# STRUCTURE AND COMPOSITION OF RIPARIAN BOREAL FOREST: NEW METHODS FOR ANALYZING EDGE INFLUENCE

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*Abstract.* Riparian ecotones at lakeshore edges are prominent features on the heterogeneous boreal forest landscape. We introduce a new method (the critical values approach), which incorporates inherent variability in interior forest, to quantify distance of edge influence at lakeshore forest edges. We use this method to examine the variation in forest structure and composition along the lakeshore forest edge-to-interior gradient in the mixedwood boreal forest. Our objectives were: (1) to quantify distance of edge influence for forest structure and composition at lakeshore forest edges; and (2) to investigate spatial pattern in vegetation along the edge-to-interior gradient. Trees, coarse woody material, saplings, shrubs, and herbs were sampled in plots at varying distances along 200-m transects established perpendicular to lakeshore forest edges. Distance of edge influence was determined by comparing mean values at different positions along the transect to critical values established from a randomization test of interior forest data. The spatial pattern of four selected species along the edge-to-interior gradient was assessed using split moving window analysis and wavelet analysis. The results suggest that a distinct lakeshore forest edge community exists. This community was ~40 m wide and was characterized by greater structural diversity, larger amounts of coarse woody material, and more saplings and midcanopy trees than interior forest. Distance of edge influence for understory composition was generally greater than for forest structure. Patterns of response for different species along the edge-to-interior gradient were related to shade tolerance. Lakeshore forest edges are distinct landscape elements, but their prominence depends on the reference forest, species, and scale.

*Key words: boreal forest; edge effects; forest structure; heterogeneity; randomization test; riparian forest; understory composition, wavelet analysis.*

## INTRODUCTION

Natural forest edges and ecotones are prominent components of the spatial heterogeneity of forested landscapes. Research on natural forest edges can contribute to our understanding of landscape pattern and process through: (1) documentation of ''edge influence,'' defined here as the change (e.g., in forest structure and composition) along the edge-to-interior gradient; and (2) characterization of the internal structure of edges. For pattern, an understanding of the distance of edge influence is necessary for determining the width of riparian forest habitat that is different from interior forest. In terms of process, the internal structure of the edge can affect boundary permeability, and therefore movement of organisms and other fluxes across the landscape (Wiens et al. 1985, Forman and Moore 1992).

Many studies have examined anthropogenically created forest edges (e.g., Ranney et al. 1981, Chen et al. 1992), but few have investigated natural, inherent edg-

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es such as forest edges adjacent to water bodies. Lakeshore forest edges differ from created edges in that they form across complex gradients of topography, hydrology, soil, light, and wind (Pabst and Spies 1998), and are dynamic, with intermittent disturbance from water table fluctuations (Naiman et al. 1993), ice scour (Holt et al. 1995), and beaver activity (Johnston and Naiman 1987). In areas managed for timber production, lakeshore riparian forest buffer zones will, over time, become the primary remaining unharvested forest in the region. However, only a few investigations of riparian forests have considered variation along a spatial gradient (Wood and Wood 1989, Hibbs and Giordano 1996, Pabst and Spies 1998).

The mixedwood boreal forest is appropriate for investigatation of lakeshore forest ecotones within a heterogeneous landscape. The aspen-dominated boreal forest in northern Alberta exhibits multi-scaled heterogeneity due to natural disturbance (insect outbreaks, fire), topography, hydrology, and its mixedwood nature (Cumming et al. 1996). Within the context of this extensive natural heterogeneity, edge influence from landscape features such as lakeshore forest edges may not be very dramatic.

We examined variation in forest structure and composition along an edge-to-interior gradient at lakeshore forest edges in the boreal mixedwood forest in order:

(1) To quantify distance of edge influence for forest structure and composition at lakeshore forest edges; and (2) To investigate spatial pattern in vegetation along the edge-to-interior gradient. In the process, we explored new applications of methods for assessing spatial pattern along the edge-to-interior gradient. Further, we developed a new ''critical values approach'' for quantifying the distance of edge influence which incorporates inherent variability in interior forest and which lacks the assumptions of most parametric tests.

## ANALYSIS OF EDGE INFLUENCE

Assessment of distance of edge influence (DEI) is essential for determining the effective size of interior forest in forest fragments and buffer strips (e.g., Laurance and Yensen 1991). However, DEI, or edge width, is difficult to quantify. Changes in forest structure and composition along edge-to-interior gradients are almost always gradual without an obvious single discontinuity (Ranney et al. 1981). Most edge influence methods are not designed to provide information on the pattern of change at the edge. In addition, they often appear to violate assumptions of independence of samples (e.g., Wales 1972, Ranney et al. 1981), and therefore cannot analyze nonnormal, autocorrelated, nonstationary data that are common in research on landscape boundaries (Gosz 1991).

Quantification of edge influence requires an objective and relevant criterion. Chen et al. (1992) provided an objective, but arbitrary, criterion for DEI as two thirds of the condition of interior forest. Few methods for determining DEI have considered the usefulness of variation within interior forest for this purpose. Laurance et al. (1998) provided an appropriate measure of the variability in interior forest through a 95% confidence interval of forest interior plots. However, their use of a fitted curve may lead to inaccurate estimates of DEI if the model of the curve is inappropriate.

We introduce a new method, the critical values approach, which quantifies DEI in the context of a community with inherent variability, and which reduces the effect of spatial autocorrelation. We define DEI as the set of distances from the edge where a given variable is significantly different from the inherent variability in interior forest (sensu ''edge width,'' Forman 1997). Statistical significance is based on comparison to critical values calculated through randomization tests on interior forest data. Randomization tests do not assume random sampling, but still maintain high statistical power (Crowley 1992).

The pattern of change along the edge-to-interior gradient, which provides a more detailed examination of the nature of the edge zone, can be assessed through edge detection techniques. These methods investigate change in vegetation along a spatial gradient, usually with the purpose of finding discontinuities or ''edges'' (defined as the areas of highest rate of change, Fortin 1994). Edge detection along one dimension is usually performed using split moving window analysis (e.g., Brunt and Conley 1990), although wavelet analysis has been recently introduced to plant ecology (Bradshaw and Spies 1992, Dale and Mah 1998). We explore these techniques to analyze the spatial pattern of selected species along an edge-to-interior gradient.

## METHODS

### Study area

Research was conducted in *Populus*-dominated mixedwood forest in Alberta, Canada (Mid-Boreal Mixedwood Ecoregion, Strong 1992), a forest type which is common throughout the southern boreal forest of western Canada (Rowe 1972, Strong 1992). This region has a boreal climate (mean summer temperature, 13.5°C; mean winter temperature, −13.2°C; annual precipitation, 397 mm, mostly in the summer; Strong 1992). Gray Luvisol soils predominate on undulating morainal plains with some Eutric Brunisol soils on more xeric sites (Rowe 1972, Strong 1992).

The study area included forest communities surrounding seven lakes (14–120 ha in size) in two regions: near Lac La Biche, Alberta (55° N, 112° W, ~610 m above sea level), and near Calling Lake, Alberta (55° N, 114° W, ~640 m above sea level). The forest edge was bounded by a zone of nonforest vegetation, 0–40-m wide, which covered the area up to the lakeshore. Slope over the first 50 m into the forest ranged from 0% to 25%. Stands ranged in age from 60 to 130 years, with canopy heights of 15 to 30 m. Forest stands were dominated by *Populus tremuloides* and *P. balsamifera* (90–100% of the total canopy tree density), with some *Betula papyrifera* and *Picea glauca.* There was a prominent shrub layer (including *Amelanchier alnifolia, Corylus cornuta, Lonicera* spp., *Ribes* spp., *Rosa acicularis, Rubus idaeus, Symphoricarpos albus,* and *Viburnum edule*) of up to 1.5 m in height, and occasionally a layer of taller *Alnus* spp., *Prunus* spp., or *Salix* spp. (2–5 m in height). The understory herb layer was diverse; *Aralia nudicaulis, Calamagrostis canadensis, Lathyrus ochroleucus, Aster* spp., *Petasites palmatus, Cornus canadensis, Maianthemum canadense,* and *Fragaria virginiana* were among the most abundant species. Lichen and moss cover was generally <10%.

### Distance of edge influence

*Sampling design.*—Two types of transects were established to sample lakeshore forest edge-to-interior gradients and upland interior forest. Twelve transects (200 m long) were established at six lakes, perpendicular to lakeshore forest edges (limit of the continuous canopy), and extended into the interior forest. All sampled edges had predominantly south-facing aspects (±60°), which we expected to have the greatest distance of edge influence (e.g., Wales 1972). Ten forest transects (200 m) were located in interior forest stands of similar composition, but 300–800 m away from any

open water and 100 m away from any major clearings. All transects were located so as to avoid conifer-dominated stands or extensive wetlands. All transects were ≥100 m apart, and there were no more than four lakeshore forest transects at a given lake, or more than two interior forest transects within 1 km². 

Plots (20 m × 5 m) were established along each transect (length perpendicular to the transect) at the following distances: 0, 5, 10, 20, 40, 60, 100, 150, and 200 m. An additional plot along the lakeshore edge transects, established in the riparian zone 10 m from the forest edge towards the lake (−10 m), was used to sample shrubs, trees, and downed coarse woody material (CWM). Within each plot, two shrub subplots (2 m × 2 m) and three herb subplots (0.5 m × 0.5 m) were established systematically along the major axis of the plot. Data were collected in summer 1996.

*Data collected.*—Trees (≥5 cm diameter at breast height; breast height = 1.3 m) and snags (≥5 cm diameter at breast height, ≥ 50 cm tall) were tallied in the 20 m × 5 m plots. For trees, we recorded species and diameter at breast height, and classified canopy position (relative height) for trees (mid-canopy, subcanopy, or canopy). Diameter was noted for all pieces of CWM (>8 cm in diameter at the intersection point; decay classes 1–3 out of 7 [Lee et al. 1995]) which intersected the major axis of the plot. Canopy cover was measured at the center of each plot using a convex spherical densiometer. We estimated percent cover of all shrub and sapling species, tallied the number of saplings, and measured the maximum height of saplings within the shrub subplots; we also estimated the cover of all forbs and dwarf woody species within the herb subplots. Cover was visually estimated to the nearest 1% up to 5%, and to the nearest 10% thereafter. Nomenclature follows Moss (1992). Data on canopy cover, and herb, shrub, and sapling composition were collected for ten of the twelve lakeshore forest edge transects (due to time constraints) and all of the upland interior forest transects.

*Data analysis.*—Additional response variables included shrub and herb species richness (per subplot) and diversity (Shannon index, Shannon and Weaver 1949), and total shrub and herb cover (sum of the cover of all species in each subplot). To summarize trends in species composition, correspondence analyses were performed on the herb and shrub species composition data along the lakeshore forest edge transects using CANOCO (ter Braak 1991). Ordination scores for subplots along the first axis were then used as response variables.

To quantify distance of edge influence (DEI), mean values at difference distances from the edge were compared to critical values based on randomization of data from the interior forest. Two different reference data sets were used to represent interior forest: (1) the adjacent riparian forest, using data from plots at 100, 150, and 200 m from the lakeshore forest edge; and (2) the

upland interior forest using data from all plots along the interior forest transects. These two data sets were used to compare edge influence to variability within the same stand and within regional interior forest, respectively. Randomizations were performed for each response variable within each reference data set using Visual Basic in Excel (Microsoft, Redmond, Washington, USA) following these steps:

1) Interior forest values were selected from each transect using one of the following (A–F) steps. For adjacent riparian forest (using only plots at 100, 150, and 200 m position):
   A) Trees and CWM: One plot value (of three possible at each transect) was randomly selected from each of the 12 transects.
   B) Shrubs and saplings: Two subplot values (of the six possible shrub subplots at each transect) were randomly selected from each of the 10 transects.
   C) Herbs: Three subplot values (of the nine possible herb subplots at each transect) were randomly selected from each of the 10 transects.

For upland interior forest (using all nine plots at each transect):

   D) Trees and CWM: One plot value (of nine possible at each transect) was randomly selected from each of the 10 transects.
   E) Shrubs and saplings: Two subplot values (of the 18 possible shrub subplots at each transect) were randomly selected from each of the 10 transects.
   F) Herbs: Three subplot values (of the 27 possible herb subplots at each transect) were randomly selected from each of the 10 transects.
2) The mean of the values obtained in Step 1 was calculated.
3) Steps 1 and 2 were repeated for a total of 5000 permutations.

Critical values were the 2.5 and the 97.5 percentiles of the 5000 permuted means (two-tailed test, $\alpha = 0.05$). Separate sets of critical values were established for each response variable and for each of the two reference data sets. Mean values at different distances from the lakeshore forest edge were considered to be significant if they lay outside the critical values. In our use of randomization tests, the null hypotheses is: The mean observed value at a given distance from the edge is no different than would be expected by chance in the reference (interior) forest (Crowley 1992). Distance of edge influence was defined as the set of consecutive distances for which mean values were significantly different than the reference forest.

Randomization tests have fewer limitations than parametric tests, but our critical values approach still does assume homogeneity of variances (between plots near the edge and those in the interior) and equivalent sample sizes. For trees and CWM, $n = 12$ at the edge
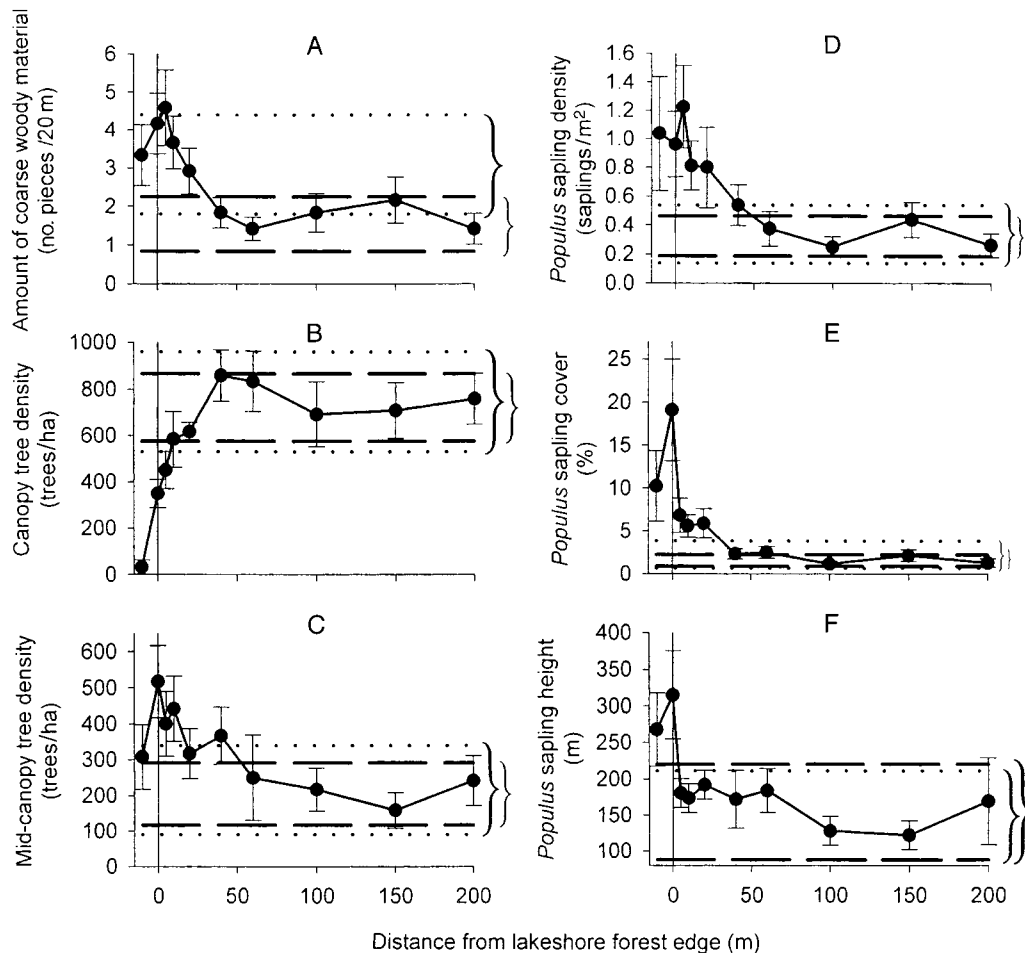
FIG. 1. Mean values along the lakeshore forest edge-to-interior gradient for forest structure: (A) amount of coarse woody material, (B) canopy tree density, (C) mid-canopy tree density, (D) *Populus* spp. sapling density, (E) *Populus* spp. sapling cover, and (F) *Populus* spp. sapling maximum height. Dashed and dotted lines indicate critical values determined by randomization tests of the adjacent riparian forest and the upland interior forest, respectively. Significant values are those that occur outside the critical values. Bars represent ± 1 SE which was calculated among all subplots for D, E, and F.

and $n = 10$ in the upland interior; thus, the type I error rate is expected to be slightly lower than 5%. The critical values approach applies only to means, and not to values at individual locations. Since our objective was to develop an understanding of the mean distance of edge influence for lakeshore forest edges in this region, we chose to maximize the number of independent replicates (transects at different locations) rather than sample thoroughly along a single transect (more subsamples). Another assumption of our approach, and of randomization tests in general, is that statistical inferences apply to samples rather than the underlying population (Crowley 1992). We infer that our results apply to our study region since we replicated transects at several sites. However, our selection of transect locations was biased towards distinct edges; vegetation patterns along edge-to-interior gradients at uneven edges may be weaker than those we report here.

*Spatial pattern analysis*

*Sampling design and data collection.*—Seven transects of contiguous 10 cm × 10 cm quadrats were set up perpendicular to lakeshore forest edges at four lakes in June 1997 for more intensive study on spatial pattern analysis. Transects began at the water's edge and extended into the forest up to 150 m from the edge. We chose three species for this part of the study based on observed strong trends along the lakeshore forest edge-to-interior gradient in our 1996 data (*Lathyrus ochroleucus, Linnaea borealis,* and *Mitella nuda*). In addition, *Calamagrostis canadensis* was chosen as a relatively shade-intolerant, disturbance-adapted species. Data included: presence/absence of *C. canadensis* and *L. ochroleucus* (six of the seven transects), and cover (to the nearest 5%, 25%, 50%, 75% or 100%, all transects) of *L. borealis* and *M. nuda.*

*Data analysis.*—We used split moving window anal-

TABLE 1. Mean values ($\pm 1$ SE) of the forest-structure response variables at different distances from the lakeshore forest edge in the nonforested riparian zone ($-10$ m) and in the upland interior forest.

| Distance from edge (m) | Canopy cover (%) | Tree density (individuals/ha) | | | | Snag density (snags/ha) | | |
|---|---|---|---|---|---|---|---|---|
| | | *Populus tremuloides* | *Populus balsamifera* | Large shrubs† | Total | *Populus tremuloides* | Large shrubs† | Total |
| $-10$ | $65 \pm 7$[ab] | $120 \pm 110$[ab] | $80 \pm 30$ | $110 \pm 60$[ab] | $380 \pm 130$[ab] | $10 \pm 10$[ab] | $110 \pm 70$[a] | $380 \pm 180$[ab] |
| 0 | $81 \pm 3$ | **$630 \pm 140$[a]** | $170 \pm 50$ | $140 \pm 90$[ab] | $990 \pm 140$ | ***$140 \pm 40$[ab]*** | $130 \pm 50$[a] | $440 \pm 90$ |
| 5 | $79 \pm 4$ | **$650 \pm 170$[a]** | $170 \pm 80$ | $60 \pm 40$ | $990 \pm 120$ | ***$200 \pm 70$[ab]*** | $50 \pm 30$ | $420 \pm 90$[ab] |
| 10 | $77 \pm 3$ | $860 \pm 190$ | **$250 \pm 150$[a]** | $30 \pm 20$ | $1260 \pm 180$ | ***$150 \pm 50$[ab]*** | $80 \pm 40$ | $510 \pm 100$ |
| 20 | $82 \pm 2$[b] | $770 \pm 100$ | **$270 \pm 90$[a]** | $30 \pm 20$ | $1180 \pm 60$ | $300 \pm 80$ | $60 \pm 40$ | $680 \pm 140$ |
| 40 | $81 \pm 2$ | $1170 \pm 200$[ab] | $140 \pm 60$ | $70 \pm 30$[a] | $1420 \pm 190$[a] | $460 \pm 100$ | $70 \pm 40$ | $620 \pm 100$ |
| 60 | $81 \pm 1$ | $790 \pm 180$ | $270 \pm 90$[a] | $30 \pm 10$ | $1210 \pm 180$ | $390 \pm 70$ | $50 \pm 30$ | $640 \pm 90$ |
| 100 | $81 \pm 2$ | $860 \pm 200$ | $120 \pm 70$ | $40 \pm 30$ | $1100 \pm 160$ | $470 \pm 120$ | $40 \pm 20$ | $630 \pm 130$ |
| 150 | $81 \pm 2$ | $840 \pm 150$ | $130 \pm 40$ | $20 \pm 20$ | $1030 \pm 140$ | $390 \pm 90$ | $40 \pm 20$ | $530 \pm 90$ |
| 200 | $76 \pm 6$ | $900 \pm 190$ | $120 \pm 60$ | $20 \pm 20$ | $1310 \pm 180$ | $310 \pm 80$ | $20 \pm 10$ | $530 \pm 100$ |
| Interior | $77 \pm 1$ | $750 \pm 60$ | $190 \pm 30$ | $40 \pm 10$ | $1120 \pm 60$ | $410 \pm 40$ | $70 \pm 20$ | $640 \pm 40$ |
| DEI (m)‡ | | | | | | | | |
| Riparian | … | 0–5 | 10–20 | … | … | 0–10 | … | … |
| Upland | … | … | … | … | … | 0–10 | … | … |

*Notes:* Superscript letters a and b designate values that were significantly different from the adjacent riparian forest and the upland interior forest, respectively. Values at two or more consecutive distances that were significantly different from either reference data set are bold; values significantly different from both reference data sets are bold italic. Eight of the 34 significant results in this table were expected due to random chance.

† Large diameter shrubs (*Salix, Alnus, Prunus*).

‡ Distance of edge influence (DEI) was defined as the set of consecutive distances that were significantly different from the adjacent riparian forest (Riparian) or upland interior forest (Upland).

ysis to investigate the magnitude of change at two different scales along the edge-to-interior gradient. In this analysis, a window of size *x* is established at the start of the transect, and a measure of dissimilarity (*D*) is calculated between the two halves of the window (Turner et al. 1991). In our case, *D* was defined as the absolute difference in mean cover or frequency for each species. The window is then moved along the transect one quadrat at a time (Turner et al. 1991). Scale can be changed by varying *x* (Brunt and Conley 1990). We tried several scales (window widths of 2, 4, 8, 12, 16, and 20 m), but only present the results for scales of 4 and 20 m. The output for these two window widths represented two different patterns: highly variable with many discontinuities at the 4-m scale, and broad changes with only a few discontinuities at the 20-m scale. We summarized the results by calculating the mean of all *D* values within 10-m intervals. Analyses were performed in Excel using Visual Basic (Microsoft, Redmond, Washington, USA).

Wavelet analysis, using the Haar wavelet, was also applied to the contiguous quadrat data. The Haar wavelet function is considered the most useful for detecting discontinuities (Bradshaw and Spies 1992), and indicates locations of sharp gradients in the data, as opposed to absolute changes (which may occur along a more gentle gradient) detected by split moving window analysis. In this method, data within the window were compared to the Haar wavelet function; values for the wavelet transform (*W*) can be visualized as the degree to which the data matched the wavelet function (Bradshaw and Spies 1992). The output is a matrix of values of *W* for all positions at all scales (Bradshaw and Spies

1992). Position variance is the mean of $W^2$ at all scales for a given distance (Dale and Mah 1998). Values of position variance were averaged within 10-m intervals.

### RESULTS

#### *Distance of edge influence*

Lakeshore forest edges were more structurally diverse than interior forest with more downed coarse woody material (CWM), saplings, and mid-canopy trees. The amount of CWM 0–20 m from the edge was significantly greater than the adjacent riparian forest, but not the upland interior forest since the two sets of critical values differed dramatically (Fig. 1A). Canopy cover and total tree density did not exhibit any significant edge influence (Table 1) since a greater number of mid-canopy trees at the edge was balanced by fewer canopy trees (Fig. 1B, C). Only four species of trees were found in the study area (*Populus tremuloides, P. balsamifera, Betula papyrifera,* and *Picea glauca*). However, at the lakeshore forest edge (0 m), there was a relatively high number of shrubs with diameter at breast height >5 cm that were classified as trees (*Alnus* spp., *Prunus* spp., and *Salix* spp.). Trends in density differed among the dominant tree species as *P. tremuloides* was significantly less dense 0–5 m from the edge, and *P. balsamifera* was significantly more dense 10–20 m from the edge, compared to the adjacent riparian forest. There was no apparent trend for overall snag density, but significantly greater numbers of snags of large diameter shrubs (only at $-10$ and 0 m) and lower numbers of *P. tremuloides* snags (DEI = 0–10 m) were found at or near the edge. Edge influence on

TABLE 2. Mean values (± SE) of the understory composition response variables at different distances from the lakeshore forest edge, in the nonforested riparian zone (−10 m) and in the upland interior forest.

| | Distance from the lakeshore forest edge (m) | | | | |
|---|---|---|---|---|---|
| Response variable | −10 | 0 | 5 | 10 | 20 |
| Ordination, first axis (shrubs) | 0.85 ± 0.29[a] | 0.30 ± 0.18[a] | 0.00 ± 0.21[a] | 0.02 ± 0.17 | 0.00 ± 0.15[a] |
| Shrub richness (no. species/0.75 m²) | 4.6 ± 0.6[ab] | 5.8 ± 0.4 | 5.8 ± 0.4 | 5.8 ± 0.5 | 5.9 ± 0.4 |
| Shrub percent cover | 62 ± 10 | 63 ± 8 | 68 ± 8 | 64 ± 10 | 58 ± 10 |
| Shrub diversity (Shannon index) | 0.92 ± 0.13[ab] | 1.22 ± 0.08 | 1.16 ± 0.09[a] | 1.30 ± 0.10 | **1.38 ± 0.06**[b] |
| Ordination, first axis (herbs) | | **0.47 ± 0.29**[a] | **0.28 ± 0.27**[a] | **0.13 ± 0.16**[a] | −0.15 ± 0.09 |
| Herb richness (no. species/0.75 m²) | | 8.8 ± 0.8 | 9.7 ± 0.7 | 10.0 ± 0.5 | *11.3 ± 0.5*[ab] |
| Herb percent cover | | 46 ± 7[ab] | 66 ± 7 | **79 ± 9**[b] | **88 ± 6**[ab] |
| Herb diversity (Shannon index) | | **1.57 ± 0.11**[a] | **1.59 ± 0.10**[a] | **1.62 ± 0.06**[a] | **1.59 ± 0.07**[a] |
| Percent cover of individual shrub species | | | | | |
| Edge-positive | | | | | |
| *Amelanchier alnifolia* | 6.8 ± 4.0[ab] | *9.8 ± 3.3*[ab] | *10.0 ± 3.0*[ab] | *6.2 ± 1.8*[ab] | *7.8 ± 2.9*[ab] |
| *Lonicera dioica* | 0.4 ± 0.3[a] | 1.2 ± 0.4 | **1.6 ± 0.7**[b] | **2.2 ± 0.6**[ab] | **1.6 ± 0.7**[b] |
| *Prunus* spp. (*P. pensylvanica* and | | | | | |
| *P. virginiana*) | 1.4 ± 0.7[a] | **1.0 ± 0.6**[a] | **3.5 ± 2.2**[ab] | **2.8 ± 1.4**[a] | **4.8 ± 3.6**[ab] |
| *Salix* spp. | 18.4 ± 6.5[ab] | *5.6 ± 3.1*[ab] | *1.3 ± 0.6*[ab] | 0.4 ± 0.3 | 1.0 ± 0.6[a] |
| *Symphoricarpos albus* | 1.3 ± 0.6 | **2.2 ± 0.7**[a] | **3.8 ± 1.7**[ab] | 1.6 ± 0.4 | *2.7 ± 1.0*[ab] |
| *Vaccinium myrtilloides* | 5.2 ± 4.1[ab] | *8.0 ± 5.6*[ab] | *2.5 ± 2.0*[ab] | *8.0 ± 4.4*[ab] | 0.5 ± 0.5 |
| Edge-negative | | | | | |
| *Alnus crispa* | 5.5 ± 3.2 | 5.0 ± 2.2 | 10.0 ± 5.9 | 7.5 ± 4.9 | *0.0 ± 0.0*[ab] |
| *Ribes triste* | 0.8 ± 0.3[b] | 2.2 ± 0.8 | 2.0 ± 0.8 | **1.3 ± 0.6**[a] | **1.1 ± 0.6**[ab] |
| *Rubus idaeus* | 7.2 ± 3.9[b] | **2.4 ± 1.1**[a] | **2.0 ± 1.0**[a] | **1.8 ± 0.6**[a] | **2.6 ± 0.7**[a] |
| Percent cover of individual herb species | | | | | |
| Edge-positive | | | | | |
| *Apocynum androsaemifolium* | | **0.8 ± 0.7**[a] | **2.9 ± 1.9**[ab] | **2.3 ± 2.3**[a] | **0.5 ± 0.4**[a] |
| *Aster conspicuus* | | 2.3 ± 0.8 | 3.2 ± 1.5[a] | 4.8 ± 1.6[ab] | 3.1 ± 1.8[a] |
| *Equisetum arvense* | | *0.6 ± 0.1*[ab] | *0.7 ± 0.2*[ab] | *0.5 ± 0.1*[ab] | *0.3 ± 0.1*[ab] |
| *Fragaria virginiana* | | 2.2 ± 0.6 | 2.7 ± 0.8 | 4.0 ± 1.0[a] | 4.2 ± 1.1[ab] |
| *Galium boreale* | | 0.7 ± 0.2 | *1.1 ± 0.2*[ab] | *0.8 ± 0.1*[ab] | *1.0 ± 0.2*[ab] |
| *Lathyrus ochroleucus* | | 2.5 ± 0.5 | **6.0 ± 1.2**[a] | **6.7 ± 1.4**[ab] | **7.3 ± 1.5**[ab] |
| *Maianthemum canadense* | | 3.3 ± 0.8 | **5.9 ± 1.6**[ab] | **8.8 ± 2.4**[ab] | **5.6 ± 1.1**[ab] |
| *Orthilia secunda* | | **0.3 ± 0.2**[a] | **0.4 ± 0.3**[a] | **0.8 ± 0.7**[ab] | **0.3 ± 0.2**[a] |
| *Petasites palmatus* | | *4.9 ± 1.5*[ab] | *3.8 ± 1.2*[ab] | *3.9 ± 1.7*[ab] | *4.4 ± 1.0*[ab] |
| *Pyrola asarifolia* | | 0.6 ± 0.2 | *1.4 ± 0.3*[ab] | *1.6 ± 0.3*[ab] | 1.0 ± 0.3 |
| *Thalictrum venulosum* | | **0.2 ± 0.2**[b] | **0.2 ± 0.2**[b] | **0.2 ± 0.1**[b] | **1.2 ± 0.7**[ab] |
| *Vicia americana* | | **0.9 ± 0.3**[b] | **1.4 ± 0.5**[ab] | **2.3 ± 0.6**[ab] | *1.2 ± 0.3*[ab] |
| Edge-negative | | | | | |
| *Aralia nudicaulis* | | **13 ± 3**[ab] | **19 ± 4**[a] | **23 ± 5**[a] | 33 ± 5[b] |
| *Cornus canadensis* | | **2.2 ± 1.0**[ab] | **3.6 ± 1.7**[b] | **2.3 ± 0.8**[ab] | 5.6 ± 2.6 |
| *Linnaea borealis* | | *0 ± 0*[ab] | *0.3 ± 0.2*[ab] | *0.8 ± 0.3*[ab] | 1.4 ± 0.7 |
| *Mitella nuda* | | *0.1 ± 0.1*[ab] | *0.3 ± 0.1*[ab] | *0.3 ± 0.1*[ab] | 0.9 ± 0.5 |
| *Rubus pubescens* | | **3.1 ± 0.9**[a] | **3.0 ± 1.1**[a] | 5.7 ± 1.4 | 7.0 ± 1.7 |

*Notes*: Superscript letters a and b designate values that were significantly different from the adjacent riparian forest and the upland interior forest, respectively. The standard error was calculated among all subplots. Values at two or more consecutive distances that were significantly different from either reference data set are set in bold type; values significantly different from both reference data sets are set in bold, italic type. We defined distance of edge influence (DEI) as the set of consecutive distances that were significantly different from the adjacent riparian forest (Riparian) or upland interior forest (Upland). For individual shrub and herb covers, species are subdivided into ''edge-positive'' and ''edge-negative'' (greater and lower cover, respectively); only common species with >10% frequency were included. Thirty of the 243 significant results in this table were expected due to random chance.

*Populus* spp. saplings extended up to 20 m, 60 m, and 0 m for density, cover, and height, respectively (Fig. 1D, E, F). The riparian zone (−10 m, Fig. 1, Table 1) was characterized by a diverse structure with greater amounts of CWM, mid-canopy trees, large diameter shrubs, and taller saplings; but lower canopy cover, overall tree density, tree diameter, and snag density than interior forest.

Herb species composition, as summarized by ordination scores along the first axis, was significantly different from the adjacent riparian forest 0–10 m and 40–60 m from the lakeshore forest edge (Table 2). The ordination of shrub composition revealed no trend along the edge-to-interior gradient. Total shrub cover and shrub richness did not show any prominent trends. Shrub diversity was significantly higher than the upland interior forest 20–150 m from the edge. Total herb cover was significantly lower at 0 m, and significantly higher further away from the edge as compared to the upland interior forest (DEI = 10–40 m). Herb species richness and diversity were significantly greater near the edge (DEI = 20–40 m and 0–40 m, respectively).

Many individual herb and shrub species exhibited strong responses along the edge-to-interior gradient.

TABLE 2. Extended.

| Distance from the lakeshore forest edge (m) | | | | | | DEI (m) | |
|---|---|---|---|---|---|---|---|
| 40 | 60 | 100 | 150 | 200 | Interior | Riparian | Upland |
| 0.06 ± 0.16 | −0.16 ± 0.23ᵃ | 0.26 ± 0.13 | 0.14 ± 0.18 | 0.07 ± 0.18 | ... | ... | ... |
| 5.8 ± 0.5 | **6.4 ± 0.4ᵇ** | **6.2 ± 0.4ᵇ** | 5.8 ± 0.4 | 5.4 ± 0.5 | 5.4 ± 0.1 | ... | 60–100 |
| 66 ± 10 | 80 ± 11ᵃᵇ | 61 ± 10 | 62 ± 9 | 56 ± 9 | 58 ± 3 | ... | ... |
| **1.32 ± 0.09ᵇ** | **1.32 ± 0.07ᵇ** | **1.37 ± 0.08ᵇ** | **1.32 ± 0.08ᵇ** | 1.25 ± 0.10 | 1.06 ± 0.04 | ... | 20–150 |
| **0.01 ± 0.03ᵃ** | **0.23 ± 0.29ᵃ** | −0.24 ± 0.06 | −0.17 ± 0.08 | −0.26 ± 0.07 | ... | 0–10, 40–60 | ... |
| ***10.8 ± 0.6ᵃᵇ*** | 9.5 ± 0.6 | 9.0 ± 0.6 | 10.1 ± 0.6 | 9.2 ± 0.5 | 9.2 ± 0.2 | 20–40 | 20–40 |
| **78 ± 8ᵇ** | 67 ± 6 | 72 ± 7 | 75 ± 7 | 71 ± 7 | 66 ± 2 | ... | 10–40 |
| **1.68 ± 0.06ᵃᵇ** | 1.44 ± 0.08 | 1.40 ± 0.08 | 1.43 ± 0.08 | 1.39 ± 0.08 | 1.53 ± 0.03 | 0–40 | ... |
| | | | | | | | |
| ***8.2 ± 2.9ᵃᵇ*** | **4.0 ± 1.0ᵇ** | 2.6 ± 0.8 | 2.1 ± 0.9 | 2.9 ± 1.2 | 1.6 ± 0.3 | 0–40 | 0–60 |
| 0.8 ± 0.3 | 1.6 ± 0.4ᵇ | **1.6 ± 0.6ᵇ** | 0.7 ± 0.2 | 1.6 ± 0.6ᵇ | 0.7 ± 0.1 | ... | 5–20, 60–100 |
| | | | | | | | |
| ***4.0 ± 2.7ᵃᵇ*** | 0.6 ± 0.5 | 0.3 ± 0.3 | 0.0 ± 0.0 | 0.6 ± 0.3 | 1.0 ± 0.3 | 0–40 | 20–40 |
| 0.1 ± 0.1 | 4.0 ± 3.0ᵃᵇ | 0.3 ± 0.3 | 0.3 ± 0.2 | 0.0 ± 0.0 | 0.3 ± 0.1 | 0–5 | 0–5 |
| ***2.2 ± 1.5ᵃᵇ*** | 1.6 ± 0.5 | 1.8 ± 0.6 | 1.2 ± 0.4 | 1.0 ± 0.3 | 1.3 ± 0.2 | 0–5, 20–40 | 20–40 |
| 0.4 ± 0.3 | 0.1 ± 0.1 | 0.2 ± 0.2 | **0.8 ± 0.5ᵇ** | 1.6 ± 1.5ᵇ | 0.2 ± 0.1 | 0–10 | 0–10, 150–200 |
| | | | | | | | |
| ***2.3 ± 1.5ᵃᵇ*** | **4.6 ± 4.5ᵇ** | 12.0 ± 6.1 | 6.8 ± 4.1 | 5.2 ± 4.0 | 10.7 ± 1.6 | 20–40 | 20–60 |
| 2.9 ± 1.2 | 1.9 ± 1.1 | 3.0 ± 1.5 | 4.4 ± 1.6 | 3.2 ± 1.5 | 3.5 ± 0.5 | 10–20 | ... |
| **1.6 ± 0.6ᵃ** | **6.0 ± 2.3ᵇ** | **6.1 ± 2.4ᵇ** | **8.2 ± 3.5ᵇ** | **7.2 ± 2.9ᵇ** | 2.3 ± 0.3 | 0–40 | 60–200 |
| | | | | | | | |
| **1.3 ± 1.3ᵃ** | **1.7 ± 1.1ᵃ** | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.6 ± 0.3 | 0–60 | ... |
| 5.2 ± 1.6ᵃᵇ | 2.4 ± 1.2 | 1.4 ± 1.0 | 1.9 ± 1.0 | 0.4 ± 0.2 | 2.0 ± 0.4 | 5–40 | ... |
| **0.2 ± 0.1ᵇ** | **0.2 ± 0.1ᵇ** | **0.2 ± 0.1ᵇ** | **0.1 ± 0.1ᵇ** | 0.1 ± 0.05 | 0.03 ± 0.01 | 0–20 | 0–150 |
| 2.1 ± 1.0 | 1.8 ± 0.6 | 1.1 ± 0.4ᵇ | 2.3 ± 0.7 | 2.5 ± 1.0 | 2.5 ± 0.3 | 10–20 | ... |
| 0.5 ± 0.1 | 0.7 ± 0.1ᵇ | 0.6 ± 0.1 | 0.6 ± 0.1 | 0.6 ± 0.1 | 0.5 ± 0.03 | 5–20 | 5–20 |
| ***6.7 ± 1.6ᵃᵇ*** | 3.3 ± 1.1 | 4.8 ± 1.3 | 3.8 ± 1.1 | 3.2 ± 0.9 | 4.1 ± 0.4 | 5–40 | 10–40 |
| **4.5 ± 0.9ᵇ** | 3.5 ± 0.7 | 4.6 ± 1.3ᵃᵇ | 3.3 ± 0.8 | 1.7 ± 0.4ᵃᵇ | 2.7 ± 0.2 | 5–20 | 5–40 |
| 0.03 ± 0.03 | 0.2 ± 0.1ᵃ | 0.1 ± 0.1 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.2 ± 0.04 | 0–20 | ... |
| 3.0 ± 0.8 | 3.4 ± 1.1ᵇ | 2.9 ± 0.9 | 2.4 ± 0.6 | 1.9 ± 0.5 | 1.7 ± 0.2 | 0–20 | 0–20 |
| 0.4 ± 0.1 | 0.3 ± 0.1 | 0.9 ± 0.3 | 0.6 ± 0.3 | 0.4 ± 0.3 | 0.6 ± 0.1 | 5–10 | 5–10 |
| **0.1 ± 0.1ᵇ** | **0.4 ± 0.2ᵇ** | **0.2 ± 0.2ᵇ** | **0.2 ± 0.1ᵇ** | **0.3 ± 0.2ᵇ** | 0.0 ± 0.0 | ... | 0–200 |
| ***1.5 ± 0.4ᵃᵇ*** | **0.7 ± 0.4ᵇ** | 1.2 ± 0.4ᵃᵇ | 0.5 ± 0.2 | 0.1 ± 0.1ᵃ | 0.3 ± 0.1 | 5–40 | 0–100 |
| | | | | | | | |
| 22 ± 4ᵃ | 28 ± 5 | 27 ± 5 | 32 ± 5 | 31 ± 5 | 24 ± 1 | 0–10 | ... |
| 7.8 ± 2.3ᵃ | **3.3 ± 1.1ᵃᵇ** | **4.2 ± 1.2ᵇ** | 7.3 ± 1.7 | 4.5 ± 1.5ᵇ | 8.5 ± 0.7 | ... | 0–10, 60–100 |
| 1.0 ± 0.4ᵃᵇ | 1.4 ± 1.0 | 2.1 ± 1.0 | 2.1 ± 0.9 | 4.8 ± 2.4 | 2.9 ± 0.4 | 0–10 | 0–10 |
| 1.0 ± 0.4 | 0.7 ± 0.3ᵇ | 0.7 ± 0.3 | 0.9 ± 0.3 | 1.3 ± 0.5 | 1.4 ± 0.2 | 0–10 | 0–10 |
| 8.2 ± 2.0 | 4.8 ± 1.3 | 7.8 ± 2.5 | 6.5 ± 2.3 | 7.0 ± 2.0 | 5.4 ± 0.6 | 0–5 | ... |

Nine of the fifteen common (>10% frequency) shrub species had significant distance of edge influence (DEI), generally up to 40 m when compared with the adjacent riparian forest (Table 2). Six species (*Amelanchier alnifolia, Lonicera dioica, Prunus* spp., *Salix* spp., *Symphoricarpos albus,* and *Vaccinium myrtilloides*) were classified as ''edge positive,'' and three species (*Alnus crispa, Ribes triste,* and *Rubus idaeus*) as ''edge negative'' (greater and lower cover near the edge, respectively). Of the 31 common herb species (>10% frequency), twelve (*Apocynum androsaemifolium, Aster conspicuus, Equisetum arvense, Fragaria virginiana, Galium boreale, Lathyrus ochroleucus, Maianthemum canadense, Orthilia secunda, Petasites palmatus, Pyrola asarifolia, Thalictrum venulosum,* and *Vicia americana*) were classified as ''edge positive,'' and five (*Aralia nudicaulis, Cornus canadensis, Linnaea borealis, Mitella nuda,* and *Rubus pubescens*) as ''edge negative'' (Table 2). For some ''edge positive'' species, DEI started at either 5 or 10 m. ''Edge positive'' species generally had greater DEI (up to 10 m or more) than ''edge negative'' species (0–5 or 0–10 m).

Most response variables were significantly different from either the adjacent riparian or the upland interior forest within 20–40 m of the lakeshore forest edge, although some differences persisted up to 60 m or more, particularly compared to the upland interior forest (Fig. 2). Within 20 m of the edge, more response variables had significant DEI when put in the context of the adjacent riparian forest, than in the context of the upland interior forest (Fig. 2A). Few forest structure response variables had DEI that extended beyond 20 m, whereas more understory species had greater DEI (Fig. 2B and C).

### Spatial pattern analysis

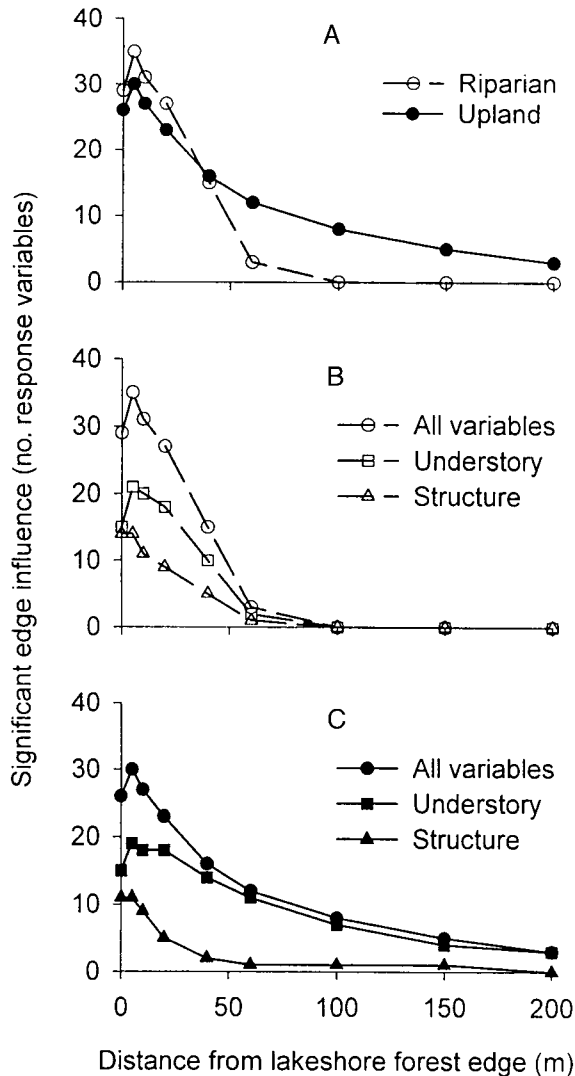All four selected species showed different patterns of abundance along the edge-to-interior gradient.

FIG. 2. Summary of the analysis of edge influence results to determine where edge influence occurs: number of response variables with significant distance of edge influence for different distances from the lakeshore forest edge. (A) Comparison between the adjacent riparian forest and the upland interior forest. (B) Comparison between understory composition and forest structure in the context of the adjacent riparian forest. (C) Comparison between understory composition and forest structure in the context of the upland interior reference forest.

Change in abundance of *Linnaea borealis* was relatively constant along the gradient, except for near 50 m (Fig. 3). *Mitella nuda* showed a marked change in cover >100 m from the edge. *Calamagrostis canadensis* and *Lathyrus ochroleucus* exhibited the greatest change in abundance just before and right at the lakeshore forest edge, respectively. Trends for the last two species were much more evident at the 20-m scale, and almost non-existent at the 4-m scale. Wavelet analysis showed very similar patterns to split moving window analysis (particularly using a window width of 20 m),

except for slightly larger peaks. However, for *Mitella nuda,* the peak near 130 m was much larger using position variance.

## DISCUSSION

### *Structure and composition of the lakeshore forest edge*

*Forest structure.*—Up to a distance of 40 m from the lakeshore forest edge, the riparian forest was structurally more complex and compositionally different than interior forest. Other studies have also shown greater structural heterogeneity in riparian forests and conform to our results of increased mid-canopy tree density, lower overstory cover, and fewer snags (McGarigal and McComb 1992, Murray and Stauffer 1995, Whitaker and Montevecchi 1997). Fewer snags and greater amounts of downed coarse woody material (CWM) at riparian edges could be the result of increased treefalls due to wind, beaver activity, or periodic flooding; and increased productivity leading to faster growth and earlier death (Malanson and Kupfer 1993).

*Understory composition.*—For several edge-positive herb species, the zone of edge influence started 5 m into the forest, although not for overall herb species composition. The cover of these species at the lakeshore forest edge (0 m) was, therefore, similar to interior forest. Immediately at the edge, greater sapling abundance could counteract the effect of increased light; in the boreal mixedwood, increased light from canopy openings is often compensated by development of the shrub layer (Constabel and Lieffers 1996). Alternatively, there could be complex interactions between water table depth and light level along the edge-to-interior gradient. According to Murcia (1995), such interactions of edge influence may be common; therefore the assumption of monotonic responses along the edge-to-interior gradient may be unrealistic.

As predicted by others (Naiman et al. 1993, Pabst and Spies 1998), we found greater herb diversity at the edge, but not herb richness (this occurred 20–40 m from the edge), shrub richness, or shrub diversity (this occurred 20–150 m from the edge). Van der Maarel (1990) suggested that low species richness would be expected at ecotones using the strict definition as a tension zone subject to high disturbance. Our lack of high species richness immediately at the lakeshore forest edge, which can experience flooding and ice scour, may lend support to his hypothesis. Increased herb diversity at the edge was due to changes in abundances of individual species; virtually no species were found only at the edge.

*Conceptual model.*—We propose the following conceptual model of edge influence on riparian forest. Exposure to wind and periodic disturbance (ice scour, water table fluctuations, and frequent beaver activity) contribute to increased tree mortality and treefalls at

Fig. 3. Change in abundance of four species along the edge-to-interior gradient using different analyses: split moving window analysis at the 4-m (dotted line) and 20-m (dashed line) scales, and position variance from wavelet analysis (solid line). Values are means for 10-m intervals along six or seven transects. Results were standardized for each analysis separately such that the mean equals 1.
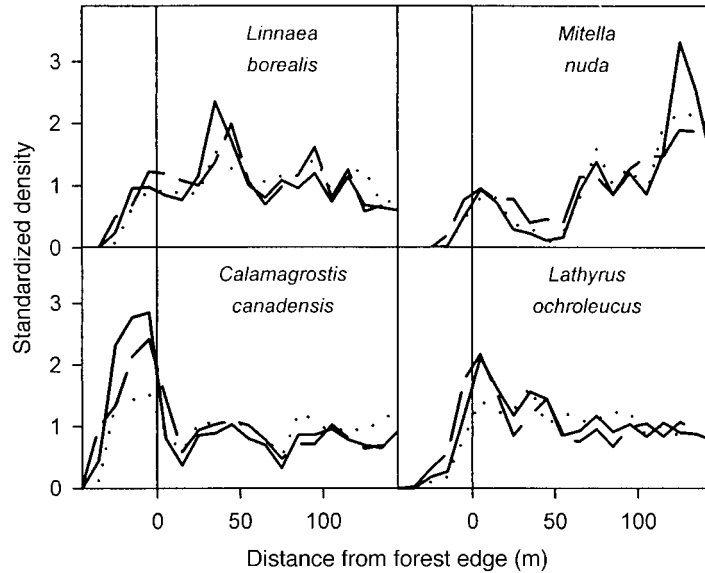
the lakeshore forest edge. The direct result is a reduction in canopy trees, more CWM, and fewer snags. Microclimatic and structural changes lead to secondary responses influenced indirectly by the edge environment, including increased sapling recruitment, and changes in understory composition. Our results indicate that edge influence extends further for these secondary responses than for primary responses. The edge environment is extended from the opening of the canopy due to structural damage at the edge. Results of greater distance of edge influence (DEI) for secondary responses from created edges (Palik and Murphy 1990, Williams-Linera 1990, Chen et al. 1992, Malcolm 1994) corroborate our hypothesis.

### Spatial pattern of the lakeshore forest edge

Lakeshore forest edges can be considered prominent landscape elements, but their distinction and pattern of the edge depends on the context, species of interest, and scale. The lakeshore forest edge community is more distinct within the context of the adjacent riparian forest, than it is within the context of the overall aspen-dominated forest on the landscape (at the edge, more variables are significantly different from the riparian forest than the upland interior forest). Patterns of response for different species along the edge-to-interior gradient suggest that the location of the highest amount of change (defined as "edge" for species composition, Fortin 1994) is related to shade tolerance. The "edge" was closer to the forest-canopy edge for understory tolerators ($-10$ m for *Calamagrostis canadensis,* 10 m for *Lathyrus ochroleucus*) than for understory obligates (40 m for *Linnaea borealis,* 120 m for *Mitella nuda*; see Lieffers 1995 for classification). For two species (*Calamagrostis canadensis* and *Lathyrus ochroleucus*) the pattern at the edge was less distinct at the smaller scale, confirming that ecotones can be scale dependent (Gosz 1991).

The lakeshore forest edge can function as habitat or as a barrier for wildlife within riparian forest stands. In the aspen-dominated mixedwood boreal forest, there is evidence that lakeshore edges may be attractive for some species (e.g., songbirds; Machtans et al. 1996), while other species appear to avoid them (e.g., Ovenbirds; Lambert 1998). Lakeshore forest edges may function as natural boundaries in the boreal forest landscape, since they have a mantel (Forman 1997) of increased sapling growth at and just outside the edge. This contradicts van der Maarel's (1990) view that only landscape elements, but not ecotones, perform barrier functions.

Plant species may respond to the edge in one of two ways: as a boundary of a patch, or as a continual gradient. The two understory species (*M. nuda* and *L. borealis*) appear to be responding to a gradient, with continual change from the lake to the forest. In contrast, the spatial patterns of the two other species, with dramatic changes in abundance before or at the edge, suggest the lakeshore forest edge is acting as a boundary. Following the cellular membrane analogy that describes boundaries as semipermeable membranes (Forman and Moore 1992), the lakeshore forest edge could theoretically be considered semipermeable to *C. canadensis,* which exhibits the greatest change in abundance on the nonforested side of the edge.

### Significance of new methods for studying edge influence

Spatial pattern analysis of selected species along the edge-to-interior gradient reveals new applications for split moving window analysis and wavelet analysis to discontinuous data. Edge detection methods using

overall species composition can reveal some information on the internal structure of the edge, such as different edge signatures for different patch structures (Brunt and Conley 1990). By examining one species at a time, however, we discovered different patterns of abundance across the edge. Wavelet analysis identified discontinuities in the data as in split moving window analysis, but provided little additional information. On this basis, it seems more practical to use the simpler method of split moving window analysis which appears to give similar results and is easier to program. Wavelet analysis does, however, have other potential applications in plant ecology (Bradshaw and Spies 1992, Dale and Mah 1998).

The critical values approach determines DEI in the context of interior forest with few assumptions. This method differs substantially from regression and other curve-fitting techniques (e.g., Chen et al. 1992, Laurance et al. 1998) which may not be appropriate for all edge data. We generally had very low $R^2$ when we fit our data to polynomial or exponential curves that assume the maximum or minimum value is at the edge (Harper 1999). Our results and others (e.g., Murcia 1995) challenge previously held ideas about edge width; the zone of edge influence may not begin exactly at the forest canopy edge.

The critical values approach for determining DEI should be flexible with regards to the type of response variable, size of plots, number of plots along transects, and number of transects. The use of randomization tests should be applicable to any ecosystem, any edge, any scale of sampling, and various sampling designs. Other methods (e.g., Chen et al. 1992, Laurance et al. 1998) may be acceptable for relatively homogeneous systems with more closed-canopy forest and very distinct edge effects, but may not be as suited to more heterogeneous ecosystems such as the mixedwood boreal forest. A further advantage is that different reference data sets can be used, providing information on edge influence in different contexts. The critical values approach is simple to understand and easy to program using standard computer software. We hope that this approach will aid in comparing DEI among different ecosystems and types of edge.

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