625 \text{ cm}^{-2}$ ) did not vary as a function of distance to the edge (Fig. 1), although species composition did change, with a greater occurrence of species typical of old fields (e.g. *Rubus* spp., *Solidago* spp., and *Aster* spp.) in the first



Fig. 4. Patch size variations with distance to the edge for different abiotic variables. Patch size is presented in cm. N.S. indicates that autocorrelation was not significant at any distance class. Distance classes larger than 76.2 cm are not presented since patch size was always smaller. *G*-test indicates whether variations along the distance gradient are significant.

few meters close to the edge than farther in the forest (P. Marchand, personal observation). However, the CV of subquadrat richness was marginally higher at the edge indicating a greater heterogeneity and suggesting a higher species turn-over between sub-quadrats ("beta" diversity) there compared to the forest interior (Table 1). This is consistent with the values of quadrat richness (2 m<sup>-2</sup>), which also tended to be higher close to the edge.

Light penetration is restricted at closed and embedded forest edges (Williams-Linera, 1990b; MacDougall and Kellman,

1992; Matlack, 1994) but is favored at open edges (Kapos, 1989; Matlack, 1993; Chen et al., 1995), where it typically enhances plant growth (Williams-Linera, 1990a; Chen et al., 1992). Indeed, light may become a limiting factor even for understory plants when the canopy is very dense (Gilliam and Turrill, 1993; Légaré et al., 2002). Edges that have been maintained by agricultural activities for a prolonged period typically develop a complex multilayered canopy and eventually become "closed". Such closed edges act similarly to the horizontal sprawl of embedded edges, decreasing edge



Fig. 5. Path analyses for three biotic variables using sub-quadrat scale data (*n* = 768). Arrow size indicates path value. Continuous lines are for positive paths; broken lines are for negative paths. Significant coefficients are indicated on the paths. OM and SM are soil organic matter and soil moisture, respectively.



Fig. 6. Path analyses for quadrat richness (n = 24). Arrow size indicates path value. Continuous lines are for positive paths; broken lines are for negative paths. Significant coefficients are indicated on the paths. OM and SM are soil organic matter and soil moisture, respectively.

Table 1 Mean (±S.E.) species turn-over (quadrat species richness/sub-quadrat species richness) at different distances to the edge

	Distance to the edge (m)				
	0	5	10	20	40
Species	$4.11\pm0.35$	$3.42\pm0.35$	$3.54\pm0.35$	$3.08\pm0.35$	3.19 ± 0.40

effects inside the forest (Didham and Lawton, 1999). The edge at our study site was of the closed type. In fact, PPFD was somewhat higher and more heterogeneous in the forest interior than near the edge (Fig. 2). A pathway between 20 and 40 m from the edge contributed to create a long and narrow canopy gap (perpendicular to the transects) that might have been responsible for higher and more heterogeneous PPFD values there (see also Watkins et al., 2003). A path or a natural canopy gap may thus have a significant impact on understory light and even mask any edge effect.

Previous studies have shown that soil moisture is typically lower at the edge than in the forest interior (Kapos, 1989; Matlack, 1993; Gehlhausen et al., 2000) in relation with higher irradiances, higher wind speeds, higher air and soil temperatures, and lower air moisture at ground level (Ries et al., 2004). However, soil moisture was higher at the edge and decreased with distance at our study site (see also Didham and Lawton, 1999): this is consistent with the fact that light was somewhat lower at the edge than in the forest interior. It is also known that soil moisture is often positively related to soil organic matter (Gupta and Larson, 1979; Jong et al., 1983). Soil organic matter was higher at the edge than in the forest interior at our site (Fig. 2), contrasting with what is usually reported in the literature (Matlack, 1993; Chen et al., 1995; but see Didham and Lawton, 1999). However, the more complex canopy stratification of closed edges implies a greater litter deposition and, therefore, a greater accumulation of organic matter. In addition, private forest owners (particularly of maple groves) frequently place pruned branches from trees near the edge at the forest border (P. Marchand, personal observation). Such a practice may have helped increase soil organic matter close to the edge and, indirectly, soil moisture.

In short, micro-environmental conditions close to the edge were not more appropriate for a diverse 'stable' mixture of old field and understory plants. Higher quadrat species richness close to the edge may be better explained by the continuous seed arrival of old field species (Ries et al., 2004; Devlaeminck et al., 2005), which live an ephemeral existence under conditions characteristic of the forest interior, along with more 'persistent' understory plants.

*Erythronium americanum* cover did not vary from the edge to the forest interior, although patch size increased with distance to the edge (Fig. 3). This result is consistent with the fact that CV of *E. americanum* cover tended to be greater near the edge (Fig. 1) suggesting a more heterogeneous distribution there. Some authors have noticed a link between increasing environmental heterogeneity (e.g. soil moisture, acidity, organic matter, and light) and decreasing species patch size for forest species (Maslov, 1989; Scheller and Mladenoff, 2002). In the present study, however, CVs of soil moisture, organic matter, and PPFD tended to be higher in the forest interior, where *E. americanum* patch size was larger. *Erythronium americanum* patch size variation may therefore indicate variations in recruitment (sexual and clonal) and in survival as environmental heterogeneity increases from the edge to the forest interior.

In sharp contrast with *E. americanum*, the cover of newly emerged *A. saccharum* seedlings (reflecting both recruitment and growth) generally declined with distance to the edge, but showed no clear response in patch size. Meiners et al. (2002) also reported complex, contrasting responses of species (tree seedlings, in their study) to edges and proposed that both the spatial pattern and species composition of regenerating forests could be affected by such species-specific responses. Edgerelated variations in e.g. granivory, herbivory, and competition (associated with variations in resource levels and abiotic conditions; Ries et al., 2004) may explain such species-specific responses to edges (Laurance, 2002). 6.2. Causal relations between environmental and biotic variables

## 6.2.1. Sub-quadrat richness

Path analysis (Fig. 5) revealed that sub-quadrat richness was positively associated with PPFD. This relation would seem to suggest light as a factor limiting fine-scale species richness in the system. However, the higher abundance of old field species at the edge and the constancy of sub-quadrat richness over the site (Fig. 1), although PPFD was higher in the forest interior, indicate that other factors associated with distance to the edge (e.g. seed dispersal) may be more important in determining plant population dynamics and community composition (Ries et al., 2004; Devlaeminck et al., 2005).

Sub-quadrat richness was also negatively associated with pH and elevation. These results are consistent with those of Beatty (1984) who found that micro-elevation played a significant role in species distribution: mounds presented less favorable growing conditions than pits, being dry, poor in nutrients, and subject to frost heaving and exposure in winter (see also Chen et al., 1999). However, elevation and pH varied with distance to the edge at our study site and indirect effects (from distance through elevation and pH) might be as or more significant for species richness than pH or elevation per se. Nevertheless, only a small proportion of the variance of the focus variable was explained by the model, indicating that other variables not considered in the present study were important determinants of sub-quadrat species richness.

## 6.2.2. Erythronium americanum cover

Path analysis revealed that E. americanum cover was influenced by most of the environmental variables. The strong relation between E. americanum cover and the variable X indicates that variations in cover were strongly associated with distance parallel to the edge (most likely a site-specific effect).

*Erythronium americanum* is a spring ephemeral plant that begins its growth in early spring and senesces with canopy closure (Muller, 1978). Light may thus be an important limiting factor for both growth and reproduction. It seems therefore reasonable to assume that sub-populations or clones that experience higher irradiances in the forest have a higher rate of increase: this would explain the observed direct positive relation between *E. americanum* cover and light on our study site.

The direct positive relation between *E. americanum* cover and elevation (reinforced by an indirect effect through soil moisture) may be explained by the fact that in spring mounds are dryer than pits, which are saturated with water at that time of the year (Beatty, 1984). This relation is also consistent with the increasing patch size of *E. americanum* at 40 m (Fig. 3), where elevation was generally higher and more homogeneous (Fig. 2). Another relation observed in the path analysis suggests that *E. americanum* may prefer low pH values. However, the biological meaning of such a preference is somewhat obscure, considering that observed pH values for the present study were constrained to a very small range.

#### 6.2.3. Acer saccharum cover

The analysis on *A. saccharum* seedling cover revealed fewer significant paths, compared to that on *E. americanum* cover, from the environmental variables (Fig. 5). Like *E. americanum* individuals, *A. saccharum* seedlings appear in spring; however, they persist over the entire growing season. We may therefore expect them to react differently to tree canopy closure and soil resources (nutrients and water). Indeed, the paths between *A. saccharum* seedling cover and PPFD, soil pH, organic matter, and moisture were all opposite in sign to those in the analysis on *E. americanum*.

The emergence of new *Acer saccharum* seedlings and the growth and survival of those newly emerged seedlings (of which seedling cover is the result) appear to have been negatively affected by the conditions prevailing in the forest interior. Indeed, the decrease of *A. saccharum* seedling cover with distance to the edge had a direct component (direct path between Y and seedling cover), but also an indirect one through PPFD, soil pH, and moisture (Fig. 5). These results are consistent with those of Meiners et al. (2002) who found lower probabilities of recruitment (attributed to higher herbivory) in the forest interior for *A. saccharum* seedlings, along a forest-old-field edge gradient.

#### 6.2.4. Model fit in the path analyses

For the three previous analyses (sub-quadrat richness, E. americanum cover, and A. saccharum cover), a better fit of the data to the model was obtained with the addition of a link between PPFD and soil moisture (LISREL, subcommand MI). Indeed, for this modified model, the minimum fit function chisquare was 13.235, with a P-value of 0.021 (d.f. = 5), the RMSEA was 0.046, with a  $P_{\text{RMSEA} < 0.05}$ -value of 0.528, and the GFI was 0.996 (the minimum fit function chi-square was 43.614, with a *P*-value < 0.001 (d.f. = 6), the RMSEA was 0.090 with a  $P_{\text{RMSEA}<0.05}$ -value of 0.004, and the GFI was 0.986 for the original model; see Section 5). PPFD measured at ground level represents the portion of light that filters through the canopy. Its intensity and heterogeneity are due, among other factors, to variations in canopy structure and in gap patterns. Similarly, rainwater reaches the ground more easily through the canopy close to gaps ('thinner' canopy) or directly in gaps (Ritter et al., 2005), often increasing soil moisture at microsites characterized by higher irradiances within the forest. Therefore, the addition of this link to our original model makes biological sense, although it has no effect on the explained proportion of variance of the focus variables.

### 6.2.5. Quadrat richness

The path analyses for quadrat richness (Fig. 6) were computed to determine whether richness at a slightly "coarser" scale (i.e.  $2 \text{ m}^2$ ) was mostly influenced by the average value of different abiotic variables or by their spatial heterogeneity. However, neither model explained a significant proportion of the variance of the focus variable, most likely because of the low number of data points (24). However, approximately the same proportion of variance ( $R^2$ ) was explained using either the mean of the variables or their CV. Thus, at the scale of these analyses, either resource availability or resource heterogeneity may be equivalent determinants of species richness (Tilman and Pacala, 1993).

# 7. Conclusion

Contrary to our expectations, light was lower, and soil moisture and organic matter were higher at the edge than in the forest interior. Probable causes are the great canopy stratification at the edge and the presence of canopy gaps in the forest interior. However, quadrat richness tended to decrease as a function of distance to the edge, a result consistent with the higher heterogeneity of species richness at the finest scale studied (per sub-quadrat), which also tended to decrease with distance to the edge. The edge brought few changes in the spatial structure of the variables, except for E. americanum cover whose patch size increased with distance and for light, which was higher and more heterogeneous in the forest interior. At the finest scale studied (sub-quadrat), only a small part of the variance of the focus variables was explained by the path models. It may be that, at this scale, stochastic processes related to mortality, predation, seed dissemination, species interactions, and other biotic factors not considered in the present study were important. At the quadrat scale, both resource availability and heterogeneity were equivalent determinants of species richness.

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