

# Spatial relationships and tree species associations across a 236-year boreal mixedwood chronosequence

Andrew Park, Daniel Kneeshaw, Yves Bergeron, and Alain Leduc

**Abstract:** We studied community development and mortality among tree species at multiple spatial scales in a 236-year mixedwood chronosequence at Lake Duparquet, Quebec. Spatial relationships, species associations, and understory–overstory replacement patterns were studied using spatial statistics, patch indices, *G* tests, and transition matrices. Results of these analyses showed that shade-intolerant and shade-tolerant tree communities formed increasingly fine-grained patches in midsuccession. These fine-grained associations appear to be partly due to suppressed stems being released into a slowly thinning canopy and partly due to new recruitment of shade-tolerant conifers. In 1-ha plots, tree species richness and evenness peaked in 25-, 100-, and 400-m<sup>2</sup> subplots during midsuccession. Forest cover type diversity also peaked in midsuccessional landscapes assessed using aerial photographs. The oldest 1-ha plot was dominated by monospecific patches of eastern white cedar (*Thuja occidentalis* L.), which was the most likely replacement for live and dead trees and the most abundant species in the numerous subplots that were occupied by trees smaller than 8 cm DBH. In spite of this dominance, long-lived paper birch (*Betula papyrifera* Marsh.) and residual fir (*Abies balsamea* (L.) Mill.) seedlings may maintain the mixedwood character of this stand into the future. The implications of our findings for stand management and conservation are discussed.

**Résumé :** Les auteurs ont étudié le développement et la mortalité de communautés d'arbres en peuplements mixtes à plusieurs échelles spatiales dans une chronoséquence de 236 ans au lac Duparquet, Québec. Les relations spatiales, les associations d'espèces et les patrons de remplacement entre les espèces du couvert dominant et celles du sous-bois ont été étudiés en utilisant des statistiques spatiales, des indices d'agglomération, des tests de *G* et des matrices de transition. Les résultats de ces analyses montrent que les communautés d'arbres intolérants et tolérants à l'ombre forment un nombre croissant d'agglomérations de petites tailles à l'étape du milieu de la succession. La formation de ces associations de petites tailles semble partiellement attribuable, d'une part, aux tiges opprimées qui sont libérées à l'intérieur d'un couvert qui s'éclaircit lentement et, d'autre part, au recrutement de conifères tolérants à l'ombre. Dans des parcelles de 1 ha, la richesse en espèces et l'équitabilité ont culminé dans des sous-parcelles de 25, 100 et 400 m<sup>2</sup> de peuplements parvenus à l'étape du milieu de la succession. La diversité du type de couvert forestier estimée à partir de photographies aériennes a aussi culminé sur des territoires parvenus à l'étape de milieu de succession. La plus vieille placette de 1 ha était dominée par des agglomérations monospécifiques de thuya occidental (*Thuja occidentalis* L.), l'espèce la plus susceptible de remplacer les arbres morts et vivants et l'espèce la plus abondante dans les nombreuses sous-parcelles occupées par des arbres dont le DHP est inférieur à 8 cm. Malgré cette dominance, les espèces à forte longévité que sont le bouleau à papier (*Betula papyrifera* Marsh.) et les semis résiduels de sapin baumier (*Abies balsamea* (L.) Mill.) peuvent maintenir la mixité d'espèces de ce type de peuplement dans le futur. Les implications de nos résultats sont discutées en regard de l'aménagement et de la conservation des forêts.

[Traduit par la Rédaction]

## Introduction

North American boreal forests have traditionally been viewed as mosaics of even-aged stands maintained by frequent, stand-replacing fires (Van Wagner 1983). However, in

the wetter climate of Canada's southeastern boreal forest, fire cycles often exceed the average life-spans of pioneer species by 100 years or more. (Bergeron et al. 1998; Bridge 2001; Kneeshaw and Gauthier 2003). Under these conditions, windthrow, tent caterpillar (*Malacosoma disstria* (Hübner)),

Received 17 June 2004. Accepted 15 November 2004. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca/> on 8 April 2005.

**A. Park,<sup>1,2</sup> D. Kneeshaw, and A. Leduc.** Groupe de recherche en écologie forestière inter-universitaire (GREFi), Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, QC H3C 3P8, Canada.

**Y. Bergeron.** Chaire Aménagement forestier durable (AFD), Université du Québec à Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.

<sup>1</sup>Present address: Biology Department and Centre for Forest Interdisciplinary Research (CFIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada.

<sup>2</sup>Corresponding author (e-mail: [a.park@uwinnipeg.ca](mailto:a.park@uwinnipeg.ca)).

and spruce budworm (*Choristoneura fumiferana* (Clem.)) have the potential to create grouped mortality among trembling aspen (*Populus tremuloides* Michx.) or balsam fir (*Abies balsamea* (L.) Mill.) to create new small-scale disturbance regimes (Bergeron et al. 1995; Kneeshaw and Bergeron 1998; McCarthy 2001; Cumming et al. 1999; Gauthier et al. 2000).

Stand-replacing fires and gap-creating secondary disturbances are likely to create different types of spatial associations within and between tree species. Where fire intervals are shorter than the life-spans of pioneer trees, spatial associations within and between postfire cohorts of different tree species are likely to be determined during the short period of postfire seedling and sprout establishment. In the case of shade-intolerant pioneer species, these patterns may persist until the next fire (Gutsell and Johnson 2000, 2002).

Fire can promote the formation of nearly monospecific patches of trees covering hundreds or thousands of square metres. On the other hand, gap formation may restrict pure-species or age-class associations to much smaller patches (Frelich and Reich 1995b). Windthrow and insect infestation create gaps large enough (up to 3000 m<sup>2</sup>, Bergeron et al. 1995; Cappuccino et al. 1998; Kneeshaw and Bergeron 1998) to promote new generations of fast-growing aspen from root sprouts (Kneeshaw and Bergeron 1996, 1999; Chen and Popadiouk 2002). Alternatively, where small gaps ( $\leq 200$  m<sup>2</sup>) result from the deaths of single trees or small groups of trees (Kneeshaw and Bergeron 1998), local replacement of the dominant pioneer trees by shade-tolerant species may be promoted.

Living and dead trees also modify the germination environment in their immediate vicinities, creating positive or negative neighbourhood effects that modify understorey-overstorey replacement patterns at the scale of individual stems (Frelich and Reich 1995b; Friedman et al. 2001; Frelich 2002). For example, trees can favor or inhibit the establishment of conspecifics or different species by modifying humus and soil conditions (e.g., Brais et al. 1995). Balsam fir and eastern white cedar (*Thuja occidentalis* L.) germinate on coarse woody debris (CWD), which accumulates as pioneer trees die (Simard et al. 1998). Longer fire intervals may, therefore, allow spatial patterns among trees to change from coarse-grained (sensu Pielou 1977) monospecific patches in young stands to fine-grained patches with several species in close spatial association in older sites (Frelich and Reich 1995b).

Forest managers and conservationists have begun to focus on the ecological consequences of species associations in mixedwood stands. Concerns have been expressed that modern forestry practices are "unmixing the mixedwoods" (Spencer 1993; Baker et al. 1995; Hobson and Bayne 2000). Silviculturalists are also experimenting with ways to reproduce mixedwood stands to simultaneously meet timber and biodiversity objectives (Greene et al. 2000; Harper and Kabzems 2003).

These conservation and management concerns imply that mixedwood species are spatially associated. However, the explicit scales at which they form spatially mixed communities have seldom been studied. In this paper, we investigate spatially explicit intraspecific and interspecific associations in a chronosequence of mixedwood stands that burned between 44 and 236 years prior to sampling. Our objective was to investigate differences in the scale, character, and possible

causes of spatial associations between tree species across this chronosequence.

Based on previous research and observations in this and other forests (e.g., Kneeshaw and Bergeron 1998; Frelich and Reich 1995b) we generated the following spatially explicit hypotheses to focus our explorations of spatial pattern: (H1) these spatially segregated patches of live and dead conspecifics will occur in midsuccession to late succession stands if trees die in contiguous groups (where a group is defined as more than three contiguous stems), (H2) landscape patches dominated by particular species or species associations will be smaller in midsuccession to late succession stands, and (H3) tree diversity of landscape patches or within small subplots will be greater in older stands if small gaps (caused by the deaths of one to three overstorey trees) favor replacement of pioneer species by shade-tolerant conifers. The null hypothesis states that proportions of subplots in specific species-richness or species-evenness categories in a given fire year were equal to the proportion of subplots in that category for all years combined.

### Location and history of study sites

Our study sites were located in the Lake Duparquet Research and Teaching Forest (LDRTF) in northwestern Quebec (48°15'N and 48°30'N; 79°15'W and 79°30'W). The regional climate is cold continental, with average annual temperatures, precipitation, and number of frost-free days of 0.8 °C, 857 mm, and 64 days, respectively (Environment Canada 1993). Black spruce (*Picea mariana* (Mill.) BSP), aspen, paper birch (*Betula papyrifera* Marsh.), balsam fir, and, in the absence of fire, eastern white cedar dominate the forest (Bergeron and Dubuc 1989). The LDRTF lies in the northern Clay Belt, an area of fine lacustrine soils deposited by the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Therefore, although there is some small-scale soil heterogeneity, all study sites were located on mesic clay soils (grey Luvisols) with moderate to good drainage (Aubin et al. 2005). Nonclay soils in the area are restricted to rocky hills that are overlain with reworked till (Kneeshaw and Bergeron 1998).

### Methods

We studied intraspecific and interspecific spatial relationships at scales of 1–45 m, and species diversity at spatial scales from 25 to 400 m<sup>2</sup> in six 1-ha plots that last burned in 1760, 1823, 1847, 1870, 1916, and 1944. To ensure that these plots shared common physiographic characteristics, they were all sited on undulating terrain with moderately well-drained grey Luvisol soils. Although differences between plots in a chronosequence can occur because of unique site characteristics rather than because of succession (Johnson 1992; Linder 1998), the plots used in this present study were positioned to represent average stand compositions observed in a more extensive data set of successional data gathered from the same region (Bergeron 2000). The broad compositional trends observed in our chronosequence have also been validated by dendrochronological studies of species turnover and fire dynamics in the LDRTF (e.g., Bergeron and Dubuc 1989; Bergeron and Charron 1994; Bergeron 2000; De Grandpré et al. 2000).

**Table 1.** Forest community definitions for (a) communities measured in 25- to 400-m<sup>2</sup> subplots in 1-ha plots, and (b) 400-m<sup>2</sup> cells on aerial photographs.

Community	Definition
<b>(a) Communities on 1-ha</b>	
Pure aspen	Importance values $\geq 0.8$ (max = 1) relative to live trees
Pure paper birch	
Pure balsam fir	
Pure cedar	
Pure white spruce	
Pure black spruce	
Pure jack pine	
Pure balsam poplar	
Pure <i>Salix</i> sp.	
Aspen–fir	
Aspen–birch	
Birch–fir	
Cedar–fir	
Mixed white spruce	Two species in plot; importance values $\geq 0.2$ but less than 0.8; dominant species mixed with any other species
Mixed cedar	
Mixed jack pine	
Mixed black spruce	
Mixed balsam poplar	
Mixed <i>Salix</i> sp.	
Three species	All importance values greater than $0 < 0.8$
Four or more species	
Dead hardwood	Importance values $\geq 0.8$ relative to live trees
Dead conifer	
<b>(b) Communities used for aerial photographs</b>	
Pure aspen	$\geq 80\%$ cover by one species only
Pure birch	
Aspen–birch mixture	Two species mix with each species $\geq 20\%$ but less than 80%
Conifer	One or more conifers occupy $\geq 80\%$
Hardwood–conifer mixture	Hardwoods and conifers, with both types less than 80% and $\geq 20\%$
Large gap	$\leq 25\%$ crown cover

Tree communities were also assessed across areas of 24–61 ha using 1 : 15 000 and 1 : 18 000 scale aerial photographs that were divided into grids of 0.16-ha (40 m  $\times$  40 m) cells. These larger aerial-photo study areas were positioned in topography similar to that of the 1-ha plots. Wherever possible, they were positioned to avoid obvious bogs, hills, and rock outcrops. Aerial-photo study areas originating in 1823, 1847, 1916, and 1944 were contiguous with the equivalent 1-ha plots, while those from 1760 and 1870 lay within 600 m of the 1-ha plots for those years.

#### Data collection in 1-ha plots

Plots were subjectively located in stand conditions that were judged to be typical of the area. Each plot was subdivided into 100-m<sup>2</sup> subplots, on which all living trees and identifiable dead trees  $\geq 5$  cm DBH were mapped to the nearest 25 cm. Distances to each tree were measured from

two perpendicular plot boundaries, with a compass and metric tape, and then converted to slope-corrected XY coordinates in the computer. Species, DBH, and condition (living, standing dead, or dead and fallen) were noted.

#### Data analysis

H1 (spatial segregation of patches of live versus dead trees in midsuccession) was addressed using univariate Ripley's  $K(t)$  analysis, and its bivariate counterpart,  $K_{(12t)}$  analysis (Ripley 1977; Diggle 1983; Upton and Fingleton 1985). H2 (smaller landscape patches in midsuccession to late succession) and H3 (greater tree diversity in midsuccession to late succession sites) were tested using landscape patch metrics on subplots of different sizes in the 1-ha plots and landscapes in aerial photographs. H3 was also tested within 1-ha plots using replicated  $G$  tests to compare between-stand differences in species richness and evenness (Sokal and Rohlf 1981). H3 was also studied using transition matrices to define subcanopy to overstory replacement probabilities.

#### Ripley's $K(t)$ and $K_{(12t)}$ analysis

Univariate ( $K(t)$ ) and bivariate  $K_{(12t)}$  Ripley's  $K$  analyses were used to compare spatial relationships within and between populations of live and dead trees. Ripley's  $K$  method compares tree-to-tree distances across a series of concentric distance classes against the null hypothesis that spatial patterns follow a cumulative Poisson distribution. An edge correction is incorporated into the algorithm to correct for the influence of trees outside the mapped area (Diggle 1983; Haase 1995). Results are subjected to either an  $L(t)$  transformation or an  $L_{(12t)}$  transformation to facilitate graphic interpretation; these transformations yield values of zero under spatial randomness and values greater or less than zero under aggregated and regular (dispersed) distributions, respectively. Distance classes were defined in 1-m increments from 1 to 45 m. The significance of univariate patterns was assessed against point-wise two-tailed 95% confidence intervals derived from 200 permutations of the tree coordinates. Bivariate randomization tests consisted of subjecting coordinates from one of the data sets to a series of random shifts that conserve relative coordinates within the data set (software developed by Moer 1993, 1997).

Bivariate spatial analyses were done between living and dead trees of each species to investigate whether tree mortality occurred in areas segregated from live trees. Populations in a given plot were included in the analyses if they were represented by 20 or more stems for both live and dead trees. Separate univariate analyses on live and dead trees were used, together with stem maps (Legendre and Fortin 1989), to aid in the interpretation of living- versus dead-tree patterns.

#### Patch size, diversity, and relationships

Patch metrics in the 1-ha plots were derived from species' importance values (Mueller-Dombois and Ellenberg 1974; Roberts-Pichette and Gillespie 2001). These metrics were used to define 24 compositional groups on 25- and 100-m<sup>2</sup> subplots. Compositional groups were determined according to criteria for dominance by single species; shared dominance by two, three, and four species mixtures; or dominance by dead trees (Table 1a). The limited resolution of the

**Table 2.** FRAGSTATS metrics used at the class and landscape scales to evaluate community structure and spatial relationships in 1-ha plots and aerial photographs.

Type of metric	Index name	Scale <sup>a</sup>	Description
Composition/ Function/ Distribution	Largest patch index (LPI)	L/C	Percentage of landscape area occupied by largest patch
	Number of patches (NP)	L/C	Number of patches within classes and landscape
	Mean patch size (PS)	L/C	Average measured within or across all patch classes (ha)
Diversity	Patch richness (PR)	L	Number of different patch types present in the landscape
Proximity	Mean nearest neighbour (MNN)	L	Distance (m) to the closest neighbour, measured between closest edges
Mixing	Contagion (Co)	L	Measures adjacency of cells of patch type <i>i</i> to cells of other patch types. Integrates mixing and dispersion of patch types. 0 less than $Co \leq 100$ ; at 100, all patch types equally adjacent
	Interspersion and juxtaposition index (IJI)	L/C	Measures the degree to which similar patch types are adjacent to each other. 0 less than $IJI \leq 100$ ; larger values have greater adjacency

<sup>a</sup>Scale refers to metrics measured at the landscape (L) scale using data from all patch classes pooled, or class (C), where statistics are calculated in each patch class. Comprehensive definitions for each metric can be seen in text by McGarigal and Marks (1994).

**Table 3.** Tree population characteristics (numbers of stems) for 1-ha plots at Lake Duparquet, Quebec.

Fire year	Live stems	Dead standing	Dead fallen	Live basal area
1760	624	728	186	38.4
1823	1829	620	313	36.0
1847	1543	352	381	43.5
1870	1316	524	212	29.0
1916	2552	754	336	29.3
1944	1737	465	249	35.6

aerial photographs necessitated measuring percent canopy cover in a smaller set of compositional categories. Each 400-m<sup>2</sup> landscape cell was assigned to one of six compositional groups based on percent canopy tree composition (e.g., hardwoods, hardwood–conifer mix, open cells with  $\leq 25\%$  canopy cover; Table 1b). Percent cover in each category was estimated visually in the quadrants of each 400-m<sup>2</sup> cell plot using a stereoscope set over a computer-generated graticule.

Compositional data from 1-ha plots and aerial photographs were converted to raster files, and their patch characteristics were analyzed using the spacial analysis program FRAGSTATS 2.0 (McGarigal and Marks 1994). FRAGSTATS uses a range of metrics gathered from cell adjacencies in raster files to identify discrete landscape patches, their characteristics, and their relationships. A subset of these metrics was used to describe the size, diversity, and spatial interspersion of landscape patches (Table 2).

### Species richness, species evenness, and community richness

Replicated *G* tests were used in chronosequence-wide comparisons of species-richness and species-evenness categories in 1-ha plots. The *G* statistic (Sokal and Rohlf 1981) can be used to test both the overall significance of a contingency table and the heterogeneity among individual contingency-table categories. Heterogeneity *G*-test statistics were assessed against the null hypothesis that proportions of subplots in specific species-richness or species-evenness categories in a given fire year were equal to the proportion of subplots in that category for all years combined. Because a spruce

budworm outbreak from 1970 to 1987 (Morin et al. 1993) produced unusually high numbers of dead fir, *G* tests were repeated with the assumption that 90% of the dead fir in each plot were still alive.

### Transition matrices

Modified transition matrices were used to estimate the probabilities of finding potential canopy species growing below large live trees, standing dead trees, and in “relative gaps”, defined as 25-m<sup>2</sup> subplots occupied only by trees of  $\leq 8$  cm DBH. Stems were counted if they were growing within 3 m of any standing dead tree or within 3 m of the largest live tree in each area of 100 subplots. Trees located less than 3 m from a plot edge were excluded from the analysis because of possible edge effects. Canopy trees were defined as having a DBH of  $\geq 15$  cm for balsam fir, eastern white cedar, or paper birch, or a DBH of  $\geq 20$  cm for trembling aspen or white spruce.

Transition probabilities were calculated using the relative frequencies of each subcanopy species, weighted by their diameters. They can be interpreted simply as weighted probabilities of finding stems of different species below larger trees. Alternatively, these transition probabilities can be interpreted as reflecting genuine replacement probabilities, an assumption that is not strictly true for communities of trees differing in shade tolerance and growth rates (McCune and Allen 1985). Interpretations of species’ potentials to replace each other in the overstory are, therefore, tentative.

## Results

### Trees in 1-ha plots

Live-stem density varied from 2552 stems-ha<sup>-1</sup> in the 1916 stand to 625 stems-ha<sup>-1</sup> in the oldest stand (Table 3). Minimum and maximum basal area were 29.3 and 43.5 m<sup>2</sup>-ha<sup>-1</sup> in midsuccessional stands that burned in 1870 and 1847, respectively. Aspen and birch dominated the two youngest stands, but balsam fir and white spruce codominated with aspen and birch in midsuccession (Fig. 1). Cedar dominated the two oldest (1823 and 1760) stands, but other species were less important in these stands than in younger stands.

Dead trees were concentrated in smaller diameter classes for all species in the three youngest stands (Fig. A1 of sup-

plementary data),<sup>3</sup> but were distributed more evenly among aspen and birch diameter classes in stands that burned before 1870. Balsam fir suffered heavy mortality in every stand. The highest (probably budworm-induced) fir mortality occurred in the oldest 1760 stand, which was dominated by conifers, where 98% of stems had died. The presence of small-diameter aspen in the 1823, 1847, and 1870 stands probably represented a second aspen cohort (Bergeron 2000), and a few large aspen and birch persisted in the oldest stands.

### Spatial analysis

Univariate analyses showed that living and dead trees were significantly aggregated in all but the oldest stand (Fig. B1 of supplementary data).<sup>3</sup> Significant aggregations extended beyond 45 m in the 1847–1944 fire-origin stands for most species, indicating that they occupied patches of at least 0.25 ha. In the oldest stand, trees were inconsistently aggregated or distributed at random. The small population of live aspen ( $n = 35$ ) was aggregated at 0–30 m in the oldest (1760) stand, but birch ( $n = 69$ ) were only aggregated at 1–4 m in the same stand.

Live versus dead trees had random or inconsistently aggregated patterns, rather than dispersed patterns. Therefore, although univariate patterns were aggregated, dead trees were interspersed among live conspecifics, rather than forming spatially discrete groups in large gaps (Fig. B2 of supplementary data).<sup>3</sup> Patterns of live versus dead aspen were aggregated in the three youngest stands (Fig. 2a), but were random or aggregated over short distances in the 1823 and 1847 stands (Fig. 2b).

Relationships between live and dead birch did not show any consistent trend with successional status of the 1-ha plots. Live versus dead birch were intermittently aggregated in the 1944, 1916, and 1823 stands (Fig. 2c: 1823 data), but were distributed at random in the 1870 stand (Fig. 2d). Live versus dead cedar (example in Fig. 2e) and fir (example in Fig. 2f) were distributed at random in the majority of plots, except for aggregations of live versus dead cedar between 2 and 44 m in the 1823 plot (Fig. 2g).

Interspersion of individual dead stems among live conspecifics was visually evident from stem maps (examples in Fig. 3). In the oldest (1760) stand, a small number of dead cedar ( $n = 59$ ) were interspersed among a bigger population of larger diameter stems ( $n = 494$ ; Fig. 3a). By contrast, dead fir of all sizes ( $n = 666$ ) were interspersed among live fir ( $n = 494$ ) in the 1823 stand (Fig. 3b). Dead aspen in the 1870 stand were small-diameter stems distributed among geographically localized clusters of live trees (Fig. 3c). By contrast, dead aspen in the 1847 stand were large-diameter stems that appeared to form local clusters of 2–4 trees, although the majority were interspersed among the aggregated live trees (Fig. 3d).

### Patch metrics

The largest homogenous patches composed of 25-m<sup>2</sup> subplots occupied 49% and 51% of the 1-ha plots in the youngest and oldest fire-origin stands, but only 3.2%–16.4% of

the total area in intervening years (Table 4). Midsuccessional stands (1823, 1847, and 1870) were also composed of many more individual patches than were the oldest and youngest plots at this scale, although overall patch richness varied little. At the same time, high values of interspersion and low values of contagion showed that patches with the same composition were clustered within midsuccessional plots.

At the 100-m<sup>2</sup> scale, there were fewer patches in the 1823–1916 stands than in either the oldest or youngest stands. However, there were no obvious chronosequence-wide trends in the distribution of patch sizes or adjacency at either the 100- or 400-m<sup>2</sup> scales. The largest patches defined by 100-m<sup>2</sup> cells occupied between 41.0% and 77.0% of the 1-ha plots and 37.1% to 78.7% of aerial-photo landscapes defined by 400-m<sup>2</sup> cells. Average patch sizes were small (0.011–0.004, 0.040–0.062, and 0.76–1.90 ha at the 25-, 100-, and 400-m<sup>2</sup> scales, respectively) and indicated strongly left-skewed patch-size distributions.

Species diversity within and between compositional groups was highest in midsuccessional stands in 25-m<sup>2</sup> subplots (Tables A1–A3 of supplementary data).<sup>3</sup> The largest patches composed of 25- and 100-m<sup>2</sup> subplots were classified as pure aspen in the youngest (1944) stand and pure cedar in the oldest (1760) stand. By contrast, patches composed of 25-m<sup>2</sup> cells in the 1823–1916 stand sequence were partitioned between two or three codominant species (Tables A1 and A2 of supplementary data).<sup>3</sup> At the 100-m<sup>2</sup> scale, between 61% and 93% of cells in the 1823–1916 stand sequence were dominated by mixtures of three, four, or more species (Table A2 of supplementary data).<sup>3</sup>

At the 400-m<sup>2</sup> scale, 75%–99% of landscapes that burned between 1823 and 1944 were dominated by aspen, birch, or an aspen–birch mixture in patches covering between 2.3 and 20 ha (Table A3 of supplementary data).<sup>3</sup> Pure conifer patches were small ( $\leq 0.2$  ha) and occupied less than 3% of the landscape in all years. However, hardwood–conifer mixtures were of greater importance in stands that burned in 1870 or earlier and occupied 69.1% of the 1760 landscape.

### Canopy openness

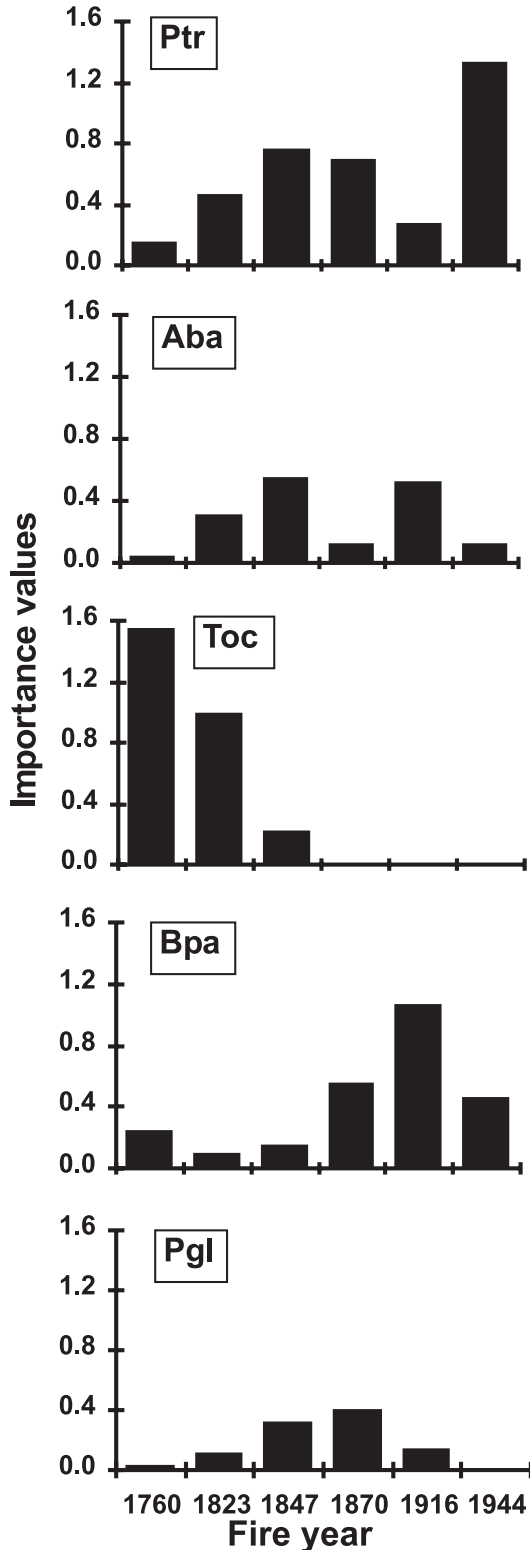
In stands that burned between 1823 and 1944, less than 5% of 25-m<sup>2</sup> subplots in 1-ha plots were without any trees larger than 5 cm DBH. Even fewer subplots were occupied by trees between 5 and 8 cm DBH (Fig. 4a). By contrast, 20.5% of 25-m<sup>2</sup> subplots lacked trees larger than 5 cm DBH in the 1760 1-ha plot. The percent openness of landscapes showed a generally increasing trend with stand age (Fig. 4b), with the oldest (1760) landscape having a mean openness of almost 60%.

### Between-stand comparisons — G tests

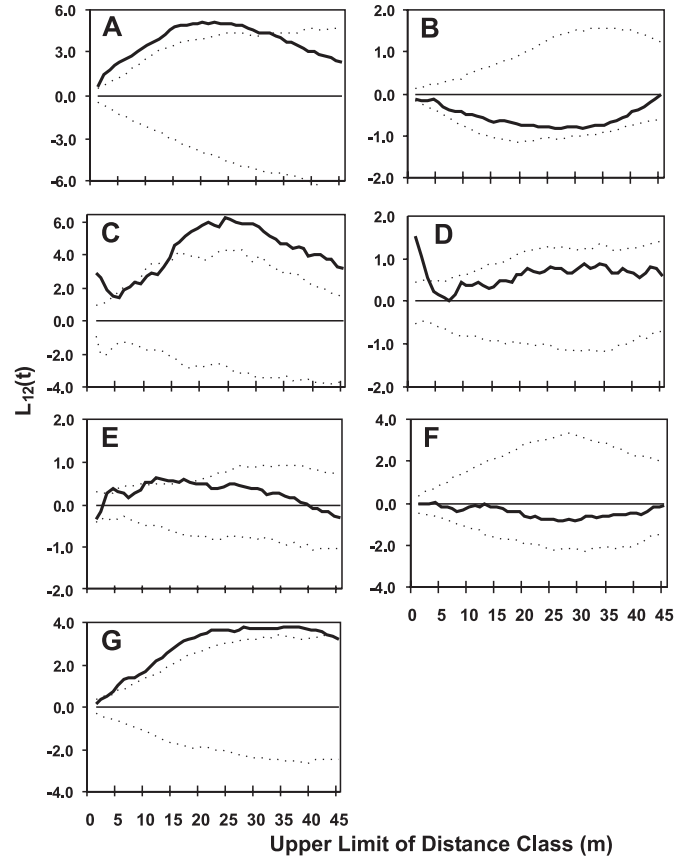
With the exception of the 1760 stand, richness and evenness of tree species were greater in older stands at the 25-, 100-, and 400-m<sup>2</sup> subplot scales. In the 1823–1916 stand sequence, all subplot scales supported more tree species larger than 5 cm DBH than would have been expected from the totals for all 1-ha plots combined ( $p \leq 0.05$ ; Fig. 5) (Table D1 of supplementary data).<sup>3</sup> Species evenness was also greater

<sup>3</sup>Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3643. For more information on obtaining material refer to [http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub\\_e.shtml](http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml).

**Fig. 1.** Importance values of the five major canopy species from the 1-ha plots. An importance value is the sum of relative density (over the whole plot) and relative dominance (basal area; Roberts-Pichette and Gillespie 2001). Relative frequency was ignored, since the entire area was enumerated. Ptr, trembling aspen; Aba, balsam fir; Toc, eastern white cedar; Bpa, paper birch; Pgl, white spruce.



**Fig. 2.** Examples of bivariate  $L_{12}(t)$  analysis for live versus dead trees for (A) aspen in 1870, (B) aspen in 1847, (C) birch in 1823, (D) birch in 1870, (E) cedar in 1760, (F) fir in 1823, and (G) cedar in 1823. Spatial patterns (solid lines) that fall above or below the upper and lower boundaries of the two-tailed 95% confidence envelopes (dotted lines) are aggregated or dispersed, respectively.



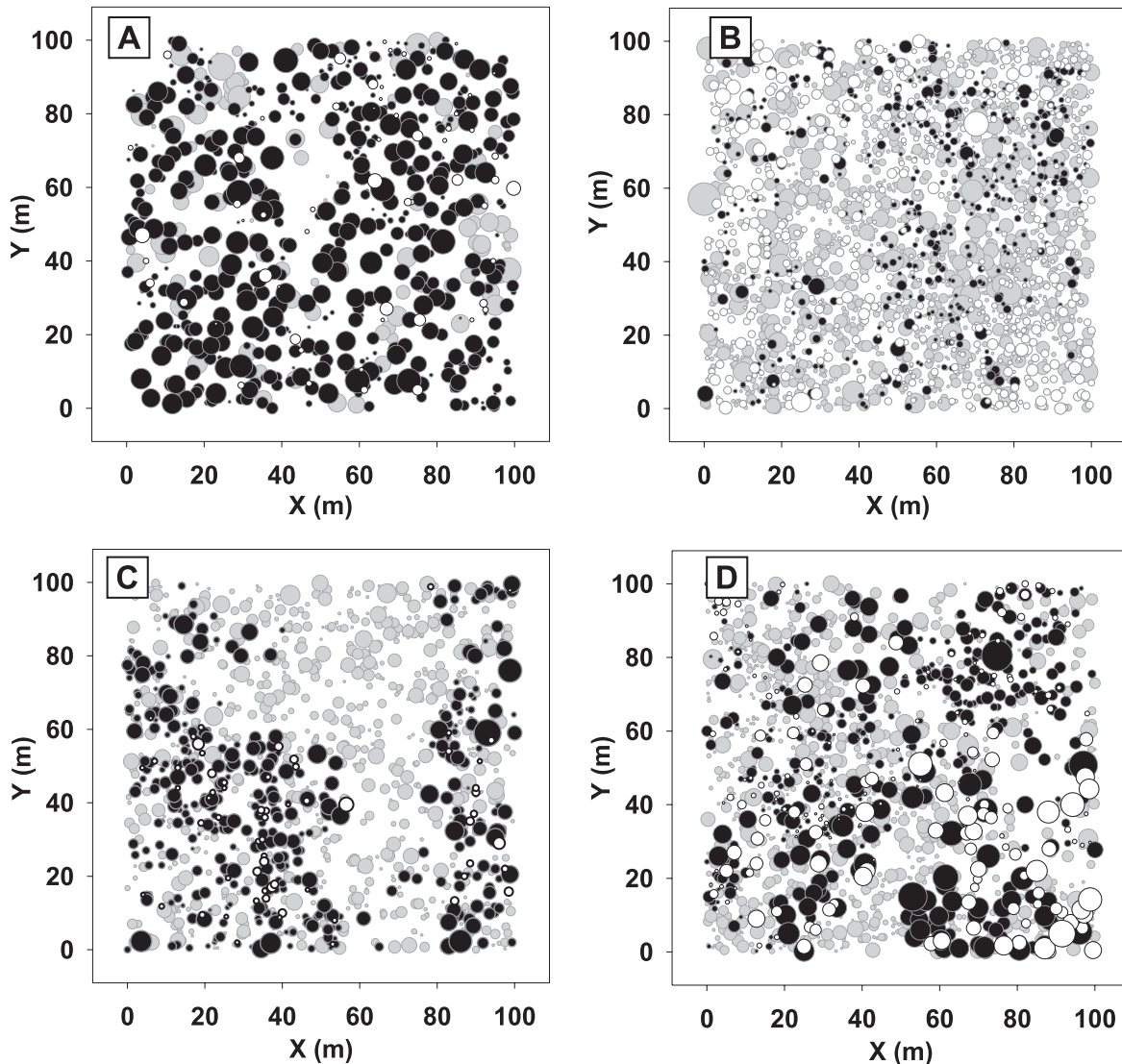
in midsuccessional plots, although this pattern was less consistent at the 400-m<sup>2</sup> scale (Table D2 of supplementary data).<sup>3</sup> Plots with low species diversity and evenness had the opposite pattern, with significantly larger numbers of single-species and low evenness plots in stands that originated in 1760 and 1944.

Including 90% of dead fir in the pool of live trees made little difference to the interpretation of species richness in 25- and 100-m<sup>2</sup> plots. Species richness was still greatest in midsuccession, although there were fewer empty 25-m<sup>2</sup> subplots. More of the 25- and 100-m<sup>2</sup> subplots had two and three tree species, respectively, after including dead fir. Inclusion of dead fir also enhanced between-stand differences in species richness in 400-m<sup>2</sup> subplots, but reduced species evenness, indicating that many subplots had been dominated by fir before the last spruce-budworm outbreak.

**Transition matrices**

Understory trees tended to grow below conspecifics in the hardwood-dominated 1916 and 1944 stands. In all other stands, however, a majority of understory trees belonged to different species from those in the overstory. Aspen and birch had moderate to high probabilities (*P*) of growing beneath their own live canopies in the 1870–1944 stands (*P* = 0.25–0.80 and 0.48–0.73 for aspen and birch, respectively; Figs. 6a and 6b) (Table C1 of supplementary data).<sup>3</sup> On the other hand,

**Fig. 3.** Plot maps of live and dead stems of (A) cedar in 1760, (B) fir in 1823, (C) aspen in 1870, and (D) aspen in 1847. The diameter of each circle is roughly proportionate to the expected diameter of tree crowns. Black circles, live stems; open circles, dead stems; light grey circles, live stems of other species.



fir was an inconsistent candidate for self-replacement beneath live conspecifics (Fig. 6c) and had consistently low probabilities for self-replacement under dead conspecifics ( $P = 0.00\text{--}0.09$ ; Fig. 6f).

Interspecific replacement of live and dead trees appeared to be more likely than intraspecific replacement in midsuccession to late succession (1847–1760 stand sequence). Aspen and birch were unlikely to grow below dead conspecifics in mid-succession and late succession (Figs. 6d and 6e) (Table C2 of supplementary data),<sup>3</sup> and cedar or fir were the most likely replacements of aspen and birch in the 1823 and 1760 stands. Birch occasionally grew below dead fir ( $p = 0.02\text{--}0.39$ ), as observed by Frelich and Reich (1995) in Minnesota (Fig. 6f) (Table C2 of supplementary data),<sup>3</sup> and aspen was moderately likely to replace dead fir ( $P = 0.11\text{--}0.51$ ) and white spruce ( $P = 0.34\text{--}0.38$ ) in the 1847 and 1870 stands.

Cedar was increasingly dominant beneath all other species in the stands that burned in 1847 or earlier. Cedar was also the most likely filler of 25-m<sup>2</sup> relative gaps in the same stands

(Fig. 7) (Table C3 of supplementary data).<sup>3</sup> However, aspen were unlikely to occupy 25-m<sup>2</sup> subplots with trees of 8 cm DBH or smaller in 1-ha plots of any age ( $P = 0.04\text{--}0.07$ ).

## Discussion

### General patterns

With the exception of the 1760 stand, small-scale compositional diversity was greater in stands that burned in 1870 and earlier than in stands that burned in 1916 and 1944. Evidence from spatial analysis suggested that this apparent trend towards increased species mixing was fostered by a regime of small gap disturbances generated by the deaths of individual trees. Contrary to H1 (segregated groups of dead trees and live residuals), dead canopy trees were generally interspersed at random among live residuals, suggesting that canopy openings were small. Small-scale species richness and evenness were at their greatest in the 1823–1870 stand sequence (partly supporting H3: higher small-scale diversity in

**Table 4.** Landscape indices measured by FRAGSTATS.

Index	Year					
	1760	1823	1847	1870	1916	1944
<b>25-m<sup>2</sup> cells</b>						
Largest patch index (%)	51.0	10.0	9.0	3.3	16.4	49.0
Number of patches	94	179	202	224	112	92
Mean patch size (ha)	0.011	0.006	0.005	0.004	0.009	0.011
Patch size coefficient of variation (%)	490.6	190.7	151.9	86.1	206.7	467.0
Mean nearest neighbour (m)	11.1	10.6	9.1	8.0	11.6	9.3
Nearest neighbour coefficient of variation (%)	109.1	120.1	71.8	78.8	116.8	86.9
Patch richness	13	17	9	12	12	12
Interspersion and juxtaposition index (%)	51.0	73.1	81.5	85.8	57.0	74.3
Contagion (%)	47.9	25.4	18.5	12.5	37.1	40.4
<b>100-m<sup>2</sup> cells</b>						
Largest patch index (%)	55.0	41.0	60.0	77.0	42.4	47.0
Number of patches	24	18	18	16	16	25
Mean patch size (ha)	0.042	0.056	0.056	0.062	0.062	0.040
Patch size coefficient of variation (%)	259.6	177.5	240.7	292.7	196.1	226.6
Mean nearest neighbour (m)	16.2	26.0	14.1	12.4	12.0	14.6
Nearest neighbour coefficient of variation (%)	54.2	119.1	50.1	49.4	45.9	48.5
Patch richness	6	8	6	5	4	9
Interspersion and juxtaposition index (%)	59.2	40.8	52.3	52.3	69.1	71.3
Contagion (%)	34.2	47.1	49.3	54.1	20.6	37.6
<b>400-m<sup>2</sup> cells</b>						
Area of landscape (ha)	26.4	36.0	60.8	30.8	29.4	24.6
Largest patch index (%)	68.48	42.05	61.97	78.65	37.1	69.48
Number of patches	24	32	24	19	26	13
Mean patch size (ha)	1.10	0.98	1.89	1.62	0.76	1.90
Patch size coefficient of variation (%)	323.2	245.0	295.1	329.2	183.5	237.8
Mean nearest neighbour (m)	79.7	54.0	101.1	110.2	65.0	94.4
Nearest neighbour coefficient of variation (%)	74.65	59.71	108.90	86.08	83.33	66.02
Patch richness	6	5	5	5	5	4
Interspersion and juxtaposition index (%)	56.5	70.2	60.8	56.5	55.6	54.0
Contagion (%)	47.9	26.8	44.1	60.1	31.7	49.2

older stands). Compositional groups in landscape patches also contained more species in midsuccessional stands, and these patches were smaller in 1-ha plots and landscapes in mid-succession (in support of H2).

High small-scale species diversity in midsuccession was accompanied by a shift from the potential replacement of canopy trees by conspecifics in the 1944 and 1916 stands to potential replacement by other species in older stands. In younger (1944 and 1916) stands, the high probability of finding aspen and birch growing beneath conspecifics probably reflected the stratification of the postfire pioneer cohort into dominant and suppressed stems. A gradual thinning of the pioneer canopy through the deaths of individual stems and small groups of trees would have allowed suppressed stems of shade-tolerant and midtolerant trees (principally fir and cedar; occasionally birch) to grow slowly into the subcanopy and canopy. Even aspen sprouts, which are reasonably common throughout the understory at the LDRTF, may be occasionally recruited to the canopy in this way (Bergeron 2000).

In the older stands, released stems from the pioneer cohorts would be augmented by new cohorts of fir and cedar. These species can germinate in large numbers on dead wood from tree falls, as well as on feathermoss substrates that de-

velop in aging mixedwood stands (Simard et al. 1998). These new trees would eventually increase small-scale tree diversity in stands where pioneer canopy trees were dying individually and were interspersed with surviving pioneer residuals.

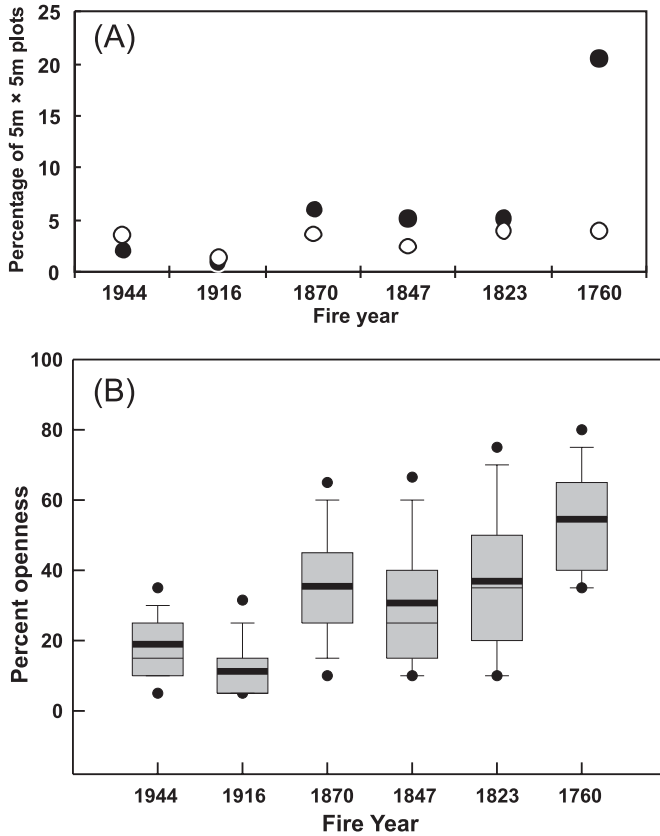
Large patches dominated by eastern white cedar, lower small-scale species diversity, and greater canopy openness distinguished the 1760 1-ha plot and landscape from all other stands. The few large aspen and birch in this plot may have been the senescent survivors of a population that was once more abundant. At the landscape scale, however, conifer-hardwood mixtures were the most important patch type in the 1760 stand, implying that hardwood populations may be more persistent in older stands than was indicated by data from the 1-ha plots.

#### **Tree replacement and the potential role of gap dynamics**

Many recent studies have emphasized gap replacement as a mechanism that promotes natural regeneration and species change in boreal forests (Coates and Burton 1997; Cumming et al. 1999; McCarthy 2001). The gap dimensions reported in these studies were small. In northeast Alberta, Cumming et al. (1999) found that 90% of aspen canopy gaps were



**Fig. 4.** Numbers of (A) 25-m<sup>2</sup> subplots in 1-ha plots having no trees  $\geq$  5 cm DBH (black circles) or only trees less than 8 cm DBH and (B) box plot of relative openness of 400-m<sup>2</sup> cells in 24- to 61-ha landscapes. Boxes bound the 25th to 75th percentiles; circles are the 5th and 95th percentiles and whiskers are standard errors. Medians and means are thin and thick lines, respectively.

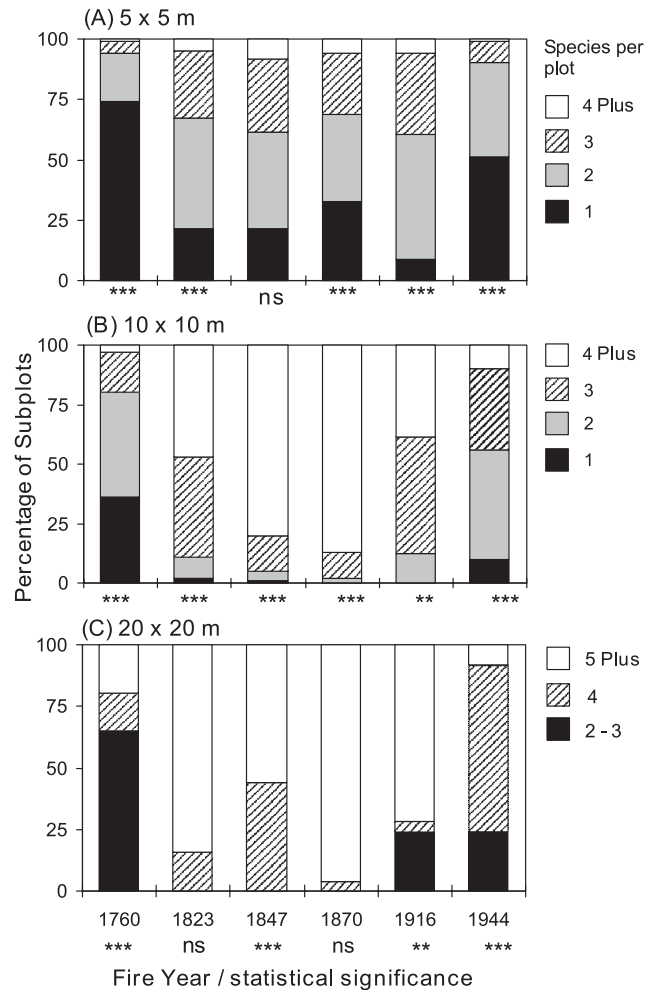


smaller than 90 m<sup>2</sup>. Similarly, although Kneeshaw and Bergeron (1998) observed that openings averaging 370 m<sup>2</sup> were created by grouped balsam fir mortality at Lake Duparquet, the majority of gaps were 25 m<sup>2</sup> or smaller in aspen-dominated stands.

Gaps of these dimensions are unlikely to be large enough to release suppressed aspen sprouts and may not always be large enough to allow shade-tolerant trees to reach the canopy. Aspen are recruited episodically in the absence of fire (Cumming et al. 1999; Bergeron 2000), but Chen and Popadiouk (2002) suggest that gaps larger than 250 m<sup>2</sup> that receive more than 40% full sunlight are needed for aspen establishment. Balsam fir seedlings can survive in less than 3% full sunlight, but need higher light levels to grow taller (Liefvers et al. 1999) and to reach sexual maturity (USDA Forest Service 1965; Messier et al. 1999). Balsam fir and white spruce under closed canopies do not produce cones until they achieve heights of 10 and 14 m, respectively (Greene et al. 2002).

Diameter distributions (Fig. A1) and age distributions (M.-C. Namroud et al., unpublished data) support the recruitment of a second aspen cohort in the 1847 and 1823 fire-origin stands. In our study, only the 1847 stand showed evidence of gaps formed by groups of large-DBH dead aspen that may have achieved the minimum dimensions specified in Chen and Popadiouk (2002) (Fig. 3d). However, the

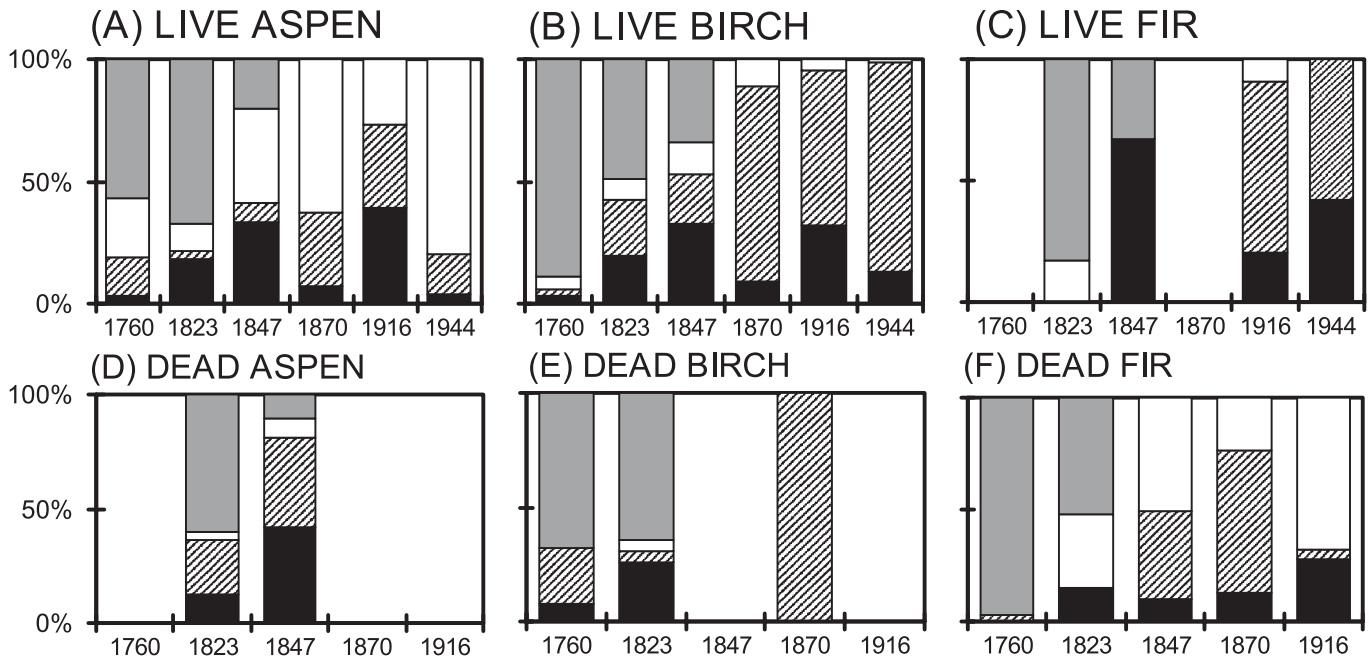
**Fig. 5.** Numbers of (A) 25-m<sup>2</sup> subplots, (B) 100-m<sup>2</sup> subplots, and (C) 400-m<sup>2</sup> subplots within 1-ha plots having various levels of species richness. Statistical significance of subplot richness in any year compared with that of all years combined is shown below the x-axis: \*,  $p \leq 0.05$ ; \*\*,  $p \leq 0.01$ ; \*\*\*,  $p \leq 0.001$ ; ns, nonsignificant.



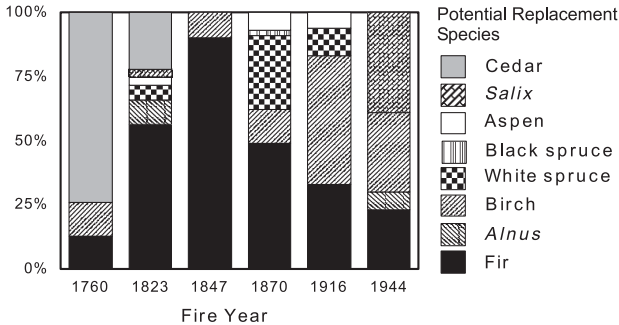
chronosequence approach suffers the disadvantage of presenting a series of snapshots of stand development. Because residence times of snags in boreal forests are generally less than 20 years (Lee 1998), current gaps (indicated by dead overstory trees) may have overlapped with older gaps for which no physical evidence was found at the time of sampling. Temporal overlap of small gaps, augmented by occasional larger scale disturbances, was cited to explain the persistence of midtolerant yellow birch (*Betula alleghaniensis* Britton) and green ash (*Fraxinus pennsylvanica* Marsh.) in a Michigan hardwood where individual gaps were smaller than 40 m<sup>2</sup> (Dahir and Lorimer 1996). Similarly, the occurrence of second cohorts of aspen and fir in our chronosequence may have been facilitated by the temporal overlap of small gaps and the cumulative thinning effects of such mortality among the original pioneer-tree populations.

Successional pathways and spatial scales of association different from those observed in our data can potentially occur because of differences in the timing, character, and severity of secondary disturbances (Frelich 2002). For example, the extensive fir mortality observed in the 1760 1-ha plot al-

**Fig. 6.** Potential replacement species for live and dead aspen, birch, and fir. Bars show percentage of potential replacement trees that were aspen (white bars), birch (diagonal stripes), cedar (grey bars), or fir (black bars). If no bars are shown for a particular year, no trees of that species were present.



**Fig. 7.** Potential replacement species in 25-m<sup>2</sup> subplots with only trees ≤ 8 cm DBH. Replacement probabilities are expressed as percentages of the total.



most certainly occurred during the 1970–1987 spruce budworm outbreak (Morin et al. 1993). The impact of the infestation on this stand may have been particularly severe, because a gradual loss of hardwood cover left the balsam fir population more exposed to budworm attack (MacLean 1996; Cappuccino et al. 1998). If rapid deterioration of large aspen clones had occurred in our younger stands (as has been observed in the southern Great Lakes, (Shields and Bockheim 1981)), our midsuccessional plots may have been dominated by larger but less diverse patches of trees. With the possible exception of the 1847 stand, such aggregated mortality was not evident in any our sites. Furthermore, recent genetics work (Namroud et al., unpublished data) demonstrates that the majority of aspen in our area were either unique ramets or clones of two to five trees.

**Future developments**

Cedar has the potential to replace all other species in the oldest stands of the chronosequence. Cedar has a strong ca-

capacity to regenerate by layering (Bergeron 2000) and lacks characteristics that would make it vulnerable to competition from other species. The dense shade cast by cedar canopies would potentially inhibit the growth, and perhaps, the survival of other species. However, it is unlikely that the 1760 stand will become a cedar monoculture. Although cedar lives two to three times longer than fir and aspen, birch is also long-lived and continued to have moderate chances of replacing other species in the 1760 stand. The 1760 fir population was decimated in the 1970–1987 spruce budworm outbreak, but fir is well adapted to budworm infestation and may continue to be recruited from surviving seedlings (Morin 1990; MacLean 1980). The persistence of mixed stands beyond 236 years after fire is confirmed by a recently discovered 400-year-old stand in the LDRTF that supports cedar, fir, and white birch (Hély et al. 2000).

**Implications for forest management and conservation**

The markedly different spatial scales and tree-species associations observed in stands of different age at Lake Duparquet reinforce Frelich’s (2002) strong recommendation to study processes in boreal and near-boreal forests at a variety of spatial scales. The importance of spatially explicit processes is also emphasized in recent studies of fire (Arseneault 2001), dispersal (Pastor et al. 1999; Asselin et al. 2001), and woody debris (Edman and Jonsson 2001).

The existence of tree associations at multiple spatial scales through time has implications for biodiversity conservation and stand-level silvicultural practices in boreal mixedwood forests. The use of silviculture to emulate landscape patterns of fire disturbance as a coarse filter for biodiversity conservation is now entrenched in forest management theory (Ontario Ministry of Natural Resources 2001). Much less attention has been paid to the importance of small-scale stand structures

that occur within landscape patches. Mixed-species stands with complex vertical structures have been associated with high levels of animal diversity, particularly that of birds (Brokaw and Lent 1999; Hobson and Bayne 2000). However, relationships between habitat quality and small-scale forest structure and (or) diversity have seldom been quantified beyond the establishment of general community-level correlations.

Our results suggest that the character of secondary disturbances in regenerating boreal mixedwood stands may have long-term effects on tree community composition at small scales. Small midsuccessional gaps, and the probability that the pioneer canopy opens in a gradual, diffuse way, appear to have allowed intolerant hardwoods and shade-tolerant conifers to associate at small scales for an extended period during midsuccession. The importance of such small-scale mixing of canopy species for wildlife should be a subject of future research. If maintaining these characteristics is to be a priority for forest management, the use of single-tree selection systems or underplanting of selection-cut overstories may be more appropriate than group selection or shelterwood systems.

## Acknowledgements

This work was supported by the ministère de l'Enseignement Supérieur et de la Science du Québec (Fonds pour la formation de chercheurs et l'aide à la recherche (FCAR) program), the ministère des Ressources Naturelles du Québec and by the Natural Sciences and Engineering Research Council of Canada. Special thanks go to Danielle Charron and Colin Kelly for original fieldwork and to Vincent Daoust for analyzing the aerial photographs. We are grateful to two anonymous reviewers for the many helpful comments they made on an earlier version of this manuscript.

## References

- Arseneault, D. 2001. Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. *Can. J. For. Res.* **31**: 1367–1374.
- Asselin, H., Fortin, M.-J., and Bergeron, Y. 2001. Spatial distribution of late successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *For. Ecol. Manage.* **140**: 29–37.
- Aubin, I., Messier, C., and Kneeshaw, D.D. 2005. Population, structure and growth acclimation of mountain maple in response to canopy openings along a successional gradient in the southern boreal forest. *Ecoscience*. In press.
- Baker, J.A., Clark, T., and Thompson, I.D. 1995. Boreal mixedwoods as wildlife habitat: observations, questions and concerns. *In Advancing Boreal Mixedwood Management in Ontario: Proceedings of a Workshop, Sault St. Marie, Ont. Edited by C.R. Smith and G. W. Crook.* Canadian Forest Service and OMNR. pp. 41–51.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Québec's southern boreal forest. *Ecology*, **81**: 1500–1516.
- Bergeron, Y., and Charron, D. 1994. Postfire stand dynamics in the southern boreal forest (Québec): a dendroecological approach. *Ecoscience*, **1**: 173–184.
- Bergeron, Y., and Dubuc, M. 1989. Succession in the southeastern part of the Canadian boreal forest. *Vegetatio*, **79**: 51–63.
- Bergeron, Y., Morin, H., Leduc, A., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Québec. *Can. J. For. Res.* **25**: 1375–1384.
- Bergeron, Y., Richard, P.J.H., Corcaillet, C., Gauthier, S., Flannigan, M., and Prairie, Y.T. 1998. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. *Conserv. Ecol.* [serial online], **2**. Available from <http://www.consecol.org/vol2/iss2/art6> [accessed 15 March 2002].
- Brais, S., Camiré, C., Bergeron, Y., and Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwest Quebec. *For. Ecol. Manage.* **76**: 181–189.
- Bridge, S.R.J. 2001. Spatial and temporal variations in the fire cycle across Ontario. *Ont. Minist. Nat. Resour. Northeast Sci. Technol.* NEST TR-043.
- Brokaw, N.V.L., and Lent, R.A. 1999. Vertical structure. *In Maintaining biodiversity in forest ecosystems. Edited by J. Malcolm and L. Hunter.* Cambridge University Press, Cambridge, UK. pp. 373–399.
- Cappuccino, N., Lavertu, D., Bergeron, Y., and Regniere, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, **114**: 236–242.
- Chen, H.H.Y., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. *Environ. Rev.* **10**: 137–166.
- Coates, K.D., and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* **99**: 337–354.
- Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J. 1999. Gap dynamics in boreal aspen stands: Is the forest older than we think? Sustainable Forest Management Network, Edmonton, Alta. Working Paper 1999-13.
- Dahir, S.E., and Lorimer, C.D. 1996. Variation in canopy gap formation among developmental stages of northern hardwood. *Can. J. For. Res.* **26**: 1875–1892.
- De Grandpré, L., Morissette, J., and Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. *J. Veg. Sci.* **11**: 791–800.
- Diggle, P.J. 1983. *The statistical analysis of spatial point patterns.* Academic Press, London.
- Edman, M., and 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.
- Environment Canada. 1993. Canadian climate normals 1961–1990. Environment Canada, Atmospheric Environment Service, Downsview, Ont.
- Frellich, L.E. 2002. *Forest dynamics and disturbance regimes: studies from temperate evergreen forests.* Cambridge University Press, Cambridge, UK.
- Frellich, L.E., and Reich, P.B. 1995a. Neighborhood effects, disturbance and succession in forests of the western Great Lakes region. *Ecoscience*, **2**: 148–158.
- Frellich, L.E., and Reich, P.B. 1995b. Spatial patterns and succession in a Minnesota boreal forest. *Ecol. Monogr.* **65**: 325–346.
- Friedman, S.K., Reich, P.B., and Frellich, L.E. 2001. Multiple-scale composition and spatial distribution patterns of the north-eastern Minnesota presettlement forest. *J. Ecol.* **89**: 538–554.
- Gauthier, S., De Grandpré, L., and Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. *J. Veg. Sci.* **11**: 781–790.
- Greene, D.F., Kneeshaw, D.D., Messier, C., Lieffers, V., Cormier, D., Doucet, R., Grover, G., Coates, K.D., and Calogeropoulos, C. 2000. Silvicultural alternatives to clearcutting and planting in southern

- boreal mixedwood stands (aspen/white spruce/balsam fir). Working Paper 2000-3. Sustainable Forest Management Network.
- Greene, D.F., Messier, C., Asselin, H., and Fortin, M.J. 2002. The effect of light availability and basal area on cone production in *Abies balsamea* and *Picea glauca*. *Can. J. Bot.* **80**: 370–377.
- Gutsell, S.L., and Johnson, E.A. 2000. The local population dynamics of trees in the boreal mixedwood forest. *In* Understanding how fire behavior characteristics shape tree population dynamics, diversity and forest patterns. Project Report 2000-22 [online]. Sustainable Forest Management Network, Edmonton, Alta. p. 13. Available from <http://www.ualberta.ca/sfm> [accessed 12 November 2003].
- Gutsell, S.L., and Johnson, E.A. 2002. Accurately aging trees and examining their height-growth rates: implications for interpreting forest dynamics. *J. Ecol.* **90**: 153–166.
- Haase, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *J. Veg. Sci.* **6**: 575–582.
- Harper, G., and Kabzems, R. 2003. Growing-space management in boreal mixedwood forests: the establishment of EP-1192.01 Fort Nelson River Site. Extension Note 64 [online]. British Columbia Ministry of Forests, Victoria, B.C. p. 8. Available from <http://www.for.gov.bc.ca/hfd/pubs/Docs/En/En64.pdf> [accessed 12 January 2004].
- Hobson, K.A., and Bayne, E. 2000. Breeding bird communities in boreal forest of western Canada: consequences of “unmixing” the mixedwoods. *Condor*, **102**: 759–769.
- Johnson, E.A. 1992. Fire and vegetation dynamics — studies from the North American boreal forest. Cambridge University Press, Cambridge, UK.
- Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. *Can. J. For. Res.* **26**: 888–898.
- Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*, **79**: 783–794.
- Kneeshaw, D.D., and Bergeron, Y. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. *Ecoscience*, **6**: 214–222.
- Kneeshaw, D.D., and Gauthier, S. 2003. Old-growth in the boreal forest: a dynamic perspective of the stand and landscape level. *Environ. Rev.* **11**: S99–S114.
- Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. *For. Ecol. Manage.* **105**: 263–272.
- Legendre, P., and Fortin, M.-J. 1989. Spatial pattern and ecological analysis. *Vegetatio*, **80**: 107–138.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* **29**: 796–811.
- Linder, P. 1998. Structural changes in two virgin boreal forest stands in central Sweden over 72 years. *Scand. J. For. Res.* **13**: 451–461.
- MacLean, D.A. 1996. Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. *For. Chron.* **72**: 399–405.
- McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* **9**: 1–59.
- McCune, B., and Allen, T.F.H. 1985. Forest dynamics in the Bitterroot Canyons, Montana. *Can. J. Bot.* **63**: 377–383.
- McGarigal, K., and Marks, B.J. 1994. FRAGSTATS: spatial analysis program for quantifying landscape structure, Version 2.0 [computer program]. Oregon State University, Corvallis, Ore.
- Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* **29**: 812–823.
- Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* **39**: 756–775.
- Moeur, M. 1997. Spatial models of competition and gap dynamics in old growth *Tsuga heterophylla/Thuja plicata* forests. *For. Ecol. Manage.* **94**: 175–186.
- Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi Region, Quebec. *Can. J. For. Res.* **23**: 1497–1506.
- Mueller-Dombois, D., and Ellenberg, H. 1974. Plotless sampling techniques. Chap. 7. *In* Aims and methods of vegetation ecology. John Wiley & Sons Inc., New York. pp. 99–133.
- Ontario Ministry of Natural Resources. 2001. Forest management guide for natural disturbance pattern emulation [online]. Available from <http://www.mnr.gov.on.ca/mnr/forests/forestdoc/ebf/guide/disturbance.html> [accessed 7 June 2004].
- Pastor, J., Cohen, Y., and Moen, R. 1999. Generation of spatial patterns in boreal forest landscapes. *Ecosystems*, **2**: 439–450.
- Pielou, E.C. 1977. Studying pattern by distance sampling. Chap. 10. *In* Mathematical ecology. John Wiley & Sons Inc., New York. pp. 148–165.
- Ripley, B.D. 1977. Modelling spatial pattern (with discussion). *J. R. Stat. Soc. B.* **41**: 368–374.
- Roberts-Pichette, P., and Gillespie, L. 2001. Section I — Canopy-tree stratum biodiversity monitoring protocols [online]. Environment Canada, Ecological Monitoring and Assessment Network. Available from <http://www.eman-rese.ca/eman/ecotools/protocols/terrestrial/vegetation/page19.html> [accessed 12 November 2003].
- Shields, W.J., Jr., and Bockheim, J.G. 1981. Deterioration of trembling aspen clones in the Great Lakes Region. *Can. J. For. Res.* **11**: 530–537.
- Simard, M.J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *J. Veg. Sci.* **9**: 575–582.
- Sokal, R.R., and Rohlf, F.J. 1981. Biometry: the principle and practice of statistics in biological research. W.H. Freeman and Company, New York.
- Spencer, J. 1993. Forest management at Weherhaeuser in Saskatchewan: past, present and future. *In* Birds in the boreal forest. Edited by H. Kuhnke. Forestry Canada, Northern Forestry Centre, Edmonton, Alta. pp. 154–162.
- Upton, G.J.G., and Fingleton, B. 1985. Spatial data analysis by example. John Wiley & Sons Inc., Chichester, UK.
- USDA Forest Service. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. Agric. Handb. 271.
- Van Wagner, R. 1983. Fire behavior in northern conifer forests and shrublands. *In* The role of northern circumpolar ecosystems. Edited by R.W. Wein and D.A. MacLean. John Wiley & Sons Inc., New York. pp. 65–80.
- Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des grands lacs glaciaires Barlow et Ojibway en territoire Québécois. *Géogr. Phys. Quat.* **31**: 357–372.