

Forest structure and composition at young fire and cut edges in black spruce boreal forest¹

Karen A. Harper, Daniel Lesieur, Yves Bergeron, and Pierre Drapeau

Abstract: We compared structure and composition at forest edges created by wildfire and clear-cutting in black spruce (*Picea mariana* (Mill.) BSP) dominated boreal forest in northwestern Quebec. Forest structure and plant species composition were sampled along transects perpendicular to eight 3- to 4-year-old fire edges and eight 2- to 5-year-old cut edges. Significance of edge influence was assessed by comparing mean values at different distances from the edge to the range of variation in interior forest. The influence of clearcut edges was minimal, generally extending only 5 m from the edge, and included greater log density and different species composition, compared with interior forest. At fire edges, prominent responses to edge creation included increased snag density and lower moss cover, compared with interior forest, extending up to 40 m into the forest. This initial structural change was likely due to partial burning extending into the forest. Overall, fire edges had more snags and a different species composition than cut edges. Our hypothesis that edge influence is more extensive at fire edges than at cut edges was supported for overstory and understory structure, but not for species composition. We suggest that there is a need for management to consider the cumulative effect of the loss of fire edges on the landscape.

Résumé : Nous avons comparé la structure et la composition des bordures de feu et de coupe dans la forêt Boréale du Nord-Ouest du Québec dominée par l'épinette noire (*Picea mariana* (Mill.) BSP). La structure et la composition ont été échantillonnées le long de transects perpendiculaires à huit bordures de feu de 3 à 4 ans et à huit bordures de coupes totales de 2 à 5 ans. L'influence de la bordure a été évaluée en comparant les valeurs moyennes aux différentes distances de la bordure à l'étendue de la variation à l'intérieur de la forêt. L'influence de la bordure des coupes totales était minimale, s'étendant généralement jusqu'à seulement 5 m de la bordure. Ces changements comprenaient une augmentation de la densité des arbres morts au sol et une composition en espèces différente de celle observée à l'intérieur de la forêt. Aux bordures de feux, une densité accrue des chicots et une diminution de la couverture de mousses, comparativement à l'intérieur de la forêt, s'étendaient jusqu'à 40 m en forêt. Ces changements structuraux étaient probablement dus au brûlage partiel qui s'est étendu dans la forêt. De façon générale, les bordures de feu avaient plus de chicots et une composition différente d'espèces comparativement aux bordures de coupes. Notre hypothèse voulant que l'influence de la bordure soit plus grande pour les bordures de feu comparativement aux bordures de coupe est supportée pour la structure des étages supérieur et inférieur de la canopée mais non pour la composition des espèces. Puisque l'influence des bordures de coupe est limitée dans la pessière noire boréale, les aménagistes forestiers devraient davantage tenir compte des effets cumulatifs de la perte d'hétérogénéité structurale des bordures issues de feu dans les paysages aménagés.

Introduction

An increased amount of edge habitat is recognized as an important consequence of fragmentation from agricultural development or forest harvesting. In the boreal forest, however, edges are also created from frequent fire disturbance. These natural edges could provide important habitat and have a prominent role in landscape-level processes. Yet, investigations of the structure and composition at natural forest edges, particularly fire edges, are limited. In the boreal

forest, recent advances have been made in developing forest management strategies that are based on our understanding of patterns and processes that occur under natural disturbances (e.g., Gauthier et al. 2004). These strategies involve combining clear-cutting, partial cutting, and selective harvesting treatments in different proportions based on the disturbance regime in the region to emulate structural development following fire and to minimize the loss of old-growth habitat. Some emphasis has been also placed on the spatial arrangement of harvest treatments by using simula-

Received 21 February 2003. Accepted 21 November 2003. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 13 February 2004.

K.A. Harper,² D. Lesieur, and P. Drapeau. Groupe de recherche en écologie forestière, Université de Québec à Montréal, C.P. 8888, succursale A, Montréal, QC H3C 3P8, Canada.

Y. Bergeron. Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue, 445, boulevard de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.

¹This paper was presented at the 4th International Workshop on Disturbance Dynamics in Boreal Forests: Disturbance Processes and their Ecological Effects, held 9–14 August 2002, Prince George, B.C., and has undergone the Journal's usual peer review process.

²Corresponding author (e-mail: c1444@er.uqam.ca).

tion models to examine landscape pattern dynamics linked to timber harvesting strategies (Franklin and Forman 1987; Wallin et al. 1994). However, these are coarse-scale strategies that cannot address the fine-scale patterns of cutblock–forest boundaries. The extent to which cut edges maintain the structural attributes of fire edges could be an important concern for biodiversity in the boreal forest landscape, where harvesting is becoming the prevalent disturbance. There may also be negative edge effects associated with harvesting for the remaining forested stands. Data on the structure and composition of fire and cut edges are needed before we can determine the management needs regarding cutblock–forest boundaries.

The influence of anthropogenically created edges on vegetation has been well documented in temperate forests in the United States (Ranney et al. 1981; Matlack 1993, Chen et al. 1992) and in tropical rain forests (Laurance et al. 1998), but has only recently been explicitly studied in subboreal (Burton 2002) and boreal forests (Esseen 1994; Harper and Macdonald 2002a; Rheault et al. 2003). Edge influence at cut edges is not as extensive or dramatic in the boreal forest as it is in other landscapes (Harper and Macdonald 2002a), perhaps because the boreal forest is a disturbance-adapted ecosystem with many inherent edges and has a relatively open, shorter canopy. Well-documented edge influence on canopy structure at cut edges includes structural damage to live and dead trees from increased wind (DeWalle 1983; Ferreira and Laurance 1997; Laurance et al. 1998; Baker and Dillon 2000) and the subsequent production of coarse woody material (Chen et al. 1992; Esseen 1994; Burton 2002). Although these effects from exposure to wind are also expected at fire edges, they may be moderated by the presence of snags in the adjacent burned area. Remnant trees and snags from the fire may also reduce effects from increased light. At cut edges, greater productivity from increased light can be manifested as increased growth of shrubs (Matlack 1993), development of a herbaceous understory (Ranney et al. 1981), invasion of non-native plants (Brothers and Spingarn 1992), or regeneration and growth of trees (Chen et al. 1992; Baker and Dillon 2000; Harper and Macdonald 2002a). Responses of individual species to edge influence may also differ between the two edge types; microhabitats following fire and clear-cutting vary in terms of forest floor disturbance (Nguyen-Xuan et al. 2000), soil characteristics, moisture, and nutrient availability (McRae et al. 2001).

Natural edges have been less well studied than anthropogenically created edges. At a landscape scale, boundary complexity has been found to be greater for fires than for human-influenced fragmented landscapes (Turner 1989; Mladenoff et al. 1993). Spatial complexity at edges might also be present at a smaller scale, which would extend the zone of edge influence at fire boundaries. Because of inherent variability in the processes leading to edge formation, gradients at natural edges are expected to be more gradual than the sharper gradients found at clearcut edges. For example, edge influence extended farther at lakeshore forest edges, which form as a result of an edaphic gradient, than at cut edges (Harper and Macdonald 2001, 2002a).

We assessed and compared the structure, composition, and extent of edge influence at young cut and fire edges in black spruce (*Picea mariana* (Mill.) BSP) boreal forest, an ecosys-

tem where edge effects on vegetation have not been previously documented. We had two objectives: (1) to compare structure and composition between fire and cut edges, and (2) to test the hypothesis that edge influence is weaker, but more extensive, at fire edges than at cut edges.

Study area

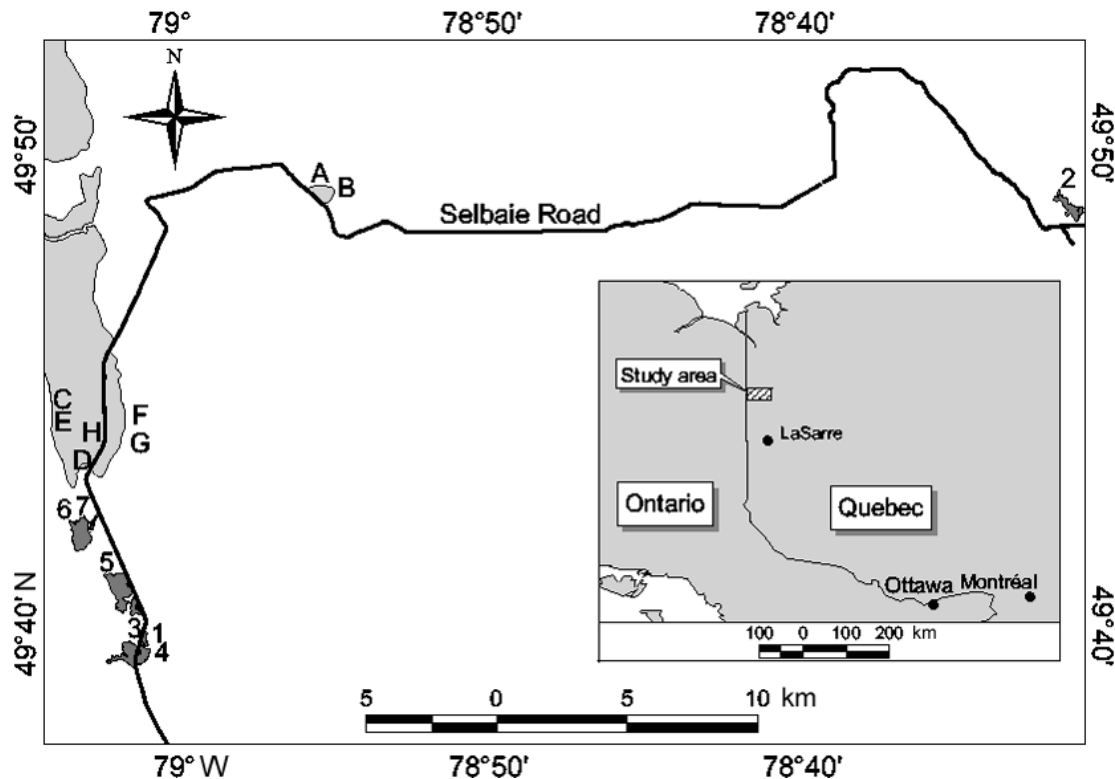
We sampled sites at the edges of fires and cutblocks in black spruce boreal forest, in the northwestern part of the Abitibi region in Quebec (49°62' to 49°87'N, 79°00' to 79°50'W; Fig. 1). The study area is part of the Lake Matagami Lowland ecoregion (Saucier et al. 1998) in the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Objibway (Vincent and Hardy 1977). The topography is relatively flat, and elevation is ca. 300 m above sea level. Soils are predominantly organic, with clay deposits and some till (Gauthier et al. 2000). According to a nearby weather station in La Sarre, Quebec (48°46'N, 79°06'W; Environment Canada 1993), mean annual temperature is 0.8 °C, annual precipitation is 856 mm, and there are 64 frost-free days. The forest mosaic in our study area is part of the *P. mariana* – moss bioclimatic domain (Saucier et al. 1998). *Picea mariana* is dominant in stands of all ages on clay and organic sites and in older stands on sand sites (Harper et al. 2002). Other tree species include jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and tamarack (*Larix laricina* (Du Roi) Koch). The region is characterized by large crown fires that kill most of the trees and aboveground vegetation (Bergeron et al. 2002). Forest harvesting in the area is done by “careful logging” of all trees larger than 9 cm DBH. Advanced regeneration and soils are protected by using machinery in parallel trails that cover no more than 30% of the harvested area (Harvey and Brais 2002). No pesticides, thinning, or field preparation was used before or after harvesting. Most of the recent fires that were easily accessible were partially or entirely salvage cut.

Methods

We established transects perpendicular to eight 3- to 4-year-old fire edges and eight 2- to 5-year-old clearcut edges (Table 1). Transects were at least 100 m away from other transects, corners of clearcuts, major forest openings, and any salvage-cut burned areas. Because we required sites with no salvage cutting, availability was very limited, and we could not control for orientation of the edges. Thus, edge aspects spanned a range of orientations for both fire and cut edges (Table 1). All edges were created in forests dominated by *P. mariana* (at least 85% of trees) on clay to organic soils. Although stand ages differed between forest stands next to fire edges and those next to cut edges, canopy cover and height were similar amongst the two sets of forest stands (means of 45% cover and 12 m height for both sets).

For each transect, we located plots at various distances from both sides of the edge to cover the full extent of the edge. Plots (20 m × 5 m, length parallel to the forest edge) were centred at the following distances along each transect:

Fig. 1. Map showing the location of the study area (inset) and the approximate locations of the cut and fire edge transects (as numbers and letters, respectively, Table 1). The transect “cut 8” is not on the map; it is located approximately 75 km east of the other transects. In the large map, light and dark shaded areas represent recent fires and cutblocks, respectively, where the transects were located. The border of the large fire is more complex than illustrated; therefore some of the fire edge transects that appear to be in the fire are actually adjacent to continuous forest.



–50, –15, –5, 0, 5, 10, 20, 40, 60, 100, 150, and 200 m from the edge into the adjacent forest; plots with negative signs were located on the disturbance side of the edge. The plot at 0 m straddled the forest edge, which was located at the edge of the continuous forest canopy; in this ecosystem, fire edges were distinct and easy to delineate. On one transect, the plot at 60 m was moved to 80 m to avoid a creek. We used data collected at 100, 150, and 200 m to characterize interior forest. Two shrub subplots (2 m × 2 m) and four herb subplots (0.5 m × 0.5 m) were established systematically along the major axis of every plot (shrub and herb subplots at either end of the 20 m × 5 m plot, and herb subplots 3 m from either side of the centre).

Sampling was conducted between June and August 2000. Trees (>5 cm DBH) and snags (standing dead trees >5 cm DBH and >50 cm tall) were tallied in the 20 m × 5 m plots and were classified as dominant, codominant, intermediate, or suppressed (Côté 2000). Decay stage was evaluated for all snags (classes 1–5; Thomas et al. 1979), and we also noted the presence of a major broken top (diameter at the break >5 cm). We tallied the number of logs (downed coarse woody material) intersecting the major axis of the plot (>5 cm diameter at the intersection point), and we evaluated decay stage (classes 1–5; Maser et al. 1979). Canopy cover was measured at the centre of each plot using a convex spherical densiometer facing both directions of the transect. Height of the tallest tree was measured in the 60 m plots.

Within the shrub subplots, we estimated the cover for each shrub species (>50 cm tall) and for all shrub species

combined, and we counted the number of *P. mariana* seedlings (<1 m tall) and *P. mariana* saplings established from layering (<1 m tall). Cover of all species of herbs, common mosses, macrolichens, and dwarf woody plants (<50 cm) was visually estimated within the herb subplots to the nearest 1% up to 5%, and to the nearest 10% thereafter. Nomenclature follows Marie-Victorin (1995). The proportion of ground covered by burned organic matter was also estimated within the herb subplots, but only for six of the eight fire edge transects. Diversity was calculated separately for shrubs, herbs, mosses, and lichens using the Shannon Index; calculations were made using cover values at the subplot level and then averaged for each plot.

We assessed edge influence at both cut and fire edges for the following categories of response variables: overstory structure (canopy cover, and tree, snag, and log densities), understory structure (cover of shrubs, herbs, moss, and lichens), regeneration (*P. mariana* layer and seedling densities), understory diversity (for shrubs, herbs, moss, and lichens), and cover of individual species (shrubs, herbs, moss, and lichens). For each response variable, we calculated both the magnitude of edge influence (MEI) and the distance of edge influence (DEI). MEI is a measure of the strength of edge influence, which we calculated as (K. Harper and E. Macdonald, unpublished)

$$[1] \quad \text{MEI} = (\bar{x}_d - \bar{x}_i) / (\bar{x}_d + \bar{x}_i)$$

where \bar{x}_d is the mean of a variable at distance d from the edge, and \bar{x}_i is the mean of a variable in interior forest (dis-

Table 1. Site and edge characteristics of forest stands, edges, and adjacent areas disturbed by fire or forest harvesting in black spruce boreal forest in northwestern Quebec.

Type of edge and transect	Year of fire or cut	Size of fire or cutblock (ha)	Edge orientation ^a (°)	Forest stand characteristics 60 m from the edge		
				Age ^b (years)	Canopy cover (%)	Height of the tallest tree (m)
Fire edge						
A	1996	10	345	175	61	15
B	1996	10	90	175	61	13
C	1997	21 476	79	na	48	10
D	1997	21 476	355	na	43	na
E	1997	21 476	95	na	40	14
F	1997	21 476	110	114	52	10
G	1997	21 476	120	114	22	8
H	1997	21 476	270	na	29	11
Cut edge						
1	1998	32	30	275	69	11
2	1995	40	70	125	54	17
3	1997	15	160	275	38	10
4	1998	32	88	275	24	10
5	1997	85	230	225	46	12
6	1998	77	345	275	28	10
7	1998	77	348	275	36	8
8	1997	18	na	80	66	17

Note: na, data are lost or not available.

^aFacing from the edge towards the forest.

^bData are from a fire reconstruction map (Bergeron et al. 2001).

tances 100, 150, and 200 m from the edge). Using this formula, MEI varies between -1 and 1 , with positive values indicating positive responses to edge influence (values greater at the edge than in interior forest) and negative values indicating negative responses (values lower at the edge than in interior forest); a result of zero means there is no edge influence.

To quantify DEI, we used the critical values approach (Harper and Macdonald 2001, 2002b), in which mean values of response variables at different distances from the edge are compared with critical values of interior forest conditions derived by resampling values from interior forest (see below), using the critical values program (Harper and Macdonald 2002b) in Visual Basic, Microsoft Excel 97 (Microsoft Corporation 1997). The critical values approach differs from a standard randomization test in that only values from interior forest are resampled and used to create a distribution of means (rather than actual values). This was done to obtain a range of variation of average interior forest conditions with which to compare edge influence, making it comparable to other methods of measuring DEI (e.g., Chen et al. 1992; Laurance et al. 1998). The critical values approach also incorporates blocking while resampling interior values to standardize variation among transects. These modifications to a standard randomization test may lead to an underestimation of the variance and greater type I error. Therefore, we also calculated DEI by comparing mean treatment values (at different distances from the edge) to a 95% confidence interval of interior forest values, as in Laurance et al. (1998). This method verified our results of significant DEI (with one exception, see Table 3) and sometimes resulted in greater DEI

than the critical values approach, which proved to be more conservative at estimating DEI with our data.

Following the critical values approach for each variable at each edge type, we determined whether mean values near the edge were significantly different than those found in interior forest using the following steps:

- (1) "Interior forest" plots or subplots were selected from each of the eight transects. For trees, canopy cover, snags, and logs, one plot (100, 150, or 200 m position) was randomly selected from each transect ($n = 8$). Two or four subplots (2 of 6 (shrub) or 4 of 12 (herb) total subplots at 100, 150, and 200 m) were randomly selected from each transect for variables measured in the shrub or herb subplots ($n = 16$ or 24 , respectively, for shrub or herb variables).
- (2) The mean of the values from the plots or subplots selected in step 1 was calculated.
- (3) These first two steps were repeated for a total of 5000 permutations.
- (4) Critical values were the 2.5 and the 97.5 percentiles of the 5000 permuted means (two-tailed test, $\alpha = 0.05$). For each edge type, mean values at different distances from the forest edge were considered to be significant if they fell outside the critical values for the corresponding interior forest.
- (5) Distance of edge influence was defined as the set of two or more consecutive distances that had values significantly different from the values in interior forest.

We compared MEI and DEI to determine whether fire edges had a more gradual gradient with lower MEI but greater DEI, as compared with cut edges (objective 2).

To compare forest structure and composition between fire and cut edges (objective 1), we determined the DEI over which there was a significant difference in response variables between the two edge types using a modification of the critical values approach (Harper and Macdonald 2002b). For each variable, we determined whether the difference in values between the two edge types, at different distances from the edge, was significant using differences in interior forest conditions corresponding to each edge type as the control, using the following steps:

- (1) Interior forest plots or subplots were randomly selected from each of the eight cut edge transects and from each of the eight fire edge transects as per step 1 described in the previous paragraph.
- (2) The t value was calculated between the two sets of values (interior forest at cut edge transects versus interior forest at fire edge transects).
- (3) These first two steps were repeated for a total of 5000 permutations.
- (4) The 5000 permuted t values were used to develop a t distribution and establish the critical values for the interior forest (2.5 and the 97.5 percentiles, two-tailed test, $\alpha = 0.05$). The t statistics were calculated for each response variable at each distance from the forest edge for fire versus cut edges and then compared with these critical values. By comparing differences at the edge to differences between the interior forest conditions near each edge type, this approach controls for regional variation that is not due to edge influence, and thus it is more appropriate than a standard t test.
- (5) The distance of edge influence within which there were significant differences between the two edge types was determined as the set of two or more consecutive distances with t statistics that fell outside the critical values from the t distribution of randomized data from the interior forest.

This paper presents the first use of this analysis and the first analysis to compare edge influence at two different edge types.

Results

Cut edges

Overstory structure was altered at clearcut edges in black spruce boreal forest compared with interior forest (Table 2), but the overall distance of edge influence (DEI) was only 5 m into the forest (Table 3, Fig. 2a). Cut edges had lower canopy cover and snag density, and greater log density than interior forest; tree density was only significantly lower within the clearcut (Table 2). The magnitude of edge influence (MEI) was strongest for changes in deadwood abundance (snag and log density) compared with other structural elements (Table 3), especially logs in decay class 1 (MEI = 0.91, results not shown).

Total cover of shrubs and moss was lower at the edge than in the interior forest (Table 2). Lower moss cover and higher lichen cover were also found farther into the forest (DEI = 40–60 and 25–60 m, respectively). There was no significant edge influence on herb cover (Table 3). Overall, DEI for understory structure generally extended only 5 m, but there were some responses farther into the forest as well (25–

60 m, Fig. 2b). MEI values for understory structure were generally low (Table 3).

Greater regeneration of *P. mariana* seedlings and reduced *P. mariana* layer density occurred only on the clearcut side of the edge (Tables 2 and 3, Fig. 2c). There was very little regeneration of other species (results not shown).

There was no significant influence on the diversity of shrubs, moss, or lichens, but herb diversity was higher at 5 to 25 m into the forest than in interior forest (Tables 2 and 3, Fig. 2d).

At cut edges, cover of understory species exhibited significant responses to edge influence up to 60 m into the forest (Table 3, Fig. 2c). Four of the eight common shrub species were negatively affected by harvesting in the clearcut and at the edge (*Cassandra calyculata* (L.) D. Don., *Kalmia angustifolia* L., *Kalmia polifolia* Wang., *Ledum groenlandicum* Retzius.), but DEI only extended 5 m (Table 3, Fig. 2e). *Cassandra calyculata* and *Kalmia polifolia* had relatively high MEIs, although *Kalmia polifolia* was found in low abundance even in interior forest (Table 2). Herbs were both positively (*Equisetum* spp., *Gaultheria hispidula* (L.) T. & G.) and negatively (*Carex* spp., *Rubus chamaemorus* L., *Smilacina trifolia* (L.) Desf.) affected by edge influence (Table 3). *Carex* spp., however, were found in significantly greater abundance in the clearcut than in the interior forest (Tables 2 and 3). Significant edge influence for *Equisetum* spp. only began at 5 m into the forest (Table 3). Other species had high MEIs, but their DEIs were not significant (Table 3) at either cut or fire edges because of high variability in interior forest and very low abundance at the edge. The proportion of herbs affected by edge influence remained above one-third up to 15 m into the forest and then decreased gradually (Fig. 2f). No herbs were abundant, even in interior forest (mostly <2% cover, Table 2). Although most moss species were affected by harvesting in the clearcut, the proportion with significant edge influence dropped to less than one-third right at the edge (Fig. 2g). Moss species were negatively affected by edge influence and had variable DEIs (*Dicranum* spp., *Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., *Sphagnum* spp.) (Table 3). One lichen (*Cladina rangiferina* (L.) Nyl.) was positively affected by edge influence, although only on the forest side of the edge (Table 3, Fig. 2h). Of the three understory taxa with mean cover in interior forest greater than 10% (*Ledum groenlandicum*, *Pleurozium schreberi*, *Sphagnum* spp.) (Table 2), all were negatively affected by edge influence, with DEIs up to 5 m on either side of the edge (Table 3).

Fire edges

One of the most prominent responses to edge influence at fire edges in black spruce forest was a greater abundance of snags compared with interior forest; MEI was very high and DEI extended up to 40 m (Tables 2 and 3, Fig. 3a). Edge influence on snag density was limited to suppressed, unbroken snags in decay class 1 (results not shown). Canopy structural change was evident as lower canopy cover and lower tree density, which extended up to 5 and 15 m, respectively (Tables 2 and 3). The density of dominant trees had a stronger MEI (–0.35) than the density of trees in other canopy posi-

Table 2. Summary of results in the disturbed area, at the edge, and in the adjacent interior forest for different response variables.

Response variable	Cut edges			Fire edges		
	Cut (-50 m)	Edge (0 m)	Interior forest (critical values)	Fire (-50 m)	Edge (0 m)	Interior forest (critical values)
Overstorey structure						
Canopy cover (%)	8 (5)	29 (4)	47–62	17 (1)	34 (4)	51–62
Tree density (no./ha)	250 (180)	1840 (290)	1800–2660	120 (130)	1120 (170)	1510–2160
Snag density (no./ha)	90 (50)	50 (20)	120–380	1710 (400)	1200 (230)	50–220
Log density (no./20 m)	7.1 (1.0)	7.4 (1.3)	1.2–2.8	3.6 (1.0)	2.8 (1.0)	1.6–3.6
Understorey structure						
Shrub cover (%)	16.4 (3.4)	19.3 (3.7)	27.6–41.9	23.7 (4.0)	38.1 (2.2)	20.9–32.5
Herb cover (%)	8.7 (2.2)	5.0 (0.8)	5.5–9.9	4.4 (1.0)	7.0 (0.9)	5.3–8.9
Moss cover (%)	35.0 (4.1)	75.7 (4.2)	82.8–92.2	20.7 (5.1)	51.6 (5.2)	73.8–83.8
Lichen cover (%)	3.8 (1.6)	7.4 (2.3)	4.2–11.9	0.0 (0.0)	3.9 (1.9)	5.3–12.3
Regeneration						
<i>Picea mariana</i> seedling density (no./m ²)	1.5 (0.6)	0.4 (0.2)	0.02–0.4	2.2 (0.9)	0.6 (0.4)	0.1–1.0
<i>Picea mariana</i> layer density (no./m ²)	2.1 (1.7)	7.6 (1.5)	7.2–12.6	0.8 (0.8)	3.5 (1.4)	4.7–9.0
Understorey diversity (Shannon index)						
Shrub diversity	0.7 (0.1)	0.9 (0.1)	0.8–1.0	0.9 (0.1)	0.9 (0.1)	0.8–1.0
Herb diversity	0.6 (0.1)	0.7 (0.1)	0.7–1.0	0.6 (0.1)	0.8 (0.1)	0.8–1.0
Moss diversity	0.5 (0.1)	0.5 (0.1)	0.4–0.6	0.3 (0.1)	0.4 (0.05)	0.4–0.6
Lichen diversity	0.2 (0.1)	0.2 (0.05)	0.1–0.2	0.0 (0.0)	0.1 (0.04)	0.2–0.3
Cover of common shrub species (%)						
<i>Alnus rugosa</i>	4.3 (2.7)	3.1 (2.0)	0.1–6.9	0.9 (0.7)	2.8 (1.4)	0.6–5.0
<i>Cassandra calyculata</i>	0.2 (0.2)	0.8 (0.3)	3.1–8.2	6.9 (2.2)	4.8 (1.3)	1.9–6.9
<i>Kalmia angustifolia</i>	0.6 (0.2)	1.8 (0.5)	2.0–6.0	0.4 (0.2)	1.1 (0.4)	0.8–2.2
<i>Kalmia polifolia</i>	0.0 (0.0)	0.0 (0.0)	0.2–0.9	0.2 (0.1)	0.1 (0.1)	0.1–0.7
<i>Ledum groenlandicum</i>	6.4 (2.1)	10.8 (2.1)	13.8–22.2	10.8 (2.2)	25.0 (3.4)	10.5–19.9
<i>Salix</i> spp.	0.6 (0.6)	0.1 (0.1)	0.0–0.8	0.4 (0.3)	0.7 (0.6)	0.0–0.7
<i>Vaccinium angustifolium</i>	2.1 (1.3)	0.2 (0.1)	0.1–0.9	1.6 (0.7)	1.5 (0.7)	0.3–2.3
<i>Vaccinium myrtilloides</i>	4.2 (1.0)	3.1 (0.7)	2.1–3.9	2.3 (0.7)	4.4 (1.0)	1.6–3.8
Cover of common herb species (%)						
<i>Carex</i> spp.	1.2 (0.5)	0.1 (0.1)	0.2–0.7	0.1 (0.1)	0.3 (0.1)	0.2–0.7
<i>Coptis groenlandica</i>	0.03 (0.03)	0.0 (0.0)	0.03–0.3	0.0 (0.0)	0.03 (0.03)	0.03–0.2
<i>Equisetum</i> spp.	1.4 (0.4)	1.1 (0.4)	0.4–1.2	3.0 (1.0)	2.7 (0.6)	0.7–2.2
<i>Gaultheria hispida</i>	1.6 (0.3)	1.6 (0.4)	0.6–1.3	0.2 (0.1)	2.2 (0.4)	1.2–3.8
<i>Limnaea borealis</i>	0.03 (0.03)	0.03 (0.03)	0.0–0.2	0.0 (0.0)	0.0 (0.0)	0.0–0.1
<i>Petasites palmatus</i>	0.1 (0.1)	0.1 (0.1)	0.0–1.2	0.2 (0.1)	0.1 (0.1)	0.0–0.2
<i>Rubus chamaemorus</i>	0.1 (0.8)	0.4 (0.2)	0.9–2.7	0.8 (0.2)	0.6 (0.2)	0.5–1.2
<i>Smilacina trifolia</i>	0.2 (0.1)	0.4 (0.1)	1.2–2.9	0.4 (0.2)	0.5 (0.2)	0.3–1.6
<i>Vaccinium oxycoccum</i>	0.3 (0.1)	0.4 (0.1)	0.4–0.8	0.5 (0.1)	0.9 (0.2)	0.7–1.2
Cover of common moss species (%)						
<i>Dicranum</i> spp.	0.1 (0.04)	0.0 (0.0)	0.1–0.9	0.2 (0.2)	0.1 (0.04)	0.4–2.5
<i>Hylocomnium splendens</i>	0.1 (0.1)	0.0 (0.0)	0.0–0.5	0.0 (0.0)	0.0 (0.0)	0.0–0.5
<i>Pleurozium schreberi</i>	10.2 (1.8)	24.8 (4.8)	17.7–30.9	0.2 (0.1)	5.4 (1.4)	11.6–22.0
<i>Polytrichum</i> spp.	0.1 (0.1)	0.03 (0.03)	0.0–1.1	1.6 (0.5)	0.5 (0.2)	0.1–0.2
<i>Ptilidium</i> spp.	1.4 (1.0)	2.6 (1.3)	1.1–6.3	0.0 (0.0)	1.6 (1.3)	1.5–5.2
<i>Ptilium crista-castrensis</i>	0.03 (0.03)	1.4 (0.9)	0.3–5.9	0.0 (0.0)	0.1 (0.1)	0.0–0.2
<i>Sphagnum</i> spp.	22.2 (4.3)	41.6 (6.1)	43.0–60.3	16.2 (5.0)	43.0 (5.3)	49.5–63.6
Cover of common lichen species (%)						
<i>Cladina mitis</i>	0.2 (0.1)	0.03 (0.03)	0.03–2.1	0.0 (0.0)	1.6 (1.1)	0.0–1.1
<i>Cladina rangiferina</i>	3.2 (1.6)	7.2 (2.3)	3.0–10.3	0.0 (0.0)	2.1 (1.1)	4.2–9.8
<i>Cladonia</i> spp.	0.4 (0.2)	0.5 (0.1)	0.3–0.8	0.03 (0.03)	0.2 (0.1)	0.4–1.1

Note: Means (standard error) are given for the plots in the disturbed area (-50 m from the edge) and at the edge (0 m). Critical values derived from resampling values in plots at 100, 150, and 200 m from the edge are given to quantify the range of variation in interior forest found near the treatment (fire or cut edges). Sample size is $n = 8$ transects; see methods for details.

Table 3. Magnitude of edge influence (MEI) and distance of edge influence (DEI) for different response variables at cut and fire edges, as well as DEI for significant differences between fire and cut edges.

Response variable	Cut edges		Fire edges		Comparison	
	MEI	DEI (m)	MEI	DEI (m)	Values higher at fire (F) or cut (C) edges	DEI (m)
Overstorey structure						
Canopy cover	-0.22	-50 to 0	-0.11	-50 to 5	C	-50 to 0
Tree density	-0.10	-50 to -5	-0.24	-50 to 15	ns	ns
Snag density	-0.65	-50 to 0	0.81	-50 to 40	F	-50 to 60
Log density	0.57	-50 to 5	0.02	ns	C	-50 to 0
Understorey structure						
Shrub cover	-0.28	-50 to 5	0.18	0 to 5	F	-50 to 5
Herb cover	-0.21	ns	-0.01	-50 to -15	C	-50 to -15
Moss cover	-0.08	-50 to 5, 40 to 60	-0.21	-50 to 40	ns	ns
Lichen cover	-0.03	-50 to -15 (-), 25 to 60 (+)	-0.38	-50 to 0	C	-50 to 0
Regeneration						
<i>Picea mariana</i> seedling density	0.38	-50 to -5	0.11	ns	ns	ns
<i>Picea mariana</i> layer density	-0.07	-50 to -5	-0.32	-50 to 5	ns	ns
Understorey diversity						
Shrub diversity	0.00	ns	0.02	ns	ns	ns
Herb diversity	0.03	5 to 25	-0.09	-50 to -5	C	-50 to -15
Moss diversity	0.05	ns	-0.42	-50 to -15	C	-50 to 15, 40 to 60
Lichen diversity	-0.07	ns	-0.03	-50 to 0, 15 to 60	C	25 to 40
Cover of common shrub species						
<i>Alnus rugosa</i>	0.07	ns	0.06	ns	C	-50 to -15
<i>Cassandra calyculata</i>	-0.76	-50 to 5	0.06	ns	F	-5 to 5
<i>Kalmia angustifolia</i>	-0.35	-50 to 0	-0.12	ns	ns	ns
<i>Kalmia polifolia</i>	-1.00	-50 to 5	-0.73	ns	F	0 to 5
<i>Ledum groenlandicum</i>	-0.25	-50 to 0	0.25	0 to 5, 25 to 40	F	-50 to 5
<i>Salix</i> spp.	-0.7	ns	0.47	ns	F	15 to 25
<i>Vaccinium angustifolium</i>	-0.31	ns	0.11	ns	ns	ns
<i>Vaccinium myrtilloides</i>	0.02	ns	0.25	40 to 60	ns	ns
Cover of common herb species						
<i>Carex</i> spp.	-0.65	-50 to -5 (+), 0 to 5 (-)	-0.22	ns	ns	ns
<i>Coptis groenlandica</i>	-1.00	ns	-0.50	-50 to -5	C	25 to 40
<i>Equisetum</i> spp.	0.19	5 to 15	0.30	-50 to 0	F	-50 to 0
<i>Gaultheria hispidula</i>	0.26	-50 to 40	-0.04	-50 to -5	C	-50 to -5, 5 to 15
<i>Linnaea borealis</i>	-0.50	ns	-1.00	ns	ns	ns
<i>Petasites palmatus</i>	-0.70	ns	0.20	ns	C	5 to 15
<i>Rubus chamaemorus</i>	-0.63	-50 to -15	-0.15	ns	F	-50 to 5
<i>Smilacina trifolia</i>	-0.67	-50 to 25	-0.26	ns	F	-5 to 0
<i>Vaccinium oxycoccos</i>	-0.14	ns	-0.02	-50 to -15	ns	ns
Cover of common moss species						
<i>Dicranum</i> spp.	-1.00	-50 to 5, 25 to 60 ^d	-0.74	ns	F	-50 to 0
<i>Hylocomnium splendens</i>	-1.00	25 to 40	-1.00	ns	ns	ns
<i>Pleurozium schreberi</i>	0.01	-50 to -5 (-)	-0.51	-50 to 0	C	-50 to -15, 0 to 5

Table 3 (concluded).

Response variable	Cut edges		Fire edges		Comparison	
	MEI	DEI (m)	MEI	DEI (m)	Values higher at fire (F) or cut (C) edges	DEI (m)
<i>Polytrichum</i> spp.	-0.85	ns	0.55	-50 to 5	F	-5 to 0
<i>Ptilidium</i> spp.	-0.16	ns	-0.32	-50 to -5	C	-50 to -15
<i>Ptilium crista-castrensis</i>	-0.33	-50 to -15	0.26	ns	ns	ns
<i>Sphagnum</i> spp.	-0.11	-50 to 5	-0.14	-50 to 25	C	-50 to -5
Cover of common lichen species						
<i>Cladina mitis</i>	-0.93	ns	0.57	ns	ns	ns
<i>Cladina rangiferina</i>	0.05	25 to 60	-0.53	-50 to 0	C	-50 to 0, 25 to 60
<i>Cladonia</i> spp.	-0.09	ns	-0.54	-50 to 0	C	-50 to -15

Note: In most instances, a negative MEI means negative edge influence (lower value at the edge compared with the interior), and a positive MEI means positive edge influence (greater value at the edge compared with the interior) within the DEI; exceptions are noted in parentheses. For DEI, negative values refer to distances within the disturbed area; significant results are reported even where DEI is limited to the disturbed area, since it indicates whether the values in the disturbed area are significantly different from those in interior forest. Only common species (>10% frequency for at least one type of edge) are included. Calculations of MEI and DEI are based on sample sizes of $n = 8$ transects; see methods for details.

^aDEI was only -50 to 5 m when compared with a 95% CI of interior forest values (see methods).

tions (results not shown). There was no significant edge influence on log density. Overall, edge influence on overstory structure extended up to 40 m into the forest from fire edges (Fig. 2a).

Structural change in the understory was also apparent at fire edges as lower cover of herbs, moss, and lichens, and greater shrub cover, compared with interior forest, with varying DEI (Tables 2 and 3). The trend of increasing moss cover along the edge-to-interior gradient mirrored a trend of decreasing cover of burned organic matter (DEI = 0 to 40 m) (Figs. 3b and 3c). Overall DEI for understory structure extended 40 m (Fig. 2b).

Significant regeneration of *P. mariana* seedlings had not yet occurred at the edge or within the burned area (Tables 2 and 3). There was reduced density of *P. mariana* saplings established from layering, with a DEI of 5 m (Tables 2 and 3, Fig. 2c).

Edge influence on diversity was generally negative and was mostly restricted to the burned area, except for lichen diversity (Table 3, Fig. 2d).

In terms of individual understory species, there was significant positive edge influence for two shrubs (*Ledum groenlandicum*, *Vaccinium myrtilloides* Michx.), which had significantly greater cover on the forest side of the edge but not in the disturbed area, compared with interior forest (Table 3, Fig. 2e). Three common herbs (*Coptis groenlandica* (Oeder) Fern., *Gaultheria hispidula*, *Vaccinium oxycoccos* L.) had significantly less cover in the burned area than in interior forest (Table 3, Fig. 2f). *Equisetum* spp. were more abundant in the burned area and right at the edge (Tables 2 and 3). Three moss species (*Ptilidium* spp., *Pleurozium schreberi*, *Sphagnum* spp.) were negatively affected by edge influence and had varying DEIs (Table 3), while *Polytrichum* spp. had significantly greater cover at the edge and in the burned area than in interior forest (Tables 2 and 3). Overall, edge influence affected almost half of the moss species right at the edge; this proportion decreased gradually to zero at 40 m into the forest (Fig. 2g). At fire edges, DEI was most

extensive for *Sphagnum* spp. compared with other individual species (-50 to 25 m; Table 3). Negative edge influence extended from the burned area up to the edge for two of the three lichen species (*Cladina rangiferina*, *Cladonia* spp.) (Table 3, Fig. 2h).

Comparison between edge types

In general, the gradient across the edge was more gradual at fire edges than at cut edges; for example, there was an abrupt change in canopy cover at cut edges, but not at fire edges (Fig. 4). In terms of DEI, greater proportions of variables for both overstory and understory structure had significant DEI on the forest side of fire edges than on the forest side of cut edges (Figs. 2a and 2b). Regeneration was more affected by edge influence (greater percentage of variables with significant DEI) on the disturbance side of the edge for cut edges, but DEI extended further for fire edges (Fig. 2c). For understory diversity, DEI also extended further at fire edges, and a greater proportion of variables were affected (Fig. 2d). Overall, fewer understory species were affected by edge influence on the forest side of fire edges than on the forest side of cut edges, except for shrubs, which had more extensive DEIs at fire edges (Figs. 2e-2h).

For overstory structure, understory structure, and regeneration, the absolute value of MEI was greater (stronger MEI) at cut edges than at fire edges for half the variables (Table 3). MEI was stronger for three of the four diversity indices at fire edges, although values were generally low (Table 3). A majority of all common shrub and herb species had stronger MEIs at cut edges than at fire edges (Table 3). The absolute value of MEI was greater at fire edges than at cut edges for about half of the moss species and two of three lichen species (Table 3).

Direct comparisons between cut and fire edges using the modified critical values approach revealed that significant differences in structure between cut and fire edges were generally restricted to the disturbed area and did not extend beyond the edge into the forest (e.g., canopy cover, log density,

Fig. 2. Percentage of response variables with significant distance of edge influence for different categories at both cut and fire edges. See Table 2 for a list of response variables in each category. Significant distance of edge influence was considered as the set of two or more consecutive distances with values significantly different from interior forest (see methods).

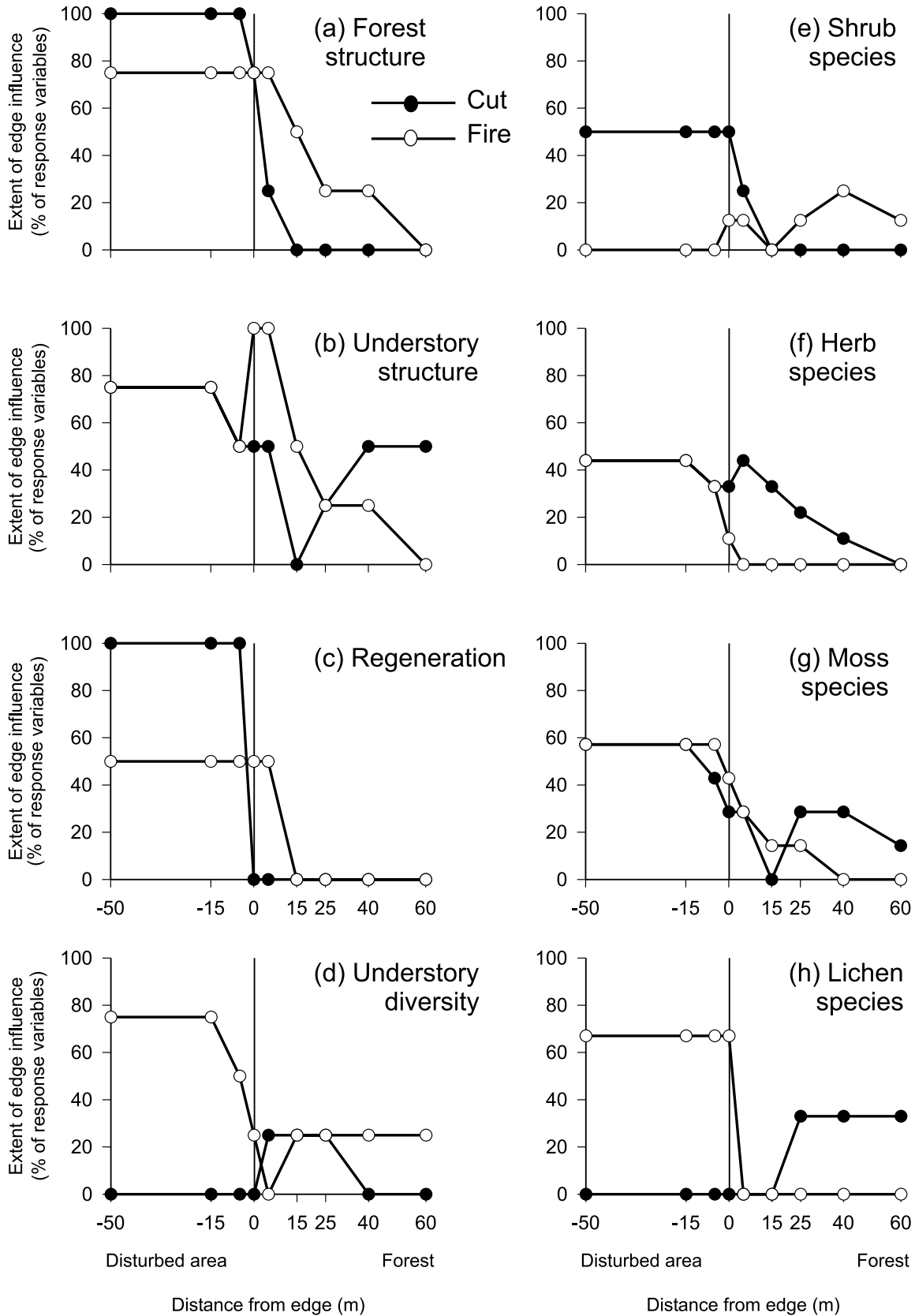
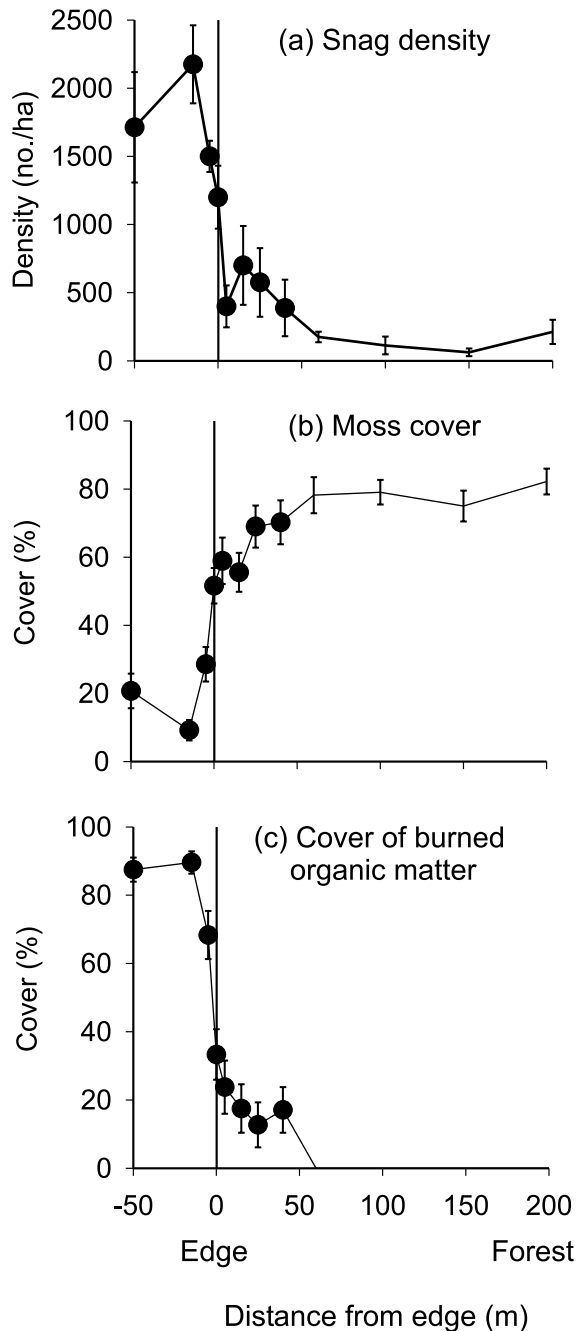


Fig. 3. Mean values along the edge-to-interior gradient at fire edges for (a) snag density, (b) moss cover, and (c) cover of burned organic matter. Solid circles represent rates that were significantly less than those in interior forest (plots 100–200 m from the edge). Data points that were not significantly different from interior forest have no symbols. Bars represent ± 1 SE; $n = 8$ plots for Figs. 3a and 3b; $n = 6$ plots for Fig. 3c.



herb and lichen cover; Table 3). The most notable exception was greater snag density at fire edges, which extended from the disturbed area up to 60 m into the forest (Table 3). Other differences on the forest side of the edge included lower density of dominant trees 15 to 40 m from fire edges (not shown), greater shrub cover at fire edges, and greater moss and lichen diversity at cut edges (Table 3). However, moss

Fig. 4. Mean canopy cover along the edge-to-interior gradient at cut and fire edges. Symbols (solid and open for cut and fire edges, respectively) represent rates that were significantly less than those in interior forest (plots 100–200 m from the edge). Data points that were not significantly different from interior forest have no symbols. Bars represent ± 1 SE; $n = 8$ plots.



and lichen diversity were not significantly affected by edge influence at cut edges (Table 3). Several shrub species (*Cassandra calyculata*, *Kalmia polifolia*, *Ledum groenlandicum*, *Salix* spp.), a few herb species (*Equisetum* spp., *Rubus chamaemorus*, *Smilacina trifolia*), and a couple of moss species (*Dicranum* spp., *Polytrichum* spp.) had significantly greater abundance on the forest side of fire edges than on the forest side of cut edges (Table 3). All of these were positively affected by edge influence at fire edges, except *Equisetum* spp. and *Polytrichum* spp., which were negatively affected by edge influence at cut edges (Table 3). Species that had greater cover on the forest side of cut edges than on the forest side of fire edges included herbs (*Coptis groenlandica*, *Gaultheria hispida*, *Petasites palmatus* (Ait.) Gray.), one moss (*Pleurozium schreberi*), and one lichen (*Cladina rangiferina*) (Table 3). Of these, *Gaultheria hispida* and *Cladina rangiferina* were positively affected by edge influence at cut edges (Table 3).

Discussion

Cut edges

Black spruce forest appears to be relatively unaffected by edge creation associated with forest harvesting, at least in the first few years. Edge influence at cut edges was much less extensive in black spruce boreal forest (overall DEI = ca. 5 m) than in subboreal (40–120 m, Burton 2002), temperate (16–137 m, Chen et al. 1992), and tropical (85–335 m, Laurance et al. 1998; 40–100 m, Mesquita et al. 1999) forests. For example, changes in overstory structure usually extend much farther into the forest than we observed at black spruce edges (e.g., Chen et al. 1992; Laurance et al. 1998; Burton 2002). Such structural changes are generally attributed to windthrow following edge creation. However, in the first few years following harvest, edge influence on

overstory structure at cut edges in black spruce forest was likely due primarily to disturbance in the harvested area. For example, the greater abundance of logs likely included logs left by harvesting activity that fell within the 0 and 5 m plots. Likewise, reduced canopy cover was probably the result of densiometer measurements that included the lack of a canopy over the cutblock. The lack of significant edge influence on tree density and lower snag density at the edge suggest that tree mortality, especially due to causes other than uprooting, was unlikely. In black spruce forest, trees are more likely to be windfirm, since they are accustomed to growing in open conditions (Harper et al. 2002), and are therefore less likely to be affected by increased wind at the edge. The forest stands in which we sampled were relatively old and, therefore, open with a discontinuous canopy (Harper et al. 2002); edge influence might be more extensive in younger, closed-canopy black spruce stands. Results for structure were similar at 5-year-old edges in aspen-dominated boreal forest in Alberta: snag density and density of dominant trees were also significantly lower right at the edge than in interior forest (with DEIs of up to 20 and 0 m, respectively, Harper and Macdonald 2002a). Tree mortality was abundant after isolation of forest fragments of up to 1 ha in Norway spruce (*Picea abies* (L.) Karst.) boreal forest in Sweden (Esseen 1994), but this may have been related to combined edge effects from different edges within the small fragments (Malcolm 1994). Although there appeared to be no effects of increased wind on structure at cut edges in our study, edge influence related to wind did affect the abundance of epiphytic lichens up to 50 m in both black spruce forest in Quebec (Rheault et al. 2003) and Norway spruce forest in Sweden (Esseen and Renhorn 1998).

Tree recruitment from seeds or vegetative regeneration is common at recently created edges (Chen et al. 1992; Sizer and Tanner 1999; Baker and Dillon 2000; Oosterhoorn and Kappelle 2000; Burton 2002; Harper and Macdonald 2002a), but had not yet occurred on the forest side of the edge in black spruce boreal forest. The lack of regeneration was likely due to the persistent *Sphagnum* layer, which hinders seedling establishment (Boudreault et al. 2002).

With regard to understory structure, our findings of lower moss cover and higher lichen cover farther into the forest are difficult to interpret but could indicate complex nonmonotonic responses to edge influence. Alternatively, greater lichen cover probably existed before the disturbance, since extensive lichen growth is unlikely in the first few years following edge creation. Lower shrub cover, which was also found following edge creation at cut edges in aspen-dominated boreal forest (Harper and Macdonald 2002a), may have been due to damage from harvesting equipment, or changes in microclimate or soil conditions at the edge.

Although edge influence on structure did not extend very far into the forest, DEI for some understory species was greater than DEI for structure variables. In general, however, edge influence for understory composition was not that extensive, possibly because of the open canopy of black spruce forest (Harper et al. 2002). The conical growth form of black spruce and sparse canopy cover allows the penetration of light to the understory even in interior forest. Therefore, when an edge is created, the effect of increased light may not penetrate very far. DEI was especially limited for shrub

species. These woody species may take more time to respond to edge influence and may only have been negatively affected by damage from harvesting equipment. Species with a greater DEI included herb, moss, and lichen species, which may be able to respond more rapidly to changes in light or moisture near the edge. Edge influence on moss species was always negative. Moss species that prefer high light conditions may not have had time to respond to edge influence or may already have been adapted to high light conditions before the edge was created. There were changes in ground level species composition further into the forest where *Cladina rangiferina*, which prefers high light conditions (Brodo et al. 2001), was positively affected by edge influence, and shade-tolerant *Hylocomnium splendens* (Foster 1985) was negatively affected by edge influence.

Fire edges

The initial structural change at fire edges is likely due to partial burning extending into the forest. Burned organic matter extended up to 40 m from the edge, the same DEI as for increased snag density, lower density of dominant trees, and lower moss cover. Thus, partial disturbance, rather than increased light and wind at the edge, may be an important factor influencing DEI at fire edges. This partial disturbance could also result in a spatially complex fire boundary at a small scale, as has been found at a larger scale (Turner 1989; Mladenoff et al. 1993); however, more research is needed to determine the spatial configuration of fire edges at a small scale.

There was little evidence of edge influence beyond the effects of partial burning. A possible exception is greater shrub cover, specifically *Ledum groenlandicum* and *Vaccinium myrtilloides*, at the edge, which could be due to release growth from increased light at the edge, or greater moisture or nutrient availability following the fire. Alternatively, greater cover of *Ledum groenlandicum* and *Vaccinium* spp. may have resulted from increased regeneration from rhizomes following light fire (Viereck 1983; Nguyen-Xuan et al. 2000). Regeneration of the dominant tree species, a common edge effect (Chen et al. 1992; Sizer and Tanner 1999; Baker and Dillon 2000; Oosterhoorn and Kappelle 2000; Burton 2002; Harper and Macdonald 2002a), had occurred in the burned area, but edge influence was not significant. Regeneration of *P. mariana* after fire is common (e.g., Viereck 1983; Nguyen-Xuan et al. 2000).

In general, distance of edge influence was greatest for response variables that were most directly affected by burning (e.g., burning of the ground moss layer, snags created by the fires). Edge influence did not extend as far for other variables, e.g., the cover of individual species. For these species, the variation due to edge effects was greater than the inherent variability in interior forest either within the burned area or very near the edge. Many common ground cover moss and lichen species were likely destroyed by partial burning (*Ptilidium* spp., *Pleurozium schreberi*, *Sphagnum* spp., *Cladina rangiferina*, *Cladonia* spp.). These species, with the exception of *Cladonia* spp., are classified as "avoiders", which establish in late-successional forest conditions (Nguyen-Xuan et al. 2000); therefore, they had not yet reestablished in the burned areas. The only ground layer and herb taxa positively affected by edge influence (*Polytrichum* and *Equisetum* spp.) probably

survived burning and resprouted from rhizoids (Viereck 1983) in the burned areas on both sides of the edge. *Polytrichum* spp. is classified as an “invader”, which is a short-lived, easily dispersed pioneer (Nguyen-Xuan et al. 2000), and had a positive edge influence by invading recently exposed burned areas. The three common herbs (*Coptis groenlandica*, *Gaultheria hispidula*, *Vaccinium oxycoccos*) that were negatively affected by edge influence responded only in the burned area and may have been directly affected by severe burning or indirectly affected by greater light, moisture, or nutrient availability in the disturbed area. *Gaultheria hispidula* is another avoider species and is negatively affected by wildfire (Nguyen-Xuan et al. 2000).

Comparison between edge types: can cut edges emulate fire edges?

Major differences exist between fire and cut edges; notably, fire edges were wider with more extensive structural change, more snags, and a different species composition than cut edges. It is important to note that these differences are only for vegetation and do not include other edge effects such as those for wildlife, and they only consider the first few years following edge creation. We introduced a new analysis to address our first objective that statistically compares responses at two different edge types. This direct comparison showed that the most extensive significant difference was greater density of snags at fire edges, but there were also differences in shrub cover, lichen diversity, and species composition. Shrub cover may have been damaged by harvesting equipment near cut edges and may have benefited from increased nutrient availability following fire in the adjacent burned area. Several individual shrub species showed similar results, particularly *Ledum groenlandicum*, a prominent shrub, although *Ledum groenlandicum* was common on 20-year-old burned and harvested sites in black spruce forest (Nguyen-Xuan et al. 2000). Results from herb species were mixed and likely reflected differences in light, moisture, and nutrient availability between burned and harvested areas and at the edges. Many of the common moss and lichen species were more abundant in the harvested areas than in burned areas, probably since fire removes more of the duff layer (Nguyen-Xuan et al. 2000). For most of these late-successional ground cover species (Nguyen-Xuan et al. 2000), the significant differences did not extend beyond the edge. Taxa with greater cover in burned areas and at the edge included shade-intolerant, short-lived *Polytrichum* spp. that invaded disturbed areas; *Polytrichum* spp. were also more abundant in 20-year-old burned areas than in harvested areas (Nguyen-Xuan et al. 2000). *Dicranum* spp. also had greater cover in burned areas in our study, but are considered late-successional species and were more abundant in 20-year-old cut areas than in 20-year-old burned areas in black spruce forest (Nguyen-Xuan et al. 2000). Lichen diversity and cover at fire edges may have been decreased by partial burning, as compared with cut edges where there was no significant reduction in lichen cover right at the edge.

Our results support the hypothesis that edge influence is more extensive at fire edges than at cut edges for structure (but not composition). For many overstory and understory structure variables, DEI extended further into the forest at fire edges than at cut edges. However, more species were af-

ected by edge influence with greater DEIs at cut edge. The hypothesis that edge influence is weaker at fire edges was not supported by our results; the number of variables with stronger MEI was just as great at fire edges as at cut edges. Therefore, it appears that for forest structure, the edge-to-interior gradient is just as strong at fire edges and extends further (because of partial burning) than at cut edges. Despite this strong, extensive edge-to-interior gradient for structure, fewer species are affected by edge influence at fire edges. A more gradual edge-to-interior gradient at fire edges may maintain microclimatic conditions that are more similar to those in the interior forest, thus affecting fewer understory species.

In black spruce boreal forest, edge effects do not penetrate very far into the forest in the first few years following edge creation. Therefore, the impact of edge influence on the remaining forest stands in a fragmented landscape may not be as much of a concern as in other forested ecosystems. Rather, a potentially important threat to biodiversity from forest management may be the loss of natural forest-fire edges on the landscape, with possible long-term effects for biodiversity. Currently, cut edges are structurally and compositionally different than fire edges. Can cut edges emulate fire edges? We think that the answer is yes, and no. Some of the structural features of natural forest edges may be emulated by harvest boundaries that are “feathered” or are partially cut to create wider edges that mimic the effects of partial burning. Research is needed to assess this possibility before such practises are added to management strategies such as those suggested by Gauthier et al. (2004). However, it is doubtful that cut edges will ever be able to emulate the high abundance of snags, one of the key characteristics of fire edges. The 40 m wide zone of a mixture of snags and live trees may provide important habitat for organisms that require both structural elements in close proximity, and it may facilitate interactions among species (Fagan et al. 1999). More research is needed on the functional role of this structural complexity at fire edges and whether it is an important component of fire-dominated landscapes for biodiversity. Since forest management is unlikely to completely emulate fire edges, fire edges should be conserved by reducing salvage logging at edges of fires. Conserving some fire edges and managing cut edges to better emulate the structure of fire edges will help maintain a unique and potentially important component of fire-dominated boreal landscapes.

Acknowledgements

We are grateful for the field assistance of Vincent D’Aoust, Daniel Denis, Mélanie Lacroix, Mario Lafond, and Samuel Pinna. Financial support was provided by Groupe de recherche en écologie forestière, Chaire industrielle en aménagement forestier durable, and the Sustainable Forest Management Network. Anonymous reviewers provided helpful comments on earlier versions of this manuscript. Ellen Macdonald helped with the analysis.

References

- Baker, W.L., and Dillon, G.K. 2000. Plant and vegetation responses to edges in the southern Rocky Mountains. *In* Forest fragmenta-

- tion in the southern Rocky Mountains. *Edited by* R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker. University Press of Colorado, Boulder, Colo. pp. 221–245.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* **31**: 384–391.
- Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable forest management of the Canadian boreal forest. *Silva Fenn.* **36**: 81–95.
- Boudreault, C., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Can. J. For. Res.* **32**: 1080–1093.
- Brodo, I.M., Sharnoff, S.D., and Sharnoff, S. 2001. Lichens of North America. Yale University Press, New Haven, Conn.
- Brothers, T.S., and Spingarn, A. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conserv. Biol.* **6**: 91–100.
- Burton, P.J. 2002. Effects of clearcut edges on trees in the Sub-boreal Spruce Zone of Northwest-Central British Columbia. *Silva Fenn.* **36**: 329–352.
- Chen, J., Franklin, J.F., and Spies, T.A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* **2**: 387–396.
- Côté, M. 2000. Dictionnaire de la foresterie. Dictionary of forestry. Ordre des ingénieurs forestiers du Québec and Les Presses de l'Université Laval, Québec, Que.
- DeWalle, D.R. 1983. Wind damage around clearcuts in the ridge and valley province of Pennsylvania. *J. For.* **81**: 158–159, 172.
- Environment Canada. 1993. Canadian climate normals 1961–1990. Canadian climate program. Atmospheric Environment Service, Downsview, Ont.
- Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biol. Conserv.* **68**: 19–28.
- Esseen, P.-A., and Renhorn, K.-E. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conserv. Biol.* **12**: 1307–1317.
- Fagan, W.F., Cantrell, R.S., and Cosner, C. 1999. How habitat edges change species interactions. *Am. Nat.* **153**: 165–182.
- Ferreira, L.V., and Laurance, W.F. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conserv. Biol.* **11**: 797–801.
- Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce) – *Pleurozium* forest of south-eastern Labrador, Canada. *J. Ecol.* **73**: 517–534.
- Franklin, J.F., and Forman, R.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landsc. Ecol.* **1**: 5–18.
- 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.
- Gauthier, S., Nguyen-Xuan, T., Bergeron, Y., Leduc, A., Drapeau, P., and Grondin, P. 2004. Developing forest management strategies based on fire regimes in northwestern Quebec, Canada. *In* Emulating natural forest landscape disturbances: concepts and applications. *Edited by* A.H. Perera, L.J. Buse, and M.G. Weber. Columbia University Press, New York. In press.
- Harper, K.A., and Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology*, **82**: 649–659.
- Harper, K.A., and Macdonald, S.E. 2002a. Structure and composition of edges next to regenerating clear-cuts in the boreal forest. *J. Veg. Sci.* **13**: 353–346.
- Harper, K.A., and Macdonald, S.E. 2002b. The critical values program for assessing edge influence. *Bull. Ecol. Soc. Am.* **83**: 61–62.
- Harper, K.A., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Structural development of black spruce forests following fire in Abitibi, Québec: a landscape scale investigation. *Silva Fenn.* **36**: 249–263.
- Harvey, B.D., and Brais, S. 2002. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. *Can. J. For. Res.* **32**: 653–666.
- Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M., and Laurance, S.G. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, **79**: 2032–2040.
- Malcolm, J.R. 1994. Edge effects in central Amazonian forest fragments. *Ecology*, **75**: 2438–2445.
- Marie-Victorin, frère. 1995. Flore laurentienne. 3^e éd. Les Presses de l'Université de Montréal, Montréal, Que.
- Maser, C., Anderson, R.G., Cromack, K., Jr., Williams, J.T., and Martin, R.E. 1979. Dead and down woody material. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S. Department of Agriculture Forest Service, Washington, D.C. pp. 78–95.
- Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* **66**: 185–194.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., and Woodley, S. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* **9**: 223–260.
- Mesquita, R.C.G., Delamonica, P., and Laurance, W.F. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biol. Conserv.* **91**: 129–134.
- Mladenoff, D.J., White, M.A., and Pastor, J. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecol. Appl.* **3**: 294–306.
- Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J., and Paré, D. 2000. The importance of forest floor disturbance in the early regeneration of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Can. J. For. Res.* **30**: 1353–1363.
- Oosterhoorn, M., and Kappelle, M. 2000. Vegetation structure and composition along an interior-edge-exterior gradient in a Costa Rican montane cloud forest. *For. Ecol. Manage.* **126**: 291–307.
- Ranney, J.W., Bruner, M.C., and Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. *In* Forest island dynamics in man-dominated landscapes. *Edited by* R.L. Burgess and D.M. Sharpe. Springer-Verlag, New York. pp. 67–95.
- Rheault, H., Drapeau, P., Bergeron, Y., and Esseen, P.-A. 2003. Edge effects on epiphytic lichens in managed black spruce forests of eastern North America. *Can. J. For. Res.* **33**: 23–32.
- Saucier, J.-P., Bergeron, J.-F., Grondin, P., and Robitaille, A. 1998. The land regions of southern Québec (3rd version): one element in the hierarchical land classification system developed by the ministère des Ressources naturelles du Québec. Ministère des Ressources naturelles du Québec, Québec, Que. Intern. Rep.
- Sizer, N., and Tanner, E.V.J. 1999. Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biol. Conserv.* **91**: 135–142.
- Thomas, J.W., Anderson, R.G., Maser, C., and Bull, E.L. 1979. Snags. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S. Department of Agriculture Forest Service, Washington, D.C. pp. 60–77.

- Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Ann. Rev. Ecol. Sys.* **20**: 171–197.
- Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley & Sons Ltd., Chichester, N.Y. pp. 201–220.
- Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaire Barlow et Ojibway en territoire québécois. *Géogr. Phys. Quat.* **31**: 357–372.
- Wallin, D.O., Swanson, F.J., and Marks, B. 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. *Ecol. Appl.* **4**: 569–580.