Negligible structural development and edge influence on the understorey at 16–17-yr-old clear-cut edges in black spruce forest

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Abstract

Questions: What is the distance of edge influence on the structure and understorey composition at 16–17-yr-old cut edges in black spruce boreal forest? How do these edges compare with more recent 2–5-yr-old cut edges in the same region?

Location: Northwestern Quebec, Canada.

Methods: Forest structure and understorey composition were sampled along transects perpendicular to ten 16–17-yr-old clear-cut edges, and compared to published results from 2–5-yr-old cut edges. We used randomization tests to assess the magnitude and distance of edge influence, and to compare edge influence between different edge ages.

Results: Black spruce forest next to the 16–17-yr-old cut edges was structurally and compositionally very similar to interior forest, with little edge influence from harvesting beyond 5 m into the forest. Edge influence on the understorey was weak (low magnitude) and not very extensive (short distance) at these edges, with no significant edge influence on the abundance of individual species. Logs peaked in abundance on the forest side of the edge, with values higher than in either adjacent ecosystem.

Conclusions: Overall, 16–17-yr-old cut edges in black spruce forest showed little evidence of further structural change compared to the 2–5-yr-old cut edges. Structural development of these edges as well as regeneration of the disturbed areas also resulted in reduced edge influence on the understorey. Instead, clear-cut edges in black spruce forest may experience more forest influence on the regenerating disturbed area.

Introduction

An increased amount of edge habitat has long been recognized as an important consequence of fragmentation following forest harvesting (e.g. Wales 1972; Ranney et al. 1981; Chen et al. 1992). However, there have been few studies on the edges of regenerating harvested areas beyond the first decade after harvesting, which are needed for a comprehensive perspective on the spatiotemporal dynamics of forest edges (but see recent studies Chabrerie et al. 2013; Dupuch & Fortin 2013). Edge structure changes over time, resulting in dynamic boundaries and subsequent effects on the adjacent plant communities. Successional processes on the forest side of created edges

are driven by microclimatic effects, changes in resource availability and population dynamics of individual species in the absence of vegetation removal or soil disturbance. Tree mortality and regeneration are key processes in the development of created edges. Resulting effects on understorey species may differ, such as between shade-tolerant and shade-intolerant understorey species (e.g. Avon et al. 2013).

At edges of regenerating clear-cuts, edge influence on the adjacent forest may decrease over time as the contrast between adjacent communities is reduced (Matlack 1994; Harper & Macdonald 2002), resulting in 'edge softening' (Harper et al. 2005). Alternatively, structural changes may continue at the edge due to wind effects on tree mortality

and structural damage, particularly in forests with slow regeneration. At these edges, changes in the understorey may persist due to long-term exposure to more light and wind before the regenerating forest has reached the same height as the undisturbed forest. Evidence of progressive edge influence on understorey plant species composition as a result of structural deterioration at created edges has been found, such as an increase in the proportion of understorey species influenced by the edge after 16 yr (Harper & Macdonald 2002) and persistence and even expansion of edge influence (increasing distance of edge influence) on understorey vegetation for 60 yr (Dupuch & Fortin 2013).

Boreal forests provide a simplified ecosystem for studying the progression of edge influence over time; in these mostly monospecific forest stands, effects of structural development at edges can be studied in isolation of effects from changes in tree species composition. We investigated forest structure and composition across 16–17-yr-old cut edges in black spruce boreal forest and compared our results with those of more recent 2–5-yr-old cut edges in forests with similar structure and composition (Harper et al. 2004). Previous studies have found that edge influence on vegetation does not extend very far at recent cut edges in boreal forests (Harper et al. 2004, 2015). The short canopy height and open canopy structure could maintain conditions for weaker and even less extensive edge influence on the forest over time as the adjacent harvested

stand regenerates, blocking out edge influence on light and wind. An alternative hypothesis is that further structural damage could occur resulting in the persistence and possible expansion of edge influence over time. We assessed edge development and change in edge influence over time in black spruce forest, focusing on edge creation after ample time for the manifestation of initial edge effects. We characterized edge structure and assessed the effects of edge development on understorey composition and diversity. Our objectives were: (1) to determine edge influence on structure and understorey plant composition at 16–17-yr-old cut edges in black spruce boreal forest, and (2) to compare these patterns of structure and composition with those across more recent 2–5-yr-old cut edges in the same region.

Methods

Study site

Our study site was in black spruce boreal forest in the Abitibi region in northwestern Québec (49°40′24″ N, 79°18′54″ W; Fig. 1). The 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 & Hardy 1977). The topography is relatively flat at an elevation of approximately 300 m a.s.l. Soils are predominantly organic, with
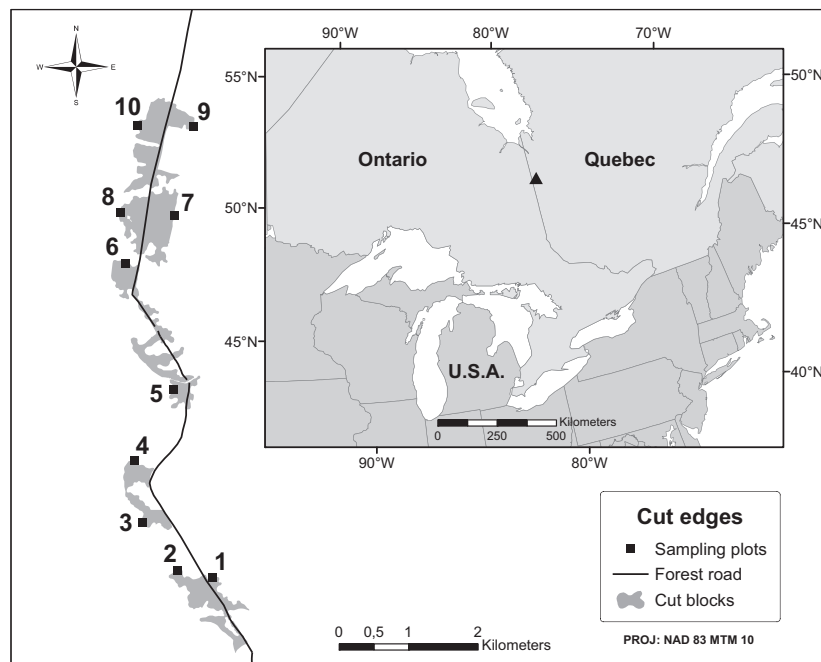

Fig. 1. Map showing the location of the transects in relation to the 1984–1985 cut blocks.

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. Mean annual wind speed was not available at the La Sarre station but ranged from 3.3 to 3.5 m·s^{-1} at other stations (Amos, Matagami and Rouyn-Noranda) in the region (Ilinca et al. 2003).

The forest mosaic in our study area is part of the *Picea mariana*–moss bioclimatic domain (Saucier et al. 1998). *Picea mariana* was dominant in all sampled forest stands; other tree species included *Pinus banksiana*, *Betula papyrifera*, *Populus tremuloides*, *Populus balsamifera* and *Larix laricina*. The average canopy cover was 40% and the average stand height was 13 m (Table 1). The region is characterized by large crown fires that kill most of the trees and above-ground vegetation (Bergeron et al. 2002). Most unharvested forest stands in our study originated from fire around 1725 or 1825, with relatively little natural or anthropogenic disturbance since then. Stands next to our studied cut edges were clear-cut in 1984 or 1985. No herbicides were used before or after harvesting. Harvested stands were not replanted; in most areas, natural regeneration had not yet become trees (>5 cm DBH) at the time of sampling. Canopy height ranged from 3 to 7 m for the few sites where trees had regenerated. The study site for the 2–5-yr-old cut edges was located 20 km to the east; these forest stands dominated by *Picea mariana* also originated from fire, mostly in the 1700s, and had 45% canopy cover and an average height of 12 m (Harper et al. 2004). Clear-cut harvesting is the only prominent land use in this forested landscape, which is otherwise dominated by a natural fire disturbance regime.

Data collection

We established a single transect perpendicular to each of ten 16–17-yr-old abrupt clear-cut edges (Fig. 1, Table 1). Sampling was conducted between Jun and Aug 2001. Transects were at least 100 m away from other transects, corners of clear-cuts and major forest openings in the forest stands or forest remnants in the cut blocks. Edges spanned a range of aspects in this study and in the study of 2–5-yr-old cut edges (Harper et al. 2004). Stand age, canopy cover and height varied among forest stands next to cut edges (Table 1).

For each transect, 20 × 5 m rectangular plots, length parallel to the forest edge, were centred at the following distances along each transect: −50, −15, −5, 0, 5, 15, 25, 40, 60, 100, 150 and 200 m from the edge into the adjacent forest (negative distances indicate the clear-cut side of the edge). The plot at 0 m straddled the forest edge, which was located at the edge of the continuous forest canopy. Plots were included on the disturbance side of the edge to encompass the entire transition zone. We used data collected at 100, 150 and 200 m to characterize interior forest. A synthesis of studies on edges in boreal forests across Canada and in Finland and Sweden found that edge influence on several vegetation responses rarely extended more than 20 m into the forest (Harper et al. 2015). Two 2 × 2 m shrub subplots and four 0.5 × 0.5 m herb subplots were established systematically along the major axis of every plot (shrub and herb subplots at either end of the 20 × 5 m plot, and two extra herb subplots 3 m from either side of the centre).

Trees (>5 cm DBH) and snags (standing dead trees >5 cm DBH and >50-cm tall) were tallied in the 20 × 5 m plots; the relative height of all trees and snags was esti-

Table 1. Site and edge characteristics of forest stands, edges and adjacent areas disturbed by forest harvesting in black spruce boreal forest in northwestern Quebec. Canopy cover and height of the tallest trees were measured 60 m from the edge.

Transect	Year of Cut	Size (ha) of Cut Block	Edge Aspect (°)[a]	Approx. Year of Origin[b]	Canopy Cover (%)	Height of the Tallest Tree (m)
Cut 1	1984	39	170	1725	69	12
Cut 2	1984	39	165	1725	34	10
Cut 3	1984	24	50	1725	15	11
Cut 4	1984	24	180	1725	33	13
Cut 5[c]	1984	10	110	1725	39	10
Cut 6	1985	45	210	1775	44	14
Cut 7	1985	56	278	1825	72	18
Cut 8	1985	56	118	1825	21	18
Cut 9	1985	54	287	1825	31	10
Cut 10[d]	1985	54	102	1825	47	10

[a]Facing from the forest towards the disturbed area.
[b]Data from a fire reconstruction map (Bergeron et al. 2004).
[c]Shrub and herb data were not collected in the 60-m plot.
[d]The −50-m plot was placed at −40 m.

mated as dominant, co-dominant, intermediate or suppressed (Côté 2000). Although we identified tree species and calculated tree species diversity, we do not report the results, which were similar to tree density, because 93% of trees were *P. mariana*. We tallied the number of logs (downed coarse woody material) intersecting the major axis of the plot (>5 cm diameter at the intersection point). Decay stage was evaluated for all snags (classes 1–5; Thomas et al. 1979) and logs (classes 1–5; Maser et al. 1979); deadwood in decay class 1 is the least decomposed. 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 using a clinometer as a proxy for canopy height, because of the uneven structure of the canopy, average tree height would not adequately characterize canopy height.

Within the shrub subplots, we visually estimated the cover for each shrub species (>50-cm tall) and for all shrub species combined, and we counted the number of seedlings (<1-m tall), saplings established from layering (<1-m tall) and taller saplings (>1-m tall, <5 cm DBH). Cover of litter and of each species of herb, ground layer common mosses and macrolichens and dwarf woody plants (<50-cm height) was visually estimated within the herb subplots to the nearest 1% up to 5% and to the nearest 10% thereafter.

Data analysis

We assessed edge influence for the following categories of response variables: overstorey structure (canopy cover, and tree, snag and log densities), understorey structure (total cover of shrubs, herbs, moss and lichens), regeneration (densities of *Picea mariana* layers, seedlings, saplings and suppressed trees) and cover of individual species (shrubs, herbs, moss and lichens). Data from subplots were averaged for each plot. 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 defined structural diversity as the number and abundance of different combinations of height, DBH and decay stages of trees, snags and logs (cf. Spies & Franklin 1988). We calculated structural diversity for each plot using the Shannon index, $H = \Sigma(p_i \ln(p_i))$, where p_i = the proportion of trees, snags or logs within specific categories of height, DBH and decay.

For each response variable, we calculated both the magnitude of edge influence (MEI) and the distance of edge influence (DEI). The MEI is a measure of the strength of edge influence, which varies between −1 and 1. We calculated MEI as $(\bar{x}_d - \bar{x}_i)/(\bar{x}_d + \bar{x}_i)$; where $\bar{x}_d$ = average of a variable at distance d from the edge and $\bar{x}_i$ = average of a

variable in interior forest (distances 100, 150 and 200 m from the edge) (Harper et al. 2005).

To quantify DEI, we used the randomization test of edge influence (RTEI; Harper & Macdonald 2011), which tests the significance of values of response variables for each distance from the edge separately using randomization tests of the data at a given distance from the edge and in the interior forest. When compared to other methods for determining DEI, RTEI was the only method that was generally invariable to sampling design while being sensitive to variation in the reference ecosystem but not at the edge (Harper & Macdonald 2011). We used RTEI with blocking using the RTEI Add-In (Harper & Macdonald 2011) in Microsoft Excel 2007. The RTEI analysis was done separately for each response variable and for each distance from the edge using the following steps (Harper & Macdonald 2011). (1) For each transect, we randomly selected an 'edge' value from the data set consisting of the value at a given distance from the edge and all interior forest values for that transect. (2) Randomized differences were calculated between the average of the randomly selected 'edge' values and the average of all the remaining 'interior' values. (3) These first two steps were repeated for a total of 5000 permutations to create a distribution of randomized differences. (4) The percentile of the observed difference between the average of the observed edge values and the average of the observed interior values within the distribution of the randomized differences was compared to the *P*-value, for which we used $P = 0.05$. DEI was then estimated as the set of two or more consecutive distances (or separated by one distance) over which the average response was significant. We used this definition of DEI in order to counteract effects of multiple testing.

We directly compared forest structure and composition between 16–17-yr-old and 2–5-yr-old cut edges using data from Harper et al. (2004), which were supplemented by two additional transects with data collected following the same methods in 2001 such that sample size was ten for both ages of cut edges. We did these comparisons regardless of whether edge influence was significant for the older cut edges because we wanted to test for differences in edge influence between edge ages, which could include edge influence at the younger but not older edges. For the analysis, we introduce the RTEI for unpaired edge comparisons, which determines the DEI over which there was a significant difference in response variables between the two time periods. It is a modification of the critical values approach for edge comparisons used in Harper et al. (2004) and we have now added it to the RTEI Add-In in Excel written using VisualBasic (Harper & Macdonald 2011). For each variable, we determined whether the difference in values between the two edge ages at different distances from the edge was significant by randomizing the

values at a given distance from the edge and interior values using the following steps. (1) For each edge age, we randomly selected an 'edge' value for each transect from a data set of the value at a given distance from the edge and all interior values for that transect. (2) We randomly assigned these 'edge' values as ten young and ten older 'edge' values. (3) We calculated a randomized *t*-value between the two sets of values (randomly selected 'edge' values for each edge age from Step (2). (4) These first two steps were repeated for a total of 5000 permutations. (5) The percentile of the observed *t*-value within the distribution of the randomized *t*-values was compared to half the *P*-value for a two-tailed test. We used the same *P*-value and procedure for estimating DEI as above. By including the interior forest conditions near each edge age, this approach controls for regional variation that is not due to edge influence, and thus is more appropriate than a standard *t*-test.

Additional comparisons of species composition between forest stands across young and older cut edges was done using ordination analysis on the combined species composition data from this study and from Harper et al. (2004). Understorey composition was assessed using the ordination scores on the first and second axes from a non-metric multidimensional scaling (NMDS) with a Bray-Curtis similarity measure with two predefined axes on the cover values of common species (overall frequency >5%, total of 31 species) of shrubs, herbs, mosses and lichens from all plots across these two sets of edges using PAST (Hammer et al. 2001). Separate analyses for DEI were performed using RTEI for the two edge ages to assess edge influence on species composition as indicated by the ordination scores (*n* = 10 transects). MEI could not be determined because of negative ordination scores.

Results

Overall, edge influence rarely extended beyond 5 m into the forest, which resulted in a narrow transition zone at 16–17-yr-old cut edges in black spruce boreal forest that was only slightly different from interior forest (Table 2). Estimates of MEI were also low (<0.2) for most variables except for canopy cover, tree and log density, litter cover, moss diversity and *Cladonia* spp. Although lower canopy cover extended 5 m into the forest, tree and snag density was only significantly lower in the clear-cut or right at the edge compared to interior forest. The only evidence of extensive structural change beyond 5 m into the forest was higher log density up to 60 m into the forest compared to interior forest. There was no significant edge influence on shrub, herb or lichen cover. Lower moss cover and higher litter cover in the disturbed area and at the edge both had a DEI of −50 to 5 m. Structural diversity on the

forest side of the edge but not on the disturbed side was generally similar to interior forest with negative edge influence on tree and snag structural diversity extending only to 0 and −5 m. Edge influence on log structural diversity was positive (higher values at the edge compared to the interior) and extended well into the forest. For species diversity, only lichen diversity had significant edge influence on the disturbed side of cut edges.

Edge influence on species composition and individual species did not extend into the forest side of the edge. Species composition as measured by the site scores along the first and second ordination axes (stress = 0.34, R^2 = 0.43 and 0.31 for axes 1 and 2, respectively) was not significantly different at the edge or in the disturbed area compared to the interior forest (RTEI analysis, results not shown). Only two species each had higher or lower cover in the disturbed area compared to interior forest with DEIs that were limited to the disturbed side of the edge (Table 2). The species with positive EI were *Cladonia* spp. and *Vaccinium myrtilloides,* and those with negative EI were *Ledum groenlandicum* and *Rubus chamaemorus.*

Overall, edge influence was more extensive (higher DEI) for a larger proportion of variables for overstorey structure and structural diversity as compared to understorey structure and species diversity (Fig. 2a,b). This comparison is particularly noteworthy within the cut area but also extends across the edge and into the forest. Edge influence on individual species was very uncommon even in the cut area and absent from the edge and the forest (Fig. 2c).

Patterns across the edge-to-interior gradient differed among different decay stages of deadwood and different sizes of regenerating trees (Fig. 3). Snags were scarce in the harvested area with larger amounts in the forest. However, different patterns were noted for logs with a peak at the forest side of the edge for less decayed logs and a decrease towards the forest for well-decayed logs. There was a slight peak in seedling density at the edge but layering increased towards the forest. For taller saplings, there was a trough in density and there were few suppressed trees within the disturbed area, indicating that regenerating saplings had not yet reached the size of trees (DBH > 5 cm).

Differences between 16–17- and 2–5-yr-old cut edges were often significant; DEI for these differences extended up to 60 m (Figs 4 and 5). Compared to the younger cut edges, tree density was lower at the older edges despite higher canopy cover 15–25 m from the edge (Fig. 4a,b). The 16–17-yr-old cut edges had more logs on the forest side of the edge but fewer logs within the harvested area than at younger cut edges (Fig. 4c). Compared to the 2–5-yr-old cut edges, the 16–17-yr-old cut edges had higher shrub and moss cover, and less litter in the disturbed area,

Table 2. Average values (± SD) in the cut (−50 m), at the edge (0 m) and in interior forest (100–200 m); magnitude of edge influence (MEI [a] at 0 m) and distance of edge influence (DEI) at 16–17-yr-old cut edges. Negative and positive MEI indicate lower and higher values at the edge compared to the interior, respectively, within the DEI. DEI was estimated as the set of two or more consecutive distances (or separated by one distance) over which MEI is significant; negative distance values refer to distances within the disturbed area. Only common species (>10% frequency) with significant DEI are included. Sample size is n = 10 transects.

	Average Values				
	Cut (−50 m)	Edge (0 m)	Forest (100–200 m)	MEI	DEI (m)
Overstorey Structure					
Canopy Cover (%)	2 ± 4	29 ± 10	43 ± 19	−0.20	−50 to 5
Tree Density (#/ha)	1.7 ± 3.8	8.0 ± 2.7	17.0 ± 6.1	−0.36	−50 to 0
Snag Density (#/ha)	1.1 ± 1.2	3.5 ± 1.7	4.1 ± 2.6	−0.08	−50 to −5
Log Density (#/20 m)	6.3 ± 3.2	7.0 ± 2.7	3.0 ± 2.1	0.40	−50 to 25, 60
Understorey					
Shrub Cover (%)	30.5 ± 19.5	27.5 ± 6.8	29.3 ± 11.0	−0.03	n.s.
Herb Cover (%)	10.0 ± 6.3	7.4 ± 5.1	8.2 ± 4.4	−0.04	n.s.
Moss Cover (%)	60.7 ± 14.2	75.8 ± 16.0	91.4 ± 10.2	−0.08	−50 to 0
Lichen Cover (%)	12.0 ± 12.9	5.1 ± 8.1	3.2 ± 7.6	−0.05	n.s.
Litter Cover (%)	19.6 ± 12.1	11.5 ± 11.1	3.1 ± 3.6	0.57	−50 to 0
Diversity (Shannon Index)					
Tree Structure	0.06 ± 018	0.96 ± 0.22	1.32 ± 0.32	−0.08	−50 to 0
Snag Structure	0.18 ± 0.39	1.04 ± 0.53	1.04 ± 0.64	−0.02	−50 to −5
Log Structure	1.22 ± 0.32	1.40 ± 0.32	0.76 ± 0.54	0.10	−50 to 5, 25, 60
Shrub Species	0.93 ± 0.26	1.04 ± 0.22	0.93 ± 0.25	0.02	n.s.
Herb Species	0.68 ± 0.35	1.04 ± 0.45	0.98 ± 0.28	−0.08	n.s.
Moss Species	0.44 ± 0.18	0.39 ± 0.20	0.32 ± 0.19	0.31	n.s.
Lichen Species	0.26 ± 0.17	0.17 ± 0.17	0.09 ± 0.12	0.11	−50 to −5
Cover (%) of Common Species					
Cladonia spp.	2.0 ± 3.3	0.5 ± 0.5	0.2 ± 0.3	0.40	−50 to −5
Ledum groenlandicum	10.3 ± 6.7	16.7 ± 9.2	20.4 ± 11.4	−0.10	−50, −5
Rubus chamaemorus	0.2 ± 0.3	1.1 ± 1.86	1.1 ± 1.1	−0.04	−50 to −15
Vaccinium myrtilloides	8.5 ± 6.1	4.5 ± 2.3	4.1 ± 4.1	0.05	−50, −5

n.s., no significant DEI.

[a]MEI = $(\bar{x}_d - \bar{x}_i)/(\bar{x}_d + \bar{x}_i)$; where $\bar{x}_d$ = average of a variable at distance d from the edge, and $\bar{x}_i$ = average of a variable in interior forest (distances 100, 150 and 200 m from the edge).

but lower moss cover 15–25 m into the forest (Fig. 4d–f). Tree diversity was lower at or near the 16–17-yr-old cut edges compared to the 2–5-yr-old ones, whereas log diversity was higher on the forest side of the older cut edges (Fig. 5a,b). At 16–17-yr-old cut edges, there was increased shrub and herb diversity at 0 m, but lower herb diversity at 15–25 m compared to the younger edges (Fig. 5c,d). The cover of five (*Gaultheria hispidula, Ledum groenlandicum, Pleurozium schreberi, Smilacina trifolia, Sphagnum* spp.) out of the 17 common species was higher (DEI up to −15, 0, −5, −5 and 60 m, respectively) at 16–17-yr-old cut edges compared to 2–5-yr-old ones, whereas no species had lower cover at the older cut edges.

Discussion

After 16–17 yr, edges of black spruce forest stands in our study region remained relatively unaffected from forest harvesting beyond 5 m into the forest. We provide further evidence that edge influence on many aspects of forest structure and composition is substantially less in the boreal forest than in other forest ecosystems (Harper et al. 2015), particularly compared to DEIs of more than 50 m at regenerating cut edges in other ecosystems (e.g. Chen et al. 1992; Burton 2002). Reasons for the smaller DEI at edges in the boreal forest include shorter canopy height, heterogeneous forest and frequent natural disturbance (Harper et al. 2015). Larger DEI has been found in other shorter open-canopied forests such as in Brazilian cerrado (Dodonov et al. 2013), but this may be due more to the invasion of non-native grasses rather than microclimate (Mendonça et al. 2015). The extremely small DEI at the older edges we studied is likely a combination of widely spaced black spruce trees with a short canopy height and very low canopy cover. Instead of edge influence, forest characteristics often extended into the disturbed area resulting in negative DEI estimates that were restricted to harvested areas away from the edge. This phenomenon, known as 'forest influence', has important implications for silviculture and biodiversity conservation (Baker et al. 2013). Baker et al.
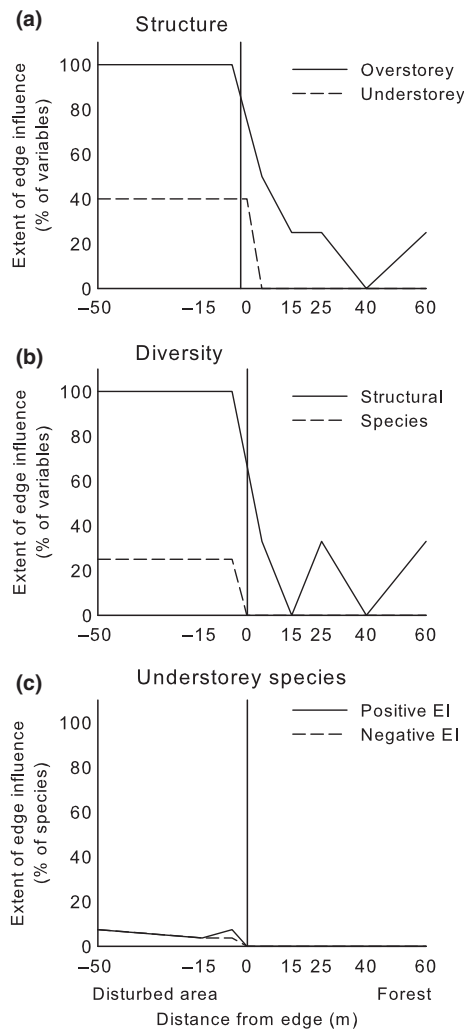
Fig. 2. Proportion of response variables with significant distance of edge influence for (a) overstorey and understorey structure, (b) structural and species diversity and (c) understorey species with positive and negative edge influence (average values greater and less than in interior forest, respectively) at cut edges. Variables for a and b are listed in Table 2 (*n* = 4 and 5 for overstorey structure and understorey, *n* = 3 and 4 for structural and species diversity). For c, significance of edge influence for species is reported in Table 2 and was tested for all species with a frequency of 10% or greater; *n* = 27 species. Significant distance of edge influence was considered as the set of two or more consecutive distances (or separated by one distance) with values significantly different from interior forest.
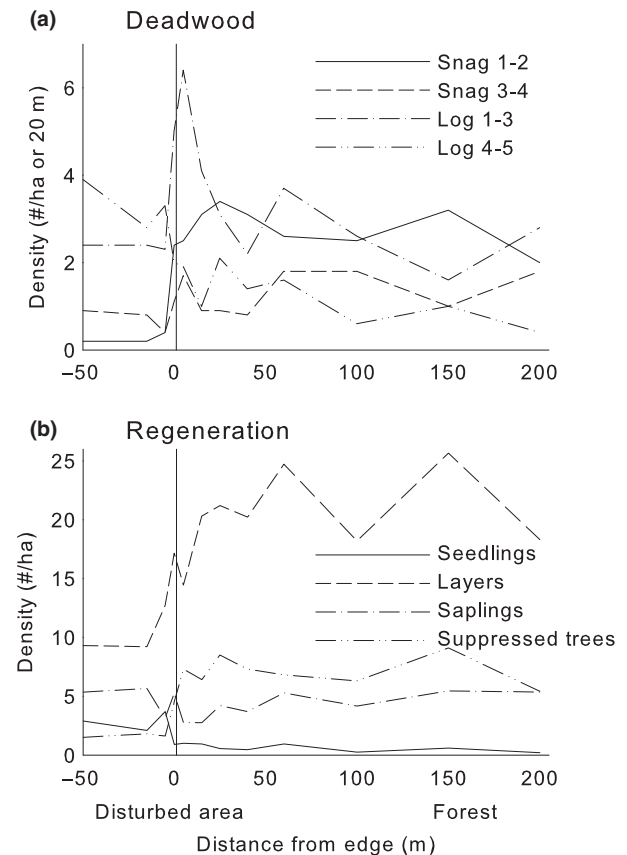
Fig. 3. Patterns of (a) deadwood and (b) regeneration at different distances across the cut forest edge. In a, snags and logs in consecutive decay stages with similar trends were grouped together for clarity (numbers for the decay stages in the legend). Edge influence was significant at distances −50 to −5 m for decay stage 1 and 2 snags, 5–15 m for decay stage 1 logs, −50 to −5, 5 and 25 m for decay stage 4 logs and −50 to 0 m for decay stage 5 logs. In b, average densities are presented for seedlings (<1 m tall), saplings (<1 m tall) established from layering (layers), taller saplings (>1 m tall, <5 cm dbh) and suppressed trees (>5 cm dbh, height well below the canopy). Edge influence was significant at distances −50 to 5 m for seedlings, −50 to −5 m for layers and suppressed trees and 5–15 m for taller saplings. Sample size is *n* = 10 transects.

(2014) found that forest influence on microclimate in Tasmania peaked at 27 yr following harvest. The influence of edges at clear-cuts in black spruce forest may have more effects on regeneration in the disturbance rather than on the adjacent undisturbed forest. Sampling multiple distances at both sides of the edge and in both reference ecosystems would allow for an assessment of the magnitude and distance of both forest influence and edge influence (e.g. Franklin et al. 2015).

Structural development of edges of clear-cuts in black spruce forest

We did not find any evidence for our hypothesis of further structural damage after 16–17 yr of edge development compared to 2–5 yr. The general lack of increased structural change at the cut edges we studied was similar to other cut edges in black spruce forest (Dupuch and Fortin 2013) and fire edges (Harper et al. 2014). The abrupt gradient in overstorey structure at these 16–17-yr-old black spruce edges continues to be sustained and even enhanced with an increase in canopy cover at older compared to
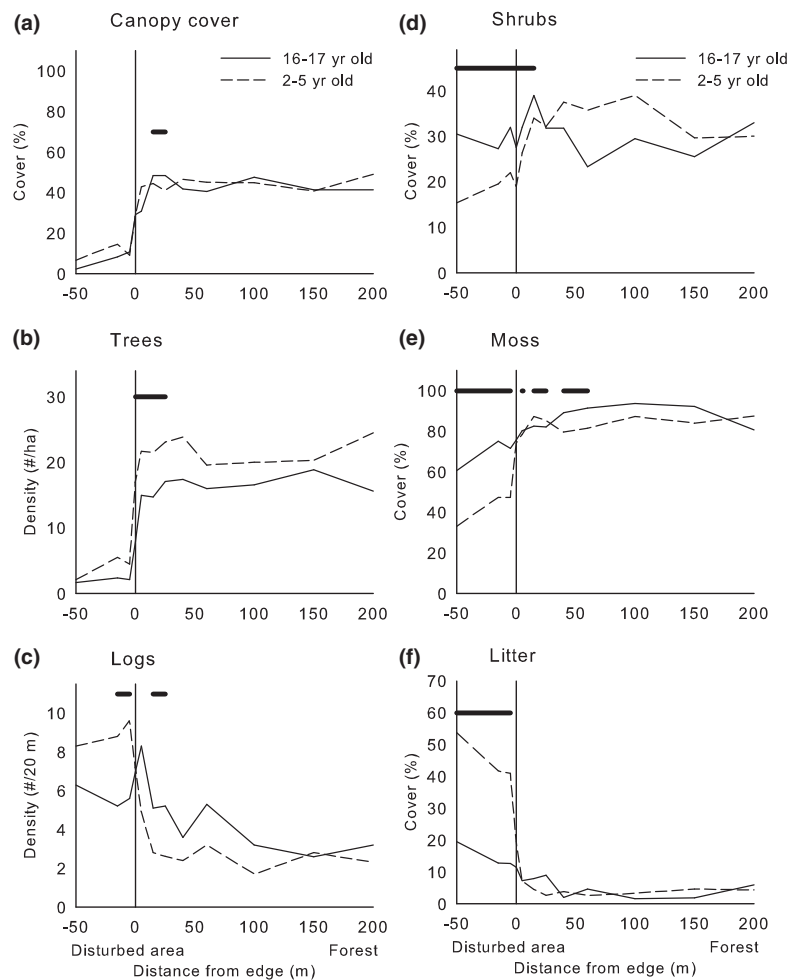
Fig. 4. Patterns of (**a**) canopy cover, (**b**) tree density, (**c**) log density, (**d**) shrub cover, (**e**) moss cover and (**f**) litter cover at different distances across 16–17 and 2–5 yr old forest edges. The solid lines at the top of the graph indicate distances where there were significant differences between the two ages of forest edge. Edge influence for snag density, herb cover and lichen cover was not significant for the difference in edge age; therefore these variables are not included. Sample size is $n = 10$ transects for each edge age.

younger cut edges. Our findings are similar to aspen-dominated boreal forest in Alberta (DEI = 0–10 m for lower canopy cover; Harper & Macdonald 2002). However, wind-throw or increased mortality due to edge influence has been observed in temperate, tropical and even sub-boreal forests (e.g. Chen et al. 1992; Laurance et al. 1998; Burton 2002), which suggests that structural damage may continue well into the first two decades following edge creation only in taller, denser forests. In our study, the resistance to increased wind-throw at their edges may be due to the uneven and relatively open canopy structure of old stands; old uneven-aged black spruce forests are less susceptible to wind-throw than even-aged younger forests (Lavoie et al. 2012). However, there was some evidence of structural change over time. Fewer trees, more logs and higher log diversity on the forest side of the edge, despite

increased canopy cover, suggests that there may have been some earlier mortality.

A peak in abundance of recently decayed logs at the edges we studied provides additional evidence for a phenomenon of larger amounts of less decayed deadwood at older edges, as was found at 13- and 25-yr-old fire edges in black spruce forest (Harper et al. 2014). There was also a higher abundance of logs at edges of 16-yr-old (but not 5-yr-old) harvested areas compared to interior forest (Harper & Macdonald 2002). Higher abundance of less decayed logs at edges compared to both adjacent ecosystems may be due to either slower decomposition at edges compared to disturbed areas or a delay in mortality and wind-throw of trees as compared to the disturbed area, as hypothesized for fire edges by Harper et al. (2014). However, Hope et al. (2003) found that post-harvest litter decomposition was
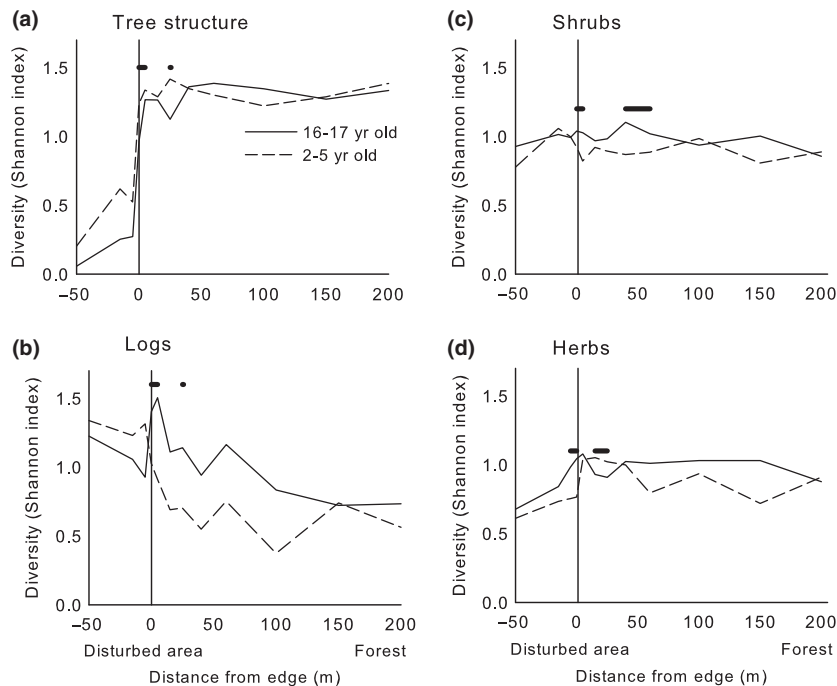
Fig. 5. Patterns of diversity of (**a**) tree structure, (**b**) log structure, (**c**) shrub species and (**d**) herb species at different distances across 16–17 and 2–5 yr old forest edges. The solid lines at the top of the graph indicate distances where there were significant differences between the two ages of forest edge. Edge influence for snag structural diversity, moss species diversity and lichen species diversity was not significant for the difference in edge age; therefore these variables are not included. Sample size is $n = 10$ transects.

not affected by distance from the edge in Douglas-fir forests and decomposition was higher for lower fire severity in black spruce forests (Boulanger et al. 2011). Redding et al. (2004) suggest that nitrification within clear-cuts may be more affected by substrate than by soil temperature and moisture. Therefore, decomposition rate may not be a factor in explaining the pattern of logs that we observed. Delayed tree mortality in forest fragments and at forest edges has been observed in many ecosystems (e.g. Esseen 1994; Laurance et al. 1998; Burton 2002). We also found evidence of earlier tree mortality following edge creation at cut edges from significantly larger amounts of recent snags at older compared to younger cut edges (results not shown), similar to Ferguson & Elkie (2003) and Jönsson et al. (2007). Even anthropogenically created edges appear to provide a different habitat in terms of deadwood than the adjacent ecosystems, and may not be simply an intermediate transition zone.

Impact of edge structural development on understorey composition

Because we found no evidence of further structural damage at cut edges in black spruce forest, it is no surprise that we also reject our second hypothesis that this would have

resulted in the persistence or even possible expansion of edge influence on the understorey. Indeed, we observed a marked decrease in edge influence on understorey structure and composition. Overall, edge influence on the understorey was much less than on the overstorey at these 16–17-yr-old edges. The understorey of the older cut areas was more developed than that of the younger clear-cuts with higher cover of shrubs and moss, and less litter; but changes at the cut edges were more modest. Without any further structural damage to the canopy, the overall effect on understorey structure was a relaxation of patterns across the cut edges, which Matlack (1994) also found for edge-related patterns of plant species composition. Dupuch & Fortin (2013) found similar results to ours at 15–46-yr-old cut edges (DEI = 10 m) but persistent and expanding edge influence at very old cut edges (>46 yr after logging) in black spruce boreal forest stands. Our combined results suggest that in black spruce forest, edge influence may remain minimal for a couple of decades following edge creation and expand after a time lag; but more research is needed to fully understand edge development over time in these forests.

We found higher regeneration only in terms of seedling density on the disturbed side of the edge, but more recruitment in terms of understorey tree density has been found

at other edges (e.g. Chen et al. 1992; Baker & Dillon 2000; Burton 2002; Harper & Macdonald 2002). More seedlings at the edge may be due to better seedbed conditions from wind-throw that causes increased soil disturbance (e.g. Esseen 1994), more favourable microclimatic conditions such as increased light and temperature (e.g. Chen et al. 1995) or the seed rain from black spruce semi-serotinous cones on the trees at the edge of the adjacent intact forest (cf. Greene & Johnson 1996). Combined with results from Dupuch & Fortin (2013) of lower regeneration at 10-yr-old edges, but higher at older edges, our findings suggest that seedling densities on the disturbed side of edges in black spruce forest start to increase at around 15 yr following edge creation. Although relatively minor at cut edges, a peak in seedling density was also found at fire edges (Harper et al. 2014), suggesting that this may be a widespread phenomenon at created edges whether anthropogenic or natural.

There was no edge influence on individual understorey plant species or overall species composition on the forest side of 16–17-yr-old clear-cut edges in black spruce forest. Although vegetation responses to edges can be variable (Alignier & Deconchat 2011), all plant species exhibited the same lack of edge influence in our study. Species either had no initial response or had recovered with time since harvesting even in the disturbed area, as indicated by higher cover at older cut edges, and significant edge influence at younger (Harper et al. 2004) but not older cut edges. Overall, it appears that in black spruce forest, responses of understorey plant species to edge creation are generally immediate and then decrease in the second decade. The absence of a lag or an increase in edge influence after 17 yr may be related to the lack of further structural change at these same edges, as predicted by Harper et al. (2005). Although Harper et al. (2005) also predicted that edge influence will not persist for long at regenerating edges, Dupuch & Fortin (2013) found the reverse, which suggests there may be a longer initial time lag than expected. We would be surprised to see larger edge influence on understorey composition at edges older than 16–17 yr old, as we expect that further structural development at the edge would result in changes in light and temperature towards interior conditions.

Edge influence on structural diversity, but not species diversity, still extended into the forest. The general lack of edge influence for understorey species diversity right at the edge was similar to younger cut edges (Harper et al. 2004), although 16–17-yr-old cut edges were more diverse than younger ones. However, at 16-yr-old cut edges in aspen stands, there was significant edge influence for herb cover and richness but not shrub richness, which was apparent at 5-yr-old cut edges (Harper & Macdonald 2002). Chabrerie et al. (2013) found an increase in species richness with edge age at maintained edges in an agricultural landscape; our contrasting results support their finding that increased edge maintenance or management intensity leads to sharper gradients at the edge.

Conclusion and applications

We conclude that 16–17-yr-old cut edges in black spruce forest showed little evidence of further structural change with time; instead, edges developed through further recruitment of seedlings and decomposition of deadwood. Structural development of these edges and regeneration of the disturbed areas resulted in much lower edge influence on the understorey in the second decade following edge creation. Our results support the hypothesis that edge influence diminishes over time as patch contrast decreases with regeneration of the adjacent forest (Harper et al. 2005), although Dupuch & Fortin (2013) suggest that there may be edge expansion for the understorey at very old cut edges (>46 yr old) in black spruce forests from eastern Québec. While long-term edge expansion could affect biodiversity and ecological processes of forest ecosystems, further study of permanent plots across edges is needed to determine the prevalence of expansion or regression of edges in different regions of the slow-growing black spruce boreal forest. Our results show that forest influence at the edges of clear-cuts may have more impact on regeneration in the disturbed area than edge influence has on the adjacent undisturbed forest in black spruce forests. This would mean that the increased amount of edges in managed landscapes might ultimately be a driver in shaping patterns of regeneration.

An increase in the abundance of harvested edges may also accentuate persistent differences between human and naturally disturbed boreal forests. We found evidence for a non-monotonic pattern (peak at or near the edge) compared to both adjacent ecosystems (rather than simply an intermediate stage) for recent logs at 16–17-yr-old cut edges. Cut edges have a reservoir of recently decayed logs; however, they differ from fire edges by the lack of snags. Lower snag abundance at cut edges suggests that this important landscape feature would be lost if harvesting replaces fire on the landscape. This highlights the importance of maintaining unharvested burned areas and their edges in boreal forest landscapes.

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