Journal of Vegetation Science 17: 625-636, 2006
© IAVS; Opulus Press Uppsala.

Changes in spatial pattern of trees and snags during structural development in *Picea mariana* boreal forests

Harper, Karen A.[1]; **Bergeron, Yves**[1,2*]; **Drapeau, Pierre**[1]; **Gauthier, Sylvie**[1,3] **& De Grandpré, Louis**[3]

[1]*Groupe de recherche en écologie forestière, Université de Québec à Montréal, CP 8888 succ. A, Montréal, QC, H3C 3P8, Canada;*
E-mail karenharper@eastlink.ca; E-mail drapeau.pierre@uqam.ca;
[2]*Université de Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada;*
[3]*Natural Resources Canada, Canadian Forest Service, Québec Region, C.P. 3800, 1055 rue du P.E.P.S., Sainte-Foy, QC, G1V 4C7, Canada; E-mail sgauthier@exchange.cfl.forestry.ca; E-mail ldegrandpre@exchange.cfl.forestry.ca;*
**Corresponding author: E-mail yves.bergeron@uqat.ca*

Abstract

Questions: How do gap abundance and the spatial pattern of trees and snags change throughout stand development in *Picea mariana* forests? Does spatial pattern differ among site types and structural components of a forest?

Location: Boreal forests dominated by *Picea mariana*, northern Quebec and Ontario, Canada.

Methods: Data on the abundance, characteristics and spatial location of trees, snags and gaps were collected along 200 m transects at 91 sites along a chronosequence. Spatial analyses included 3TLQV, NLV and autocorrelation analysis. Non-parametric analyses were used to analyse trends with time and differences among structural components and site types.

Results: Gaps became more abundant, numerous and more evenly distributed with time. At distances of 1-4 m, tree cover, sapling density and snag density became more heterogeneous with time. Tree cover appeared to be more uniform for the 10-33 m interval, although this was not significant. Patch size and variance at 1 m were greater for overstorey than for understorey tree cover. Snags were less spatially variable than trees at 1 m, but more so at intermediate distances (4 - 8 m). Few significant differences were found among site types.

Conclusions: During stand development in *P. mariana* forest, gaps formed by tree mortality are filled in slowly due to poor regeneration and growth, leading to greater gap abundance and clumping of trees and snags at fine scales. At broader scales, patchy regeneration is followed by homogenization of forest stands as trees become smaller with low productivity due to paludification.

Keywords: Chronosequence; Forest structure; Forest stand development; Gap dynamics; New local variance; Spatial autocorrelation; Three-term local quadrat variance.

Abbreviations: 3TLQV = Three-term local quadrat variance; NLV = New local variance.

Introduction

Changes in the spatial pattern of forest structure with time can provide insight into processes that occur throughout stand development. Clumping and regular distributions of plants have been linked with the interactions of facilitation and competition for limited resources, respectively (Malkinson et al. 2003). In early stages of forest stand development, competitive self-thinning leads to a more regular distribution of trees (Christensen 1977; Kenkel 1988; Moeur 1993; Peterson & Squires 1995; Lee et al. 1997), logs (Harmon et al. 1986) and small gaps (Spies et al. 1990; Bradshaw & Spies 1992; Kuuluvainen 1994). During later phases of development, spatial pattern dynamics are driven by fine-scale disturbances (Kuuluvainen et al. 1998) such as windthrow or insect outbreaks, resulting in a more clumped distribution of deadwood (Harmon et al. 1986) and more gaps of all sizes (Spies et al. 1990; Bradshaw & Spies 1992; Tyrrell & Crow 1994; Lertzman et al. 1996; Kneeshaw & Bergeron 1998; Chen & Popadiouk 2002). Present knowledge thus indicates that gap abundance and the spatial heterogeneity of trees and snags increases with time since disturbance. Although many studies have examined spatial pattern at different stages of development, only an investigation that spans all developmental stages following disturbance will be able to detect the full extent of trends in spatial pattern during succession. Likewise, the simultaneous examination of trends in gaps and the spatial pattern of both trees and snags will be able to link gap formation and the resulting spatial patterns of forest structure.

Spatial pattern of trees and gaps can also be affected by factors other than stand development, which could obscure trends with time since disturbance. Edaphic factors such as soil moisture can affect the distribution of trees and stand structure (Parish et al. 1999; Druckenbrod et al. 2005); autocorrelation of plants may be greater on more productive soils because of better growth of newly dispersed plants next to parent plants (Miller et al. 2002). Heterogeneity in the micro-environment could also cause clumping (McDonald et al. 2003). The abundance and spatial pattern of gaps can also differ among different forest types (Bartemucci et al. 2002). Therefore, the pattern of forest (and gap) structure may differ among sites with different species composition, productivity and superficial deposits. In particular, trends in spatial pattern with time may differ among sites that are continuously dominated by one species compared with sites that undergo succession of the dominant tree species during stand development.

We investigated gaps and spatial pattern of forest structure along a chronosequence following fire in three different site types in a boreal coniferous forest. Our main objective was to identify effects of self-thinning and fine-scale disturbance on the spatial pattern of trees and snags throughout stand development. Whereas most studies on spatial pattern include only a few sites, we developed new methods to compare spatial pattern among many sites along a chronosequence. We also assessed if there were differences in spatial pattern among different structural components (trees and snags of different sizes and decay stages) to indirectly infer changes related to forest structural development. Finally, we compared the spatial pattern of trees and snags, as well as the abundance of gaps, among three different site types (organic, clay and sand) to assess any differences in spatial pattern due to species composition or soil type.

Methods

Study area

We sampled sites in *Picea mariana* boreal forest in the northwestern part of the Abitibi region in Québec and in the Abitibi Lake Model Forest in Ontario (48°92' to 49°93' N; 78°64' to 80°64' W; Harper et al. 2005). This region is part of the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Objibway (Vincent & Hardy 1977). The topography is flat at an elevation of ca. 300 m a.s.l. Soils are predominantly organic, with clay deposits and some till (Gauthier et al. 2000). Mean annual temperature is 0.8/0.9 °C, annual precipitation is 856/792 mm, and there are 64/90 frost-free days (period 1961-1990, La Sarre, Québec and Iroquois Falls, Ontario weather stations respectively; Environment Canada, Anon. 1993).

Picea mariana is dominant in stands of all ages on clay and organic sites, and in older stands on sand sites (Harper et al. 2003). *Pinus banksiana* is often abundant on early-intermediate aged drier sites such as outwash deposits, old beaches and eskers, and some clay sites (Harper et al. 2003). Other early successional species (*Populus tremuloides* and *Salix* spp.) can be abundant in early-intermediate aged clay and sand stands (Gauthier et al. 2000; Harper et al. 2003). Therefore, structural development of the canopy coincides with changes in dominant species composition on sand sites, but is independent of species replacement in stands on organic sites which are always dominated almost exclusively by *Picea mariana* (Harper et al. 2002, 2003).

The disturbance regime in this region is characterized by large crown fires that kill most of the trees and above-ground vegetation (Harper et al. 2003). The recent fire history for the entire study area is available from a fire reconstruction by dendrochronology and aerial photograph interpretation (Bergeron et al. 2004).

Data collection

To determine changes in spatial pattern with time since fire, 91 sites were located in separate forest stands at least 1 km apart along a chronosequence (Fig. 1). Using the reconstructed fire history for the region to determine time since the most recent fire (Bergeron et al. 2004), we selected site locations to span a variety of ages. Accessibility and the lack of harvesting were also prerequisites for sites to be selected. Time since last fire was verified from tree age data collected from ten trees at each site. Sites were classified as organic-hydric, mesic to subhydric-clay and xeric-sand (cf. Gauthier et al. 1996) based on a combination of superficial deposit and hydric regime which were sampled at each site. Organic sites (25 sites) had an organic layer more than 60 cm thick and poor drainage; clay sites (45 sites) had clay deposits with moderate drainage; and well-drained sandy sites (20 sites) were designated as sand. This rough classification was used since the distinction between the three site types was usually clear with very few intermediate cases. The different types of sites were quite well interspersed (Fig. 1); therefore we assumed that differences among site types were not a result of random variation across the landscape that might occur if the site types were clumped.

Data were collected on the abundance, characteristics and spatial location of trees, snags and gaps along transects at all sites in 1996 and 1997. At each site, a 200-m transect was established except for 21 sites in small stands where 100-190 m transects were necessary to avoid logged areas or abrupt changes in environmental conditions. Gap diameter was measured as the distance along the transect between the first living branches on

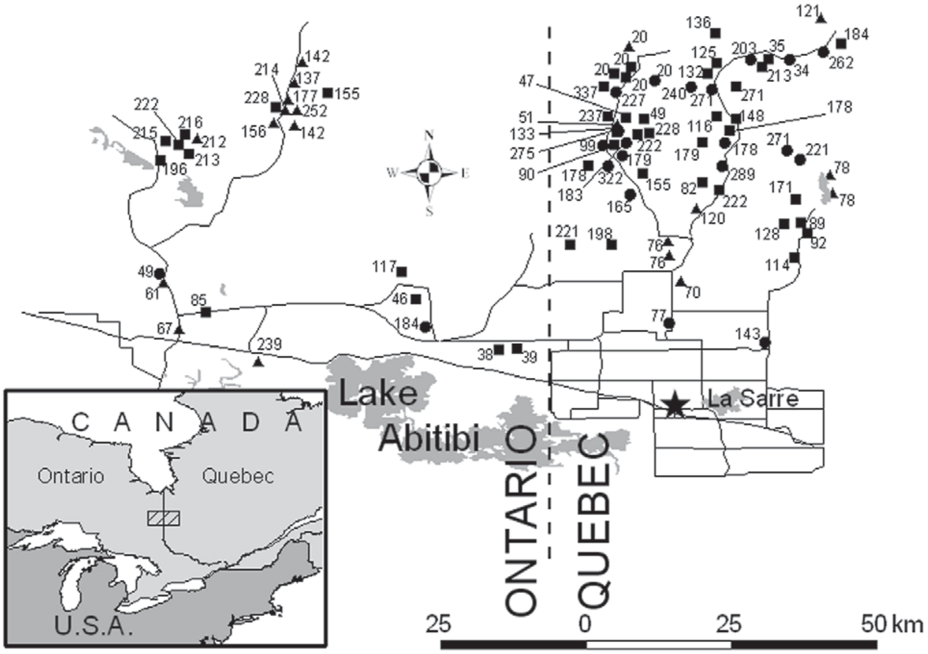


Fig. 1. Map of all the sites. Symbols represent the site type: organic (circles), clay (squares), sand (triangles). Sites are labelled with the time since the most recent fire. The inset map shows the location of the study area within Canada. Reprinted from Harper et al. (2005), Copyright (2006), with permission from Elsevier.

either side of a gap with evidence of a treefall. The vertical projection of the tree canopy was mapped to the nearest 10 cm along the transect; cover above and below 3 m was also noted separately as overstorey and understorey tree cover, respectively. All live trees and snags with DBH greater than or equal to 1 cm within a 200 m × 4 m wide rectangular plot centered on each transect were mapped with a accuracy of 1 m such that density was measured within a grid of 800 1 m × 1 m subplots. All trees and snags were measured for height and diameter at breast height. The results for saplings (height class 1-5 m and diameter class 1-5 cm) are presented in the main text; results of other size classes and decay classes for snags are presented in App. 2.

Spatial analyses

For each site, we used a combination of different spatial analyses to determine: (1) the patch size and variance for total, understorey (height less than 3 m) and overstorey (height greater than 3 m) tree cover; and (2) the degree of autocorrelation of tree, snag and sapling densities. To estimate the size of patches of trees for each site, we employed new local variance (NLV; Galiano 1982; Dale 1999) on the tree cover data: (1)

$$V_N(b) = \frac{\sum_{i=1}^{n-2b} \left| \left(\sum_{j=1}^{i+b-1} x_j - \sum_{j=i+b}^{i+2b-1} x_j \right)^2 - \left(\sum_{j=i+1}^{i+b} x_j - \sum_{j=i+b+1}^{i+2b} x_j \right)^2 \right|}{2b(n-2b)}$$

where $V_N(b)$ is the NLV for block size b (size of a block of quadrats, distance or 'scale'), n is the number of 'quadrats' or 10 cm segments along the transect and x is the tree cover (presence/ absence). In this paper, we use the term 'distance' or 'distance class' for the analysis of the data to identify the distance or spacing between sampling units (Dungan et al. 2002). The results of NLV are graphs of $V_N(b)$ vs. b. We assigned the patch size as the block size corresponding to the first tall peak by visually inspecting each graph. Since NLV determines the smaller of either patch or gap size, we converted gap size to patch size by dividing by the ratio of gap to tree cover if the ratio was less than one. Although there may be other scales of pattern, broader scales will likely be groups of patches or gaps.

The spatial pattern of forest structure at each site was assessed using both a paired quadrat variance method on the tree cover data and correlation analysis on the tree, snag and sapling density data. Three-term local quadrat variance (3TLQV) measured the amount of variability in tree cover at difference distances (Dale 1999): (2)

$$V_3(b) = \frac{\sum_{i=1}^{n+1-3b} \left(\sum_{j=1}^{i+b-1} x_j - 2\sum_{j=i+b}^{i+2b-1} x_j + \sum_{j=i+2b}^{i+3b-1} x_j \right)^2}{8b(n+1-3b)}$$

where $V_3(b)$ is the 3TLQV for block size b. Results for 3TLQV, consisting of graphs of $V_3(b)$ vs b, are usually interpreted on a site-by-site basis; although comparisons have been made among few sites (e.g. Dale & Blundon 1990; Bradshaw & Spies 1992; Dale & Zbigniewicz

1997). In order to assess the trends of spatial pattern with time since fire, we used a new method to summarize spatial pattern analysis results to allow comparisons among a large number of sites (cf. Bartemucci et al. 2002). First, we standardized the 3TLQV results by dividing $V_3(b)$ by the sample variance (Rossi et al. 1992), which enabled comparisons of trends in pattern, irrespective of trends in abundance. Mean values were then calculated over non-overlapping distance classes; we used 0.0-2.0, 2.1-6.0, 6.1-10.0 and 10.1-33.0 m. The first three intervals were chosen to complement results from correlation analysis of trees and snags (1, 4, 8 m; see below); and 33 m was the maximum possible block size for the shortest transect. Greater average variance would indicate greater relative heterogeneity in tree cover and therefore aggregation of trees within the particular distance class. We performed NLV and 3TLQV analyses on total, understorey and overstorey tree cover.

We also assessed trends in spatial pattern of trees, snags and saplings using correlograms. The correlogram statistic is calculated as (cf. 1 – Geary's C, Dale 1999; autocorrelation, Miller et al. 2002; statistic for a correlogram, Scheller & Mladenoff 2002): (3)

$$\rho = 1 - \frac{(n-1)\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}\left(x_i - x_j\right)^2}{2\sum_{i=1}^{n}\left(x_i - \bar{x}\right)^2 \sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}}$$

where ρ = autocorrelation coefficient, n = number of quadrats, w_{ij} are weights with the values 1 or 0 if the pair x_i and x_j are included or not, respectively, and x is the number of trees, snags or saplings in the quadrat. The correlogram statistic is calculated for each distance separately. For a distance of 1 m, we used the grid of 1 m × 1 m subplots as quadrats; $w_{ij} = 1$ when pairs of quadrats were adjacent (including diagonal adjacency). For additional distances of multiples of 4 m up to 32 m, numbers of trees, snags or saplings were combined within 4 m × 4 m quadrats, resulting in a transect of contiguous quadrats; for these distances, $w_{ij} = 1$ when pairs of quadrats were 1, 2 and 8 quadrats apart. Analyses were only conducted if there were five or more trees, snags or saplings per transect. We used this inverse of Geary's C, which still varies between 0 and 1, so that greater values represent greater spatial autocorrelation or spatial structure (similar values) at the specific distance and therefore less heterogeneity or clumping. Correlelograms were determined for live tree, snag and sapling density.

Statistical analyses

Non-parametric statistical analyses were used to determine trends with time since fire and differences among sites for gap abundance and spatial pattern after tests of normality revealed that data for many variables did not satisfy assumptions of normal error distributions. Response variables for all analyses included: gap proportion, density, average length and diversity (estimated as the standard deviation of gap lengths); total, overstorey and understorey tree cover patch size (NLV results); standardized 3TLQV for four different distance classes (0-2, 2-6, 6-10, 10-33 m) for total, overstorey and understorey tree cover; autocorrelation coefficient for four different distances (1, 4, 8 and 32 m) for total live tree density, total snag and sapling density. Since we conducted multiple tests, we modified the p-value for groups of tests using the sequential Bonferroni test (Rice 1989). We applied this method separately for each test and for each site type (organic, clay, sand or all sites combined), where appropriate. We also separated the variables into two groups before applying the sequential Bonferroni test: general variables (all variables listed above except saplings) and trees and snags in different classes of dbh, height and decomposition (all variables in App. 2 plus saplings). The number of tests considered for multiple testing are stated where the original results are reported (Tables 1, 2; Tables A1, A2 in App. 1; Tables B1, B2, B3 in App. 2).

Spearman's coefficient of rank correlation (Sokal & Rohlf 2001) for all sites combined was used to test for significant overall trends with time since fire. Correlations were also calculated separately for each of the three site types. Correlations were only calculated when non-zero data were available for ten sites or more. We also used Kruskal-Wallis analyses to test differences in spatial pattern among site types irrespective of time since fire. These and all other statistical tests were carried out by use of SPSS (Anon. 2004)

Additional analyses were carried out to test differences in spatial pattern among different forest structural components. The Wilcoxon signed ranks test was used to assess the difference in patch size and 3TLQV results of the four distance classes (0-2, 2-6, 6-10, 10-33 m) between the understorey (< 3 m) and overstorey (> 3 m) tree cover; sites with missing data were omitted. The Wilcoxon signed ranks test was also used to assess differences in the spatial pattern between live trees and snags using the autocorrelation coefficients at all four distances (1, 4, 8 and 32 m).

Results

Trends with time since fire

Gap abundance increased with time since fire, reaching proportions greater than 80% of stand area and densities greater than 10 per 100 m on some sites (Fig. 2A). There was no significant trend with time since fire for average gap length (Fig. 2A) or patch size (App. 1, Table A1). Gaps were more evenly distributed among all size classes in older forests, as indicated by greater variation (standard deviation) in gap size (Fig. 2A).

Tree cover became significantly more variable with time since fire for the 0-2 m distance class (Fig. 2B). There was an apparent decrease in variability with time for the 10-33 m interval, but it was not significant likely

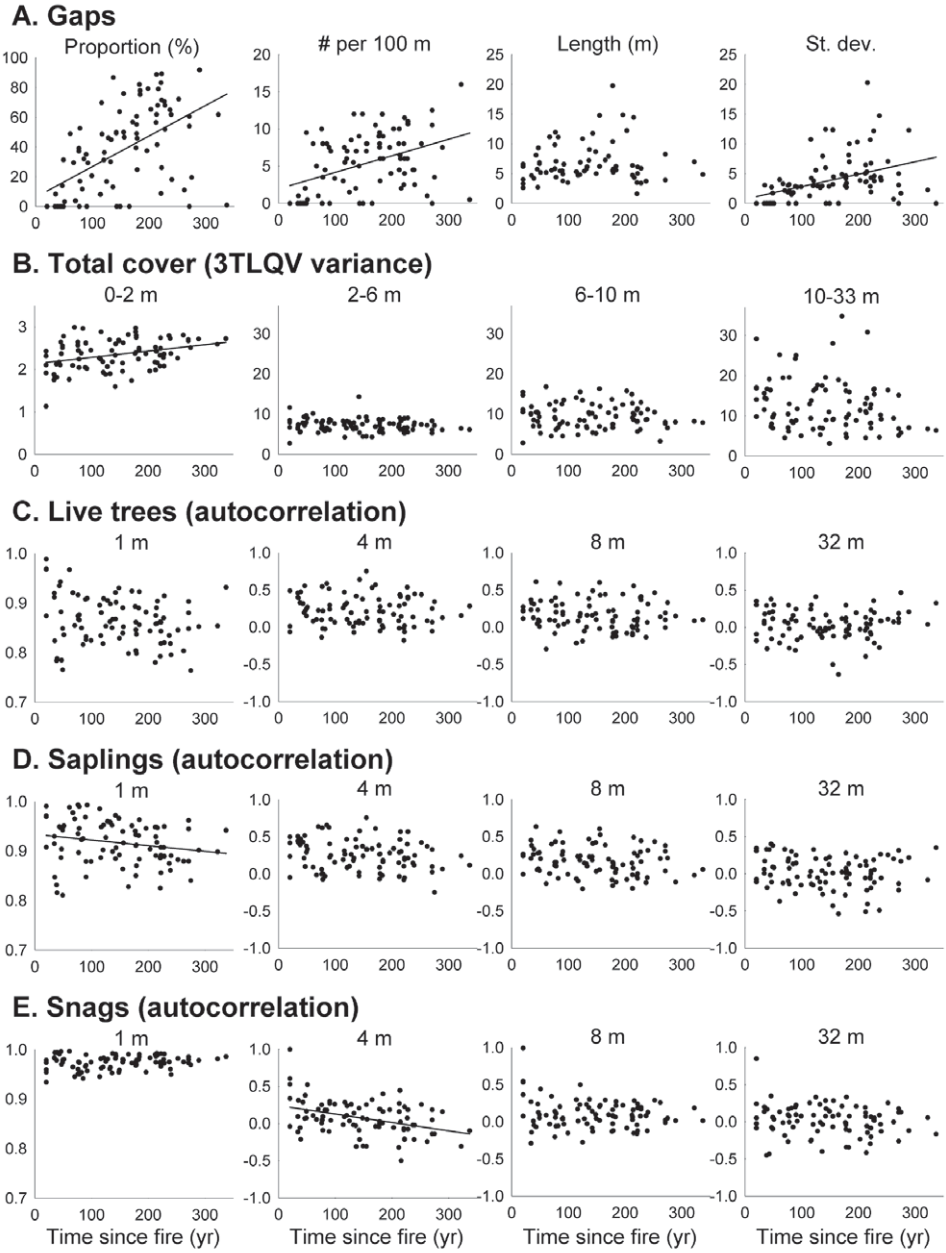


Fig. 2. Trends with time since fire on all sites combined for: **A**. Gap proportion, density, length and standard deviation of length; **B.** Spatial variance in total canopy cover (3TLQV results) for all four distance classes; **C**. Autocorrelation coefficient for live trees at all four distances; **D.** Autocorrelation coefficient for saplings (DBH 1–5 cm) at all four distances; **E.** Autocorrelation coefficient for snags at all four distances. Solid regression lines were added where the trends were significant ($\alpha < 0.05$) as a visual aid; the trend for saplings at 1 m was only marginally significant ($\alpha < 0.1$). Note that for **B**-**D**, the scale of the y-axis for 0-2 m and 1 m is different from the other distances. Statistics on non-parametric Spearman correlations are in App. 1, Table A1.

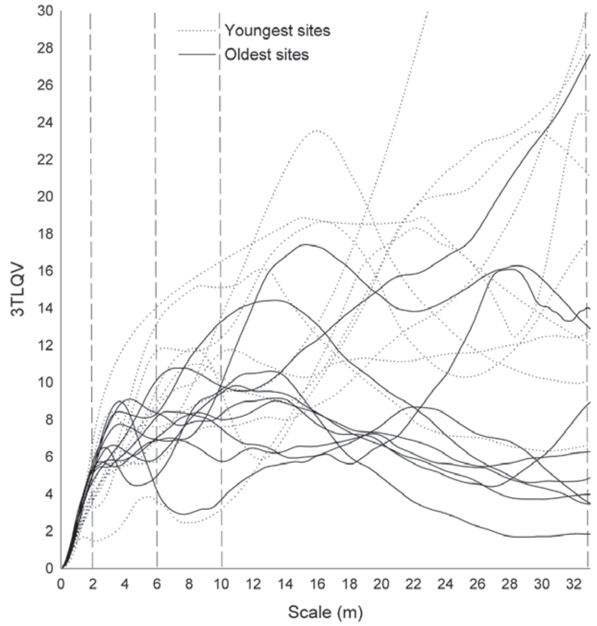


Fig. 3. Standardized 3TLQV results for total canopy cover on the ten youngest (< 40 years, dotted lines) and the ten oldest sites (≥ 240 years, solid lines) as a function of distance. Note that the variance was greater for the oldest sites in the distance class 0-2 m, and for the youngest sites in the distance class of 10-33 m, while no trends with time since fire can be seen in the distance classes 2-6 and 6-10 m (boundaries between distance classes are represented by dashed lines).

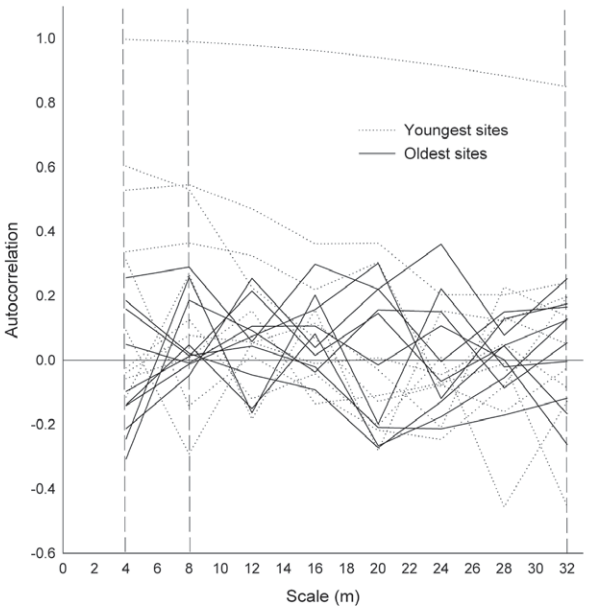


Fig. 4. Spatial structure of snags on the ten youngest (< 40 years, dotted lines) and the ten oldest sites (≥ 240 years, solid lines) as a function of distance between observation points. Note that the variance was greater for the youngest sites at 4 m, but there were no significant trends with time since fire at 8 and 32 m (these three distances are represented by dashed lines).

due to the presence of three intermediate-aged outlier stands with very high variance. These results are also evident from the graph of 3TLQV results for total canopy cover on the ten youngest and ten oldest sites which shows greater variance for the oldest sites at 0-2 m, and for the youngest sites at 10-33 m (Fig. 3). Overall, variance in cover increased with distance. There were no significant trends with time since fire when understorey and overstorey cover were considered separately (App. 1, Table A1).

Change in the spatial structure of live tree density with time since fire was not significant at any distance, although a non-significant decrease with time was apparent at 1 m (Fig. 2C). Saplings (DBH 1-5 cm) became less homogeneous with time at the 1 m distance (Fig. 2D). The spatial structure of saplings less

Table 1. Comparison of spatial pattern between overstorey and understorey tree cover. Mean values and *p*-values from Wilcoxon sign ranks tests for patch size (NLV results) and spatial variance for four different distance classes (3TLQV results). Sample size is *n* = 87.

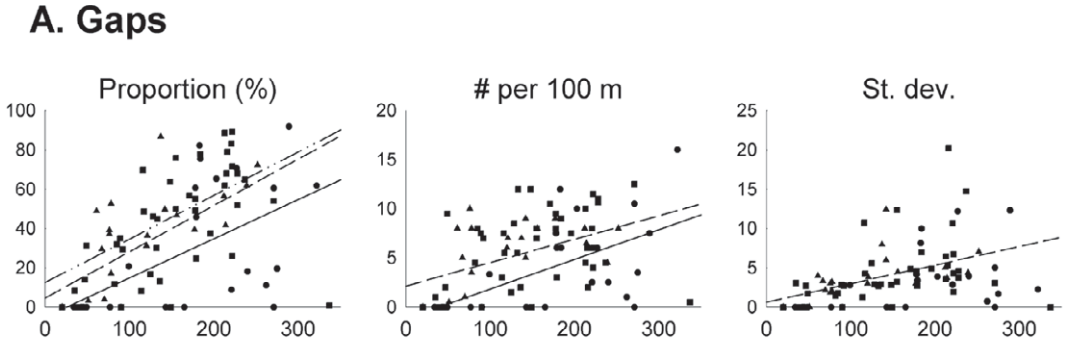
	Understorey cover	Overstorey cover	*p*-value
patch size	1.45	2.15	0.000*
0-2 m	0.373	0.292	0.000*
2-6 m	0.777	0.783	0.862
6-10 m	1.009	1.012	0.896
10-33 m	1.581	1.393	0.488

* = Significant at α = 0.05 with the sequential Bonferroni test where the number of tests considered is *k* = 5.

Table 2. Comparison of spatial pattern between live trees and snags. Mean values and *p*-values from Wilcoxon sign ranks tests for autocorrelation analysis at four different distances. Sample size is *n* = 89.

	Live trees	Snags	*p*-value
1 m	0.864	0.974	0.000*
4 m	0.225	0.072	0.000*
8 m	0.163	0.095	0.009*
32 m	0.036	0.018	0.503

* = Significant at α = 0.05 with the sequential Bonferroni test where the number of tests considered is *k* = 4.



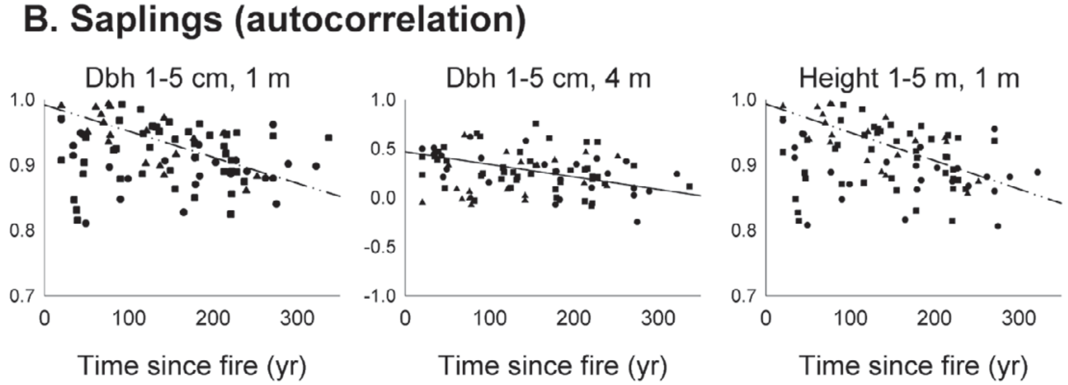


Fig. 5. Trends with time since fire for each of the three site types for: **A**. Gap proportion, density and standard deviation of length; **B**. Autocorrelation coefficient for saplings (DBH 1-5 cm) at 1 and 4 m and for saplings (height 1-5 m) at 1 m. Only results which are significant for some site types but not others are shown. Solid regression lines were added where the trends were significant ($\alpha < 0.05$) as a visual aid: solid for organic sites, dashed for clay sites and dash-dot-dot for sand sites; the trend for saplings at 1 m was only marginally significant ($\alpha < 0.1$). Statistics on non-parametric Spearman correlations are in App. 1, Table A1.

than 5 m tall exhibited no significant trends with time (App. 1, Table A1). For snags, the autocorrelation coefficient at 4 m decreased with time since fire from relatively high values in very young sites indicating a more uniform distribution of snags after fire (Fig. 2E). The correlogram results for snag density on the youngest and oldest sites (Fig. 4) also illustrates this trend.

Trends with time since fire varied among site types (Fig. 5). Gap density and proportion increased significantly with time since fire on organic and clay sites but not on sand sites (although an increase in gap proportion was significant at the $\alpha = 0.1$ level on sand sites; Fig. 5A). Gap standard deviation increased significantly with time since fire only on clay sites (Fig. 5A). For saplings, the autocorrelation coefficient decreased significantly with time at 1 m for sand sites and at 4 m for organic sites (Fig. 5B). The decrease in homogeneity with time of saplings at 1 m on sand sites appeared to be due to relatively high values of the autocorrelation coefficient in young sites (Fig. 5B).

Comparisons among structural components

Patch size was significantly greater for overstorey than for understorey tree cover (Table 1). There was significantly greater variance in understorey tree cover than overstorey cover for the 0-2 m distance class (Table 1). Snags were more homogeneous (higher autocorrelation coefficient) than trees at 1 m, but less so at 4 and 8 m (Table 2). Results for the autocorrelation coefficient for trees and snags of different sizes and for snags in different decay stages are presented in App. 2.

Differences among site types

There was only one significant difference among site types (App. 1, Table A2). There was a decrease in variability in overstorey tree cover for the 0-2 m interval from organic to clay to sand sites (Fig. 6).

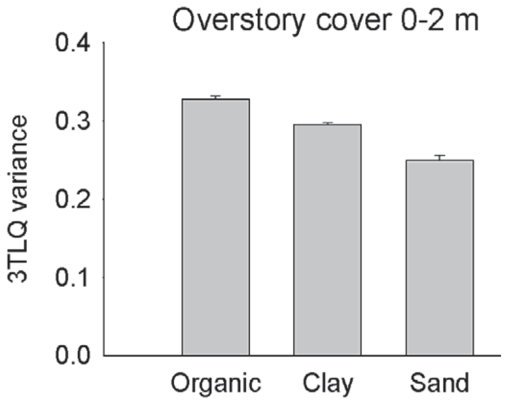


Fig. 6. Significant differences among site types for overstorey cover at a distance class of 0-2 m. This was the only significant difference among site types. Bars represent average values with standard error. Statistics on the Kruskal Wallis tests are in App. 1, Table A2.

Discussion

Direct evidence for changes in pattern during stand development

Our results show changes of the spatial pattern of several important *Picea mariana* boreal forest characteristics during stand development. The observed increase in the proportion of gaps with time since fire, also found in many other forests (Tyrrell & Crow 1994; Lertzman et al. 1996; Kneeshaw & Bergeron 1998), was due to greater densities of gaps in older forest stands, rather than larger gaps as observed in other forests (Spies et al. 1990; Liu & Hytteborn 1991; Bradshaw & Spies 1992; Hill et al. 2005). Some small gaps arise after self-thinning (Bradshaw & Spies 1992), but gap abundance primarily increases due to mortality brought about by fine-scale disturbance in later successional stages. An increase in gap size usually occurs as the result of larger tree sizes (Tyrrell & Crow 1994), enlargement of gaps (Young & Hubbell 1991; Hill et al. 2005) or a change in mortality from self-thinning to windthrow which usually removes clumps of trees. Franklin et al. (2002) suggest that gap development and expansion in later developmental stages may not occur in ecosystems with frequent stand-replacing disturbance. However, Chen & Popadiouk (2002) found that, even in the boreal forest which experiences frequent disturbance by fire, gaps expand in the final stage of development. We may not have observed an increase in gap length in the *Picea mariana* forest because trees in older stands are often small due to low productivity, and because windthrow is more likely to act on single trees in the more open canopied forests (Harper et al. 2005). Changes in forest structure (smaller trees and an open canopy) result from paludification which is the process by which the development of thick moss and organic layers lowers soil temperature and decreases nutrient availability (Paré & Bergeron 1995; Gower et al. 1996; Lavoie et al. 2005). The change in gap diversity from small gaps to a more even distribution of gaps on gap size classes is also found by other studies (Spies et al. 1990; Bradshaw & Spies 1992; Tyrrell & Crow 1994; Kneeshaw & Bergeron 1998).

Changes in the spatial pattern of trees during structural development can be partly attributed to the differential mortality of trees, particularly through two major processes: competitive thinning and patchiness of disturbance agents. Self-thinning of smaller, notably clumped trees during the stem exclusion stage is likely to increase the distance between trees, so that the surviving, larger trees have a more regular distribution (Christensen 1977; Kenkel 1988; Peterson & Squires 1995; Lee et al. 1997; Malkinson et al. 2003). Since our chronosequence approach spanned a long time period, we were unable to detect a change from a clumped to a more regular distribution at the early stem exclusion stage (approx. 40-100 years in this ecosystem, Harper et al. 2005).

Mortality of individual trees leads to a more heterogeneous pattern of tree density and cover (Harmon et al. 1986; Kuuluvainen et al. 1998). We found that significant trends in spatial pattern during stand development usually occurred at the scale of individual trees (0-2 m). Other studies find variation in canopy cover or tree density at short distances (3.5 m, Kenkel 1988; < 1 m, Kuuluvainen et al. 1996; <7 m, Kuuluvainen & Linkosalo 1998; Kuuluvainen et al. 1998) where direct interactions with neighbouring trees take place (Kenkel 1988). Aggregation results from the clumping of trees that have established in gaps (Frelich & Reich 1995; McDonald et al. 2003). In later stages of development, saplings establish in gaps created by individual tree mortality or fine-scale secondary disturbances such as windthrow or insect outbreaks (Christensen 1977; Kuuluvainen et al. 1996; Parish et al. 1999; Awada et al. 2005; Wolf 2005). In the *Picea mariana* forest, further clumping of saplings at these fine scales may arise by layering (vegetative reproduction as a result of rooting from lower branches) from neighbouring trees.

Aggregation in later stages of development may also be due to the lack of replacement of large trees because paludification hinders tree growth (Harper et al. 2005). Spatial autocorrelation or spatial dependence in organic layer thickness can occur at distances of up to 80 m in *Picea mariana* sites but is highly variable (M. Lavoie et al. In press). Without site-specific data for the spatial pattern of organic matter thickness it is hard to assess the extent to which paludification affects the spatial pattern of forest structural characteristics.

Concurrently, tree cover becomes more uniform at larger distances (10-33 m). Although this trend was not significant, a visual inspection of the graph and the change in the trend with time as the distance increases indicates that the trend of increasing homogeneity with time at broader scales may warrant further investigation. In deciduous boreal forest, spatial homogeneity of trees within stands also increases with age (Lee et al. 1997). Clumping in young stands may be due to local seed dispersal or facilitation as established plants improve conditions for others nearby in a heterogeneous environment (Malkinson et al. 2003); this effect would diminish with time creating a more homogeneous pattern. Alternatively, heterogeneous cover in young *Picea mariana* stands may be created by variation in fire severity. Recruitment and growth are greater in areas with exposed mineral soil compared to areas where fire severity is low (Lecomte et al. 2006). Over time, patches in which fire severity was low will remain open, while dense stands that established in areas with high fire severity will become more open with time due to paludification (Harper et al. 2005; Lecomte et al. 2006). The overall effect at broad scales is homogenization of tree cover forming open canopied forest across all older stands.

Snag density followed a trend of increasing heterogeneity with time since fire at a distance of 4 m. As for trees, deadwood was also expected to be evenly distributed during self-thinning at early stages of development, and more aggregated later in development due to increasing importance of mortality agents that act on finer scales (Harmon et al. 1986; Kuuluvainen et al. 1998).

Comparison among structural components

Greater patch size for overstorey than for understorey tree cover implies that patches enlarge or coalesce as trees grow. However, average patch sizes are small (1-2 m) with only 1-3 trees in each patch and there is no trend in patch size with time. Therefore, the difference in patch size may be attributable to the growth of trees or the formation of small patches as trees enter the canopy. Other studies report coalescence of patches leading to an increase in patch size during succession (Yarranton & Morrison 1974; Christensen 1977).

We find differences in heterogeneity between the understorey and overstorey tree cover only at the smallest distance (1 m) where variance was greater in the understorey due to the patchy distribution of saplings which generally cluster within gaps (Christensen 1977; Kuuluvainen et al. 1996; Parish et al. 1999). This result opposes the general trend of increasing heterogeneity with time since fire, from which we would predict overstorey tree cover to become more heterogeneous as trees entered the canopy during stand development. A reason why the overstorey cover is more regular than the understorey tree cover may be that differences in spatial pattern between the two canopy levels is unrelated to time since fire. As saplings grow into the canopy, their spatial distribution becomes more variable at intermediate scales, due to mortality from secondary disturbances such as windthrow or insect outbreaks. Reduced homogeneity for larger trees at intermediate scales, as compared to smaller trees, is found in some studies (Svensson & Jeglum 2000; Antos & Parish 2002a), while in others density-dependent mortality or competition for light is reported to maintain more uniform distributions among larger trees (Moeur 1993; Ward et al. 1996; Rouvinen et al. 2002; Druckenbrod et al. 2005). Differences between studies in these respects may be due to differences in stand age, stand composition or site factors which favour density-dependent vs. density-independent mortality processes. In these *Picea mariana* stands, density-dependent mortality of saplings may be more likely to be clustered at fine scales because of layering or vegetative reproduction close to the parent trees.

Differences in spatial structure between live and dead trees provide insight into patterns of mortality. Greater variability in snag distribution at intermediate scales reflects the patchy nature of mortality from secondary disturbances such as windthrow or insect outbreaks. Relatively clumped distributions of snags are also found in some (Kenkel 1988; Kuuluvainen et al. 1998), but not all (Lee et al. 1997; Druckenbrod et al. 2005) other studies. The more even distribution of snags than trees at 1 m was surprising and may simply reflect lower densities of snags. Antos & Parish (2002b) report similar results for short distances (< 5 m): clumping of live trees but not of dead trees, suggesting that mortality was spatially random at these scales.

Differences among site types

Our results that relatively few variables differ in spatial pattern of forest structural characteristics among site types accords with Scheller & Mladenoff (2002). However, we did find one exception for overstorey tree cover, which provides some evidence that edaphic conditions influence tree spatial patterns (Ward & Parker 1989; Miller et al. 2002). In stands with better and more homogeneous light and soil conditions, the establishment and growth of newly dispersed plants near the parent plants will be favoured resulting in greater autocorrelation or spatial homogeneity (Miller et al. 2002), particularly at short distances. Our findings of lower variance for overstorey cover on clay and sand sites with relatively high productivity compared with organic sites, as well as a more homogeneous distribution of saplings at 1 m distance on young sand sites, support this hypothesis. Our results indicate that trends with time since fire vary among site types for gaps in addition to saplings. On sand sites, the presence of *Pinus banksiana* may obscure trends in gap abundance and diversity since time since fire may be confounded with a change in dominance (Harper et al. 2003), particularly in the early-intermediate aged sites.

Conclusions

The spatial pattern of forest structural characteristics in *Picea mariana* boreal forest provides insight into processes that occur during stand development. The shift in the cause of mortality from density-dependent self-thinning to secondary disturbances affects many aspects of spatial pattern including an increase in gap abundance and diversity, and greater variability in tree cover and snag density at short distances. Trees establish in clusters within gaps as seedlings; these patches then enlarge or coalesce as trees grow into the canopy. Once trees enter the canopy, the patchy nature of mortality from fine-scale disturbances leads to greater variability at intermediate distances. These processes and the associated patterns are common during stand development in many forest stands. However, we also note other trends that reflect unique processes in *Picea mariana* forest. Patchy regeneration and tree growth immediately after fire are followed by homogenization of forest stands at broad scales. Factors other than stand development influence spatial pattern, as evidenced by the large variation in our results for trends with time since fire. Particularly on sand sites, a varied species composition obscures spatio-temporal trends.

Acknowledgements. We thank Yong Ban, Catherine Boudreault, Eric Desjardins, Marie-Hélène Longpré and Thuy Nguyen for collecting and entering the data. Alain Leduc and Kim Lowell provided valuable assistance with data analysis. We also thank Joseph Antos, two anonymous reviewers and especially Rune Økland for their helpful comments. This research was funded by the Sustainable Forest Management Network, les Fonds Forestiers du Ministère des Ressources Naturelles du Québec, Lake Abitibi Model Forest, Natural Sciences and Engineering Research Council of Canada and the Fonds Forestier du Québec.

References

Anon. 1993. *Canadian climate normals 1961-1990*. Canadian climate program. Atmospheric Environment Service, Environment Canada, Downsview, ON, CA.

Anon. 2004. *SPSS for Windows. Release 12*. SPSS, Chigaco, IL, US.

Antos, J.A. & Parish, R. 2002a. Dynamics of an old-growth, fire-initiated, subalpine forest in southern interior British Columbia: tree size, age, and spatial structure. *Can. J. For. Res*. 32: 1935-1946.

Antos, J.A. & Parish, R. 2002b. Structure and dynamics of a nearly steady-state subalpine forest in south-central British Columbia, Canada. *Oecologia* 130: 126-135.

Awada, T., Henebry, G.M., Redmann, R.E. & Sulistiyowati, H. 2004. *Picea glauca* dynamics and spatial pattern of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest. *Ann. For. Sci*. 61: 789-794.

Bartemucci, P., Coates, K.D., Harper, K.A. & Wright, E.F. 2002. Gap disturbances in northern old-growth forests of British Columbia. *J. Veg. Sci*. 13: 685-696.

Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85: 1916-1932.

Bradshaw, G.A. & Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *J. Ecol*. 80: 205-215.

Chen, H.Y.H. & Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. *Environ. Rev*. 10: 137-166.

Christensen, N.L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. *Am. Midl. Nat*. 97: 176-188.

Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, UK.

Dale, M.R.T. & Blundon, D.J. 1990. Quadrat variance analysis and pattern development during primary succession. *J. Veg. Sci*. 1: 153-164.

Dale, M.R.T. & Zbigniewicz, M.W. 1997. Spatial pattern in boreal shrub communities: effects of a peak in herbivore density. *Can. J. Bot*. 75: 1342-1348.

Druckenbrod, D.L., Shugart, H. H. & Davies, I. 2005. Spatial pattern and process in forest stands within the Virginia piedmont. *J. Veg. Sci*. 16: 37-48.

Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-

Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M. & Rosenberg, M.S. 2002. A balanced view of scale in spatial statistical analysis. *Ecography* 25: 626-640.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage*. 155: 399-423.

Frelich, L.E. & Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr*. 65: 325-346.

Galiano, E.F. 1982. Détection et mésure de l'hétérogénéité spatiale des espèces dans les paturages. *Acta Oecol*. 3: 269-278.

Gauthier, S., Leduc, A. & Bergeron, Y. 1996. Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. *Environ. Mon. Assess*. 39: 417-434.

Gauthier, S., De Grandpré, L. & Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. *J. Veg. Sci*. 11: 781-790.

Gower, S.T., McMurtrie, R.E. & Murty, D. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends Ecol. Evol*. 11: 378-382.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.J. & Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res*. 15: 133-302.

Harper, K.A., Bergeron, Y., Gauthier, S. & Drapeau, P. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Quebec: a landscape scale study. *Silva Fenn*. 36: 249-263.

Harper, K.A., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S. & Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environ. Rev*. 11: S79-S98.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S. & De Grandpré, L. 2005. Structural development following fire in coniferous eastern boreal forest. *For. Ecol. Manage*. 206: 293-306.

Hill, S.B., Mallik, A.U. & Chen, H.Y.H. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. *Can. J. For. Res*. 35: 1942-1951.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology* 69: 1017-1024.

Kneeshaw, D.D. & Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79: 783-794.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann. Zool. Fenn*. 31: 35-51.

Kuuluvainen, T. & Linkosalo, T. 1998. Estimation of a spatial tree-influence model using iterative optimization. *Ecol. Modell*. 106: 63-75.

Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. *Silva Fenn*. 30: 315-328.

Kuuluvainen, T., Syrjanen, K. & Kalliola, R. 1998. Structure of a pristine *Picea abies* forest in northeastern Europe. *J. Veg. Sci*. 9: 563-574.

Lavoie, M., Paré, D., Fenton, N., Groot, A. & Taylor, K. 2005. Paludification and management of forested peatlands in Canada: a literature review. *Environ. Rev*. 13: 21-50.

Lavoie, M., Harper, K.A., Paré, D. & Bergeron, Y. In press. Spatial pattern in the organic layer and tree growth: A case study from regenerating *Picea mariana* stands prone to paludification. *J. Veg. Sci*. 18.

Lecomte, N., Simard, M. & Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. *Écoscience* 13: 152-163.

Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H. & Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. *Ecol. Appl*. 7: 691-701.

Lertzman, K.P., Sutherland, G.D., Inselberg, A. & Saunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology* 77: 1254-1270.

Liu Q. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *J. Veg. Sci*. 2: 391-402.

Malkinson, D., Kadmon, R. & Cohen, D. 2003. Pattern analysis in successional communities – An approach for studying shifts in ecological interactions. *J. Veg. Sci*. 14: 213-222.

McDonald, R.I., Peet, R.K. & Urban, D.L. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a Piedmont forest. *J. Veg. Sci*. 14: 441-450.

Miller, T.F., Mladenoff, D.J. & Clayton, M.K. 2002. Old-growth northern hardwood forests: spatial autocorrelation and patterns of understory vegetation. *Ecol. Monogr*. 72: 487-503.

Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci*. 39: 756-775.

Paré, D. & Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. *J. Ecol*. 83: 1001-1007.

Parish, R., Antos, J.A. & Fortin, M.-J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. *Can. J. For. Res*. 29: 1347-1356.

Peterson, C.J. & Squiers, E.R. 1995b. An unexpected change in spatial pattern across 10 years in an aspen-white-pine forest. *J. Ecol*. 83: 847-855.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Rossi, R.E., Mulla, D.J., Journel, A.G. & Franz, E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr*. 62: 277-314.

Rouvinen, S., Kuuluvainen, T. & Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in vienansalo wilderness, eastern Fennoscandia. *Silva Fenn*. 36: 127-145.

Scheller, R.M. & Mladenoff, D.J. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecol. Appl*. 12: 1329-1343.

Sokal, R.R. & Rohlf, F.J. 2001. *Biometry*. 3rd. ed. W.H. Freeman and Company, New York, NY, US.

Spies, T.A., Franklin, J.F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res*. 20: 649-658.

Svensson, J.S. & Jeglum, J.K. 2001. Structure and dynamics of an undisturbed old-growth Norway spruce forest on the rising Bothnian coastline. *For. Ecol. Manage*. 151: 67-79.

Tyrrell, L.E. & Crow, T.R. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* 75: 370-386.

Vincent, J.S. & Hardy, L. 1977. L'Évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. *Geogr. Phys. Quart*. 31: 357-372.

Ward, J.S. & Parker, G.R. 1989. Spatial dispersion of woody regeneration in an old-growth forest. *Ecology* 70: 1279-1285.

Ward, J.S., Parker, G.R. & Ferrandino, F.J. 1996. Long-term spatial dynamics in an old-growth deciduous forest. *For. Ecol. Manage*. 83: 189-202.

Wolf, A. 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. *For. Ecol. Manage*. 215: 212-223.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol*. 62: 417-428.

Young, T.P. & Hubbell, S.P. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* 72: 1464-1471.

Received 20 May 2005;
Accepted 19 June 2006;
Co-ordinating Editor: R.H. Økland.

For App. 1 and 2, see also JVS/AVS Electronic Archives;
www.opuluspress.se/

App. 1. Detailed statistical results for trends in spatial pattern in *Picea mariana* boreal forest.

Table A1. Detailed results of Spearman correlation analyses with time since fire as the independent variable. Results are reported for each of the three site types separately only where results are significant for some site types but not others.

	n	r_s	*p*-value	*k*
All sites combined				
Gap proportion	91	0.611	0.000*	27
Gap density	91	0.445	0.000*	27
Gap length	71	0.250	0.037	27
Gap standard deviation	91	0.546	0.000*	27
Total cover[1] patch size	90	-0.133	0.212	27
Total cover[1] 0-2 m	90	0.336	0.001*	27
Total cover[1] 2-6 m	90	-0.178	0.093	27
Total cover[1] 6-10 m	90	-0.105	0.325	27
Total cover[1] 10-33 m	90	-0.250	0.018	27
Understorey tree cover[1] patch size	89	-0.175	0.101	27
Understorey tree cover[1] 0-2 m	89	0.224	0.035	27
Understorey tree cover[1] 2-6 m	89	0.166	0.121	27
Understorey tree cover[1] 6-10 m	89	-0.118	0.270	27
Understorey tree cover[1] 10-33 m	89	-0.150	0.160	27
Overstorey cover[1] patch size	88	-0.144	0.182	27
Overstorey cover[1] 0-2 m	88	0.075	0.490	27
Overstorey cover[1] 2-6 m	88	-0.054	0.614	27
Overstorey cover[1] 6-10 m	88	0.048	0.655	27
Overstorey cover[1] 10-33 m	88	0.069	0.523	27
Live tree density[2] 1 m	89	-0.227	0.033	27
Live tree density[2] 4 m	89	-0.138	0.196	27
Live tree density[2] 8 m	89	-0.139	0.194	27
Live tree density[2] 32 m	89	0.015	0.888	27
Saplings (DBH 1-5 cm)[2] 1 m	89	-0.271	0.010	52
Saplings (DBH 1-5 cm)[2] 4 m	89	-0.221	0.038	52
Saplings (DBH 1-5 cm)[2] 8 m	89	-0.203	0.057	52
Saplings (DBH 1-5 cm)[2] 32 m	89	-0.115	0.284	52
Saplings (height 1-5 m)[2] 1 m	88	-0.321	0.002**	52
Saplings (height 1-5 m)[2] 4 m	88	-0.222	0.038	52
Saplings (height 1-5 m)[2] 8 m	88	-0.191	0.075	52
Saplings (height 1-5 m)[2] 32 m	88	-0.157	0.143	52
Snag density[2] 1 m	89	0.142	0.183	27
Snag density[2] 4 m	89	-0.352	0.001*	27
Snag density[2] 8 m	89	-0.085	0.427	27
Snag density[2] 32 m	89	-0.171	0.109	27
Organic sites only				
Gap density	25	0.635	0.000*	27
Gap proportion	25	0.655	0.000*	27
Gap standard deviation	25	0.634	0.001	27
Saplings (DBH 1-5 cm)[2] 1 m	25	-0.269	0.194	52
Saplings (DBH 1-5 cm)[2] 4 m	25	-0.619	0.001*	52
Saplings (height 1-5 m)[2] 1 m	25	-0.337	0.099	52
Clay sites only				
Gap density	45	0.486	0.001*	27
Gap proportion	45	0.682	0.000*	27
Gap standard deviation	45	0.602	0.000*	27
Saplings (DBH 1-5 cm)[2] 1 m	44	-0.039	0.802	52
Saplings (DBH 1-5 cm)[2] 4 m	44	-0.303	0.045	52
Saplings (height 1-5 m)[2] 1 m	43	-0.116	0.460	52
Sand sites only				
Gap density	20	0.374	0.104	27
Gap proportion	20	0.667	0.001**	27
Gap standard deviation	20	0.510	0.022	27
Saplings (DBH 1-5 cm)[2] 1 m	20	-0.673	0.001*	48
Saplings (DBH 1-5 cm)[2] 4 m	20	-0.351	0.129	48
Saplings (height 1-5 m)[2] 1 m	20	-0.700	0.001*	48

[1] Analysed using 3TLQV.

[2] Analysed using spatial autocorrelation analysis.

* Significant at $\alpha = 0.05$ with the sequential Bonferroni test where the number of tests considered is *k*.

** Significant at $\alpha = 0.1$ with the sequential Bonferroni test where the number of tests considered is *k*.

App. 1 and 2. Internet supplement to: Harper, K.A.; Bergeron, Y.; Drapeau, P.; Gauthier, S. & De Grandpré, L. 2006. Changes in spatial pattern of trees and snags during structural development in *Picea mariana* boreal forests.
J. Veg. Sci. 17: 625-636.

Table A2. Detailed results for the Kruskal Wallis tests among site types.

	n	χ^2	*p*-value	*k*
Gap proportion	91	3.44	0.179	27
Gap density	91	4.45	0.044	27
Gap length	71	1.08	0.584	27
Gap standard deviation	91	6.26	0.108	27
Total cover[1] patch size	90	1.61	0.446	27
Total cover[1] 0-2 m	90	2.67	0.263	27
Total cover[1] 2-6 m	90	6.89	0.032	27
Total cover[1] 6-10 m	90	6.80	0.033	27
Total cover[1] 10-33 m	90	3.54	0.170	27
Understorey tree cover[1] patch size	89	5.65	0.059	27
Understorey tree cover[1] 0-2 m	89	0.546	0.761	27
Understorey tree cover[1] 2-6 m	89	1.12	0.572	27
Understorey tree cover[1] 6-10 m	89	0.741	0.690	27
Understorey tree cover[1] 10-33 m	89	0.694	0.707	27
Overstorey cover[1] patch size	88	6.58	0.037	27
Overstorey cover[1] 0-2 m	88	12.50	0.002*	27
Overstorey cover[1] 2-6 m	88	3.56	0.038	27
Overstorey cover[1] 6-10 m	88	4.13	0.127	27
Overstorey cover[1] 10-33 m	88	2.38	0.304	27
Live tree density[2] 1 m	89	1.59	0.451	27
Live tree density[2] 4 m	89	2.82	0.244	27
Live tree density[2] 8 m	89	1.66	0.436	27
Live tree density[2] 32 m	89	3.49	0.175	27
Saplings (DBH 1-5 cm)[2] 1 m	89	11.52	0.003	52
Saplings (DBH 1-5 cm)[2] 4 m	89	2.52	0.245	52
Saplings (DBH 1-5 cm)[2] 8 m	89	0.148	0.929	52
Saplings (DBH 1-5 cm)[2] 32 m	89	2.31	0.315	52
Saplings (height 1-5 m)[2] 1 m	88	11.94	0.003	52
Saplings (height 1-5 m)[2] 4 m	88	3.92	0.141	52
Saplings (height 1-5 m)[2] 8 m	88	0.751	0.687	52
Saplings (height 1-5 m)[2] 32 m	88	1.73	0.421	52
Snag density[2] 1 m	89	1.70	0.427	27
Snag density[2] 4 m	89	0.389	0.823	27
Snag density[2] 8 m	89	2.45	0.294	27
Snag density[2] 32 m	89	0.047	0.977	27

[1] Analysed using 3TLQV.

[2] Analysed using spatial autocorrelation analysis.

* Significant at $\alpha = 0.05$ with the sequential Bonferroni test where the number of tests considered is *k*.

App. 2. Spatial structure of different types of structural components following fire in *Picea mariana* boreal forest.

We also examined trends in the autocorrelation coefficient for different types of live trees and snags in *Picea mariana* boreal forest with time since fire and on different site types with an additional objective of comparing the spatial pattern of trees and snags among different sizes and decay stages. All trees and snags were measured for height (classes: 1-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35 m) and diameter at breast height (classes: 1-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40 cm). The decay stage of all snags was determined (classes 1-4, similar to stages 3-6 in Thomas et al. 1979). Analyses described in the methods section of the main text were also applied to autocorrelation coefficient results for distances of 1, 4, 8 and 32 m for trees and snags in DBH classes 5-15, 15-25 and > 25 cm, trees in height classes 5-15 and > 15 m, snags in height classes 1-5 and 5-25 m, and snags in decay classes 1 and 2-4. See the main text for a discussion of multiple testing using the sequential Bonferroni test (Rice 1989). In addition, to test differences in spatial pattern (autocorrelation coefficients at the four different distances) in trees and snags among different height, DBH and decay classes, we used Kuskal Wallis tests for three or more groups with class as a random factor, or Mann Whitney tests for two groups (SPSS Inc., Anon. 2004).

The only significant trend with time since fire was a decrease in variability for tall trees (height >15 m) during stand development at 1 m (Table B1). There were only a couple of differences in trends with time since fire among site types that were marginally significant at $\alpha = 0.1$ (Table B1). On organic sites, there was a negative trend in autocorrelation coefficients with time at 1 m for medium-sized trees (DBH 5-15 cm). Taller snags had decreasing autocorrelation coefficients at 4 m on sand sites only. There were no significant differences in autocorrelation coefficients of trees or snags of different sizes or decay stages among site types (Table B2). Differences in the autocorrelation results of trees among DBH and height classes were significant at 1 and 4 m (Table B3). Larger and taller trees tended to more homogeneous at 1 m, but less so at greater distances, compared to other sizes of trees. Differences for different types of snags were significant only at 1 m (Table B3). Greater autocorrelation coefficients were found for larger, taller snags that were not as well decayed.

Taller trees became more uniform with time, likely due to competitive thinning of more crowded stems which leads to more regular patterns in stable habitat (Moeur 1993; Malkinson et al. 2003; McDonald et al. 2003). More uniform patterns of larger, taller trees compared to smaller trees at 1 m, but more variable at 4 and 8 m, can be attributed to the same causes as for less variable overstorey cover compared to understorey tree cover (see discussion in the main text). Other studies found that larger trees have a more regular distribution and are less clumped due to density-dependent mortality (Christensen 1977; Ward & Parker 1989; Moeur 1993; Kuuluvainen et al. 1996; Ward et al 1996; Parish et al. 1999; Antos & Parish 2002a; Rouvinen et al. 2002; Druckenbrod et al. 2005). The reverse trend that we found at intermediate distances is likely due to patchiness from fine-scale disturbance. A few other studies also found this decrease in homogeneity with growth (Svensson & Jeglum 2000; Antos & Parish 2002a).

Small snags generated by self-thinning during the earlier stem exclusion phase could be more clumped at fine scales due to crowding, compared to the density-independent more uniform fine-scale disturbance later in stand development. This conclusion is supported by greater autocorrelation coefficients for larger and taller snags that would have been formed from secondary disturbance as opposed to small snags formed from self-thinning. Parish et al. (1999) and Rouvinen and Kuuluvainen (2001) also found that taller snags were less clustered than smaller snags, and Edman and Jonsson (2001) found comparable results for logs. The more variable pattern of well-decayed snags compared to recent snags suggests that aggregated damage to snags from wind creates a more clumped distribution of remaining snags.

Additional references

Edman, M. & Jonsson, B.G. 2001. Spatial pattern of downed logs and wood-decaying fungi in an old-growth *Picea abies* forest. *J. Veg. Sci*. 12: 609-620.

Rouvinen, S. & Kuuluvainen, T. 2001. Amount and spatial distribution of standing and downed dead trees in two areas of different fire history in a boreal Scots pine forest. *Ecol. Bull*. 49: 115-127.

Thomas, J.W., Anderson, R.G., Maser, C. & Bull, E.L. 1979. Snags. In: Thomas, J.W. (ed.) *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*, pp. 60-77. U.S. Department of Agriculture Forest Service, Washington, DC, US.

Table B1. Detailed results for the Spearman correlation analyses of structural components at different distances with time since fire as the independent variable. Results are reported for each of the three site types separately only where results are significant at some site types but not others.

	n	r_s	p-value	k
All sites combined				
Trees				
DBH 5-15 cm, 1 m	88	–0.060	0.578	52
DBH 5-15 cm, 4 m	88	0.072	0.503	52
DBH 5-15 cm, 8 m	88	0.088	0.416	52
DBH 5-15 cm, 32 m	88	0.014	0.896	52
DBH 15-25 cm, 1 m	68	0.210	0.086	52
DBH 15-25 cm, 4 m	68	0.010	0.933	52
DBH 15-25 cm, 8 m	68	–0.007	0.954	52
DBH 15-25 cm, 32 m	68	0.192	0.117	52
Height 5-15 m, 1 m	84	0.088	0.427	52
Height 5-15 m, 4 m	84	–0.004	0.968	52
Height 5-15 m, 8 m	84	0.174	0.112	52
Height 5-15 m, 32 m	84	0.159	0.148	52
Height >15 m, 1 m	60	0.484	0.000*	52
Height >15 m, 4 m	60	–0.287	0.026	52
Height >15 m, 8 m	60	–0.0758	0.567	52
Height >15 m, 32 m	60	0.006	0.962	52
Snags				
DBH 1-5 cm, 1 m	30	0.410	0.024	52
DBH 1-5 cm, 4 m	30	–0.414	0.023	52
DBH 1-5 cm, 8 m	30	–0.095	0.619	52
DBH 1-5 cm, 32 m	30	–0.201	0.286	52
DBH 5-15 cm, 1 m	81	0.176	0.117	52
DBH 5-15 cm, 4 m	81	–0.229	0.040	52
DBH 5-15 cm, 8 m	81	–0.201	0.072	52
DBH 5-15 cm, 32 m	81	–0.117	0.299	52
DBH 15-25 cm, 1 m	61	0.026	0.845	52
DBH 15-25 cm, 4 m	61	–0.121	0.352	52
DBH 15-25 cm, 8 m	61	–0.060	0.644	52
DBH 15-25 cm, 32 m	61	–0.082	0.529	52
Height 1-5 m, 1 m	89	0.112	0.295	52
Height 1-5 m, 4 m	89	–0.260	0.014	52
Height 1-5 m, 8 m	89	–0.067	0.532	52
Height 1-5 m, 32 m	89	–0.052	0.627	52
Height >5 m, 1 m	70	0.337	0.004	52
Height >5 m, 4 m	70	–0.213	0.076	52
Height >5 m, 8 m	70	0.042	0.732	52
Height >5 m, 32 m	70	–0.076	0.530	52
Decay class 1, 1 m	70	0.332	0.005	52
Decay class 1, 4 m	70	–0.225	0.061	52
Decay class 1, 8 m	70	0.082	0.500	52
Decay class 1, 32 m	70	–0.073	0.548	52
Decay classes 2-4, 1 m	89	0.127	0.237	52
Decay classes 2-4, 4 m	89	–0.271	0.010	52
Decay classes 2-4, 8 m	89	–0.109	0.308	52
Decay classes 2-4, 32 m	89	–0.077	0.474	52
Organic sites only				
Trees DBH 5-15 cm, 1 m	25	–0.594	0.002**	52
Snags height > 5 m, 4 m	16	–0.570	0.021	52
Clay sites only				
Trees DBH 5-15 cm, 1 m	44	0.191	0.215	52
Snags height > 5 m, 4 m	38	0.068	0.685	52
Sand sites only				
Trees DBH 5-15 cm, 1 m	19	0.350	0.141	48
Snags height > 5 m, 4 m	16	–0.701	0.002**	48

* Significant at $\alpha = 0.05$ with the sequential Bonferroni test where the number of tests considered is k.

** Significant at $\alpha = 0.1$ with the sequential Bonferroni test where the number of tests considered is k.

Table B2. Detailed results for different structural components for the Kruskal Wallis tests among site types. Differences in trees and snags with > 25 cm DBH were not analysed due to low sample sizes. No variables were significantly different among site types at $\alpha = 0.05$ or $\alpha = 0.1$ with the sequential Bonferroni test where the number of tests considered is $k = 52$.

	n	χ^2	*p*-value
Trees			
DBH 5-15 cm, 1 m	88	1.68	0.433
DBH 5-15 cm, 4 m	88	0.180	0.914
DBH 5-15 cm, 8 m	88	2.62	0.270
DBH 5-15 cm, 32 m	88	0.367	0.833
DBH 15-25 cm, 1 m	68	5.23	0.073
DBH 15-25 cm, 4 m	68	1.82	0.403
DBH 15-25 cm, 8 m	68	0.193	0.908
DBH 15-25 cm, 32 m	68	0.734	0.693
Height 5-15 m, 1 m	84	1.57	0.457
Height 5-15 m, 4 m	84	0.459	0.795
Height 5-15 m, 8 m	84	1.98	0.372
Height 5-15 m, 32 m	84	0.428	0.807
Height >15 m, 1 m	60	3.12	0.210
Height >15 m, 4 m	60	0.182	0.913
Height >15 m, 8 m	60	0.143	0.931
Height >15 m, 32 m	60	3.74	0.154
Snags			
DBH 1-5 cm, 1 m	30	3.88	0.144
DBH 1-5 cm, 4 m	30	4.90	0.086
DBH 1-5 cm, 8 m	30	3.70	0.157
DBH 1-5 cm, 32 m	30	1.84	0.400
DBH 5-15 cm, 1 m	81	4.20	0.123
DBH 5-15 cm, 4 m	81	1.18	0.572
DBH 5-15 cm, 8 m	81	0.157	0.924
DBH 5-15 cm, 32 m	81	0.191	0.909
DBH 15-25 cm, 1 m	61	7.25	0.027
DBH 15-25 cm, 4 m	61	0.046	0.977
DBH 15-25 cm, 8 m	61	0.215	0.898
DBH 15-25 cm, 32 m	61	6.74	0.034
Height 1-5 m, 1 m	89	4.05	0.132
Height 1-5 m, 4 m	89	0.267	0.875
Height 1-5 m, 8 m	89	0.690	0.708
Height 1-5 m, 32 m	89	0.851	0.653
Height > 5 m, 1 m	70	5.40	0.067
Height > 5 m, 4 m	70	0.153	0.926
Height > 5 m, 8 m	70	0.424	0.809
Height > 5 m, 32 m	70	2.94	0.230
Decay class 1, 1 m	70	1.30	0.522
Decay class 1, 4 m	70	1.77	0.413
Decay class 1, 8 m	70	1.58	0.459
Decay class 1, 32 m	70	0.197	0.906
Decay classes 2-4, 1 m	89	3.37	0.185
Decay classes 2-4, 4 m	89	0.089	0.956
Decay classes 2-4, 8 m	89	0.169	0.919
Decay classes 2-4, 32 m	89	0.005	0.998

Table B3. Detailed results for differences in trees and snags among different classes of DBH, height and decay stage for Kruskal Wallis tests among different structural classes or Mann Whitney tests where there are only two groups. Groups are as follows: DBH 1-5 cm, 5-15 cm, 15-25 cm and >25 cm for tree and snag DBH groups 1-4; height 1-5 m, 5-15 m, >15 m for tree height groups 1-3; height 1-5 m, >5 m for snag groups 1-2; and decay class 1, classes 2-4 for snag decay groups 1 and 2.

	Average values						
	Group 1	Group 2	Group 3	Group 4	*n*	χ^2 or *U*	*p*-value
Trees							
DBH, 1 m	0.917	0.945	0.984	0.996	251	113.2	0.000*
DBH, 4 m	0.254	0.137	0.104	0.067	251	23.13	0.000*
DBH, 8 m	0.166	0.107	0.073	0.099	251	8.38	0.015
DBH, 32 m	0.015	0.039	–0.003	–0.123	251	1.94	0.378
Height, 1 m	0.911	0.952	0.981		232	102.7	0.000*
Height, 4 m	0.266	0.137	0.140		232	18.59	0.000*
Height, 8 m	0.176	0.138	0.084		232	7.16	0.028
Height, 32 m	0.017	0.021	–0.003		232	1.22	0.543
Snags							
DBH, 1 m	0.987	0.982	0.993	0.994	179	52.64	0.000*
DBH, 4 m	0.056	0.089	0.020	0.042	179	5.34	0.069
DBH, 8 m	0.058	0.097	0.081	0.077	179	0.660	0.719
DBH, 32 m	–0.053	0.031	0.049	0.035	179	5.54	0.063
Height, 1 m	0.981	0.990			159	1178	0.000*
Height, 4 m	0.053	0.057			159	3066	0.864
Height, 8 m	0.078	0.044			159	2738	0.190
Height, 32 m	0.005	–0.009			159	2888	0.432
Decay, 1 m	0.990	0.981			159	1402	0.000*
Decay, 4 m	0.061	0.073			159	2904	0.463
Decay, 8 m	0.024	0.074			159	2640	0.100
Decay, 32 m	0.020	0.016			159	3098	0.953

*Significant at $\alpha = 0.05$ with the sequential Bonferroni test where the number of tests considered is $k = 20$.