

Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia

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Summary

1. Although anthropogenic edges are an important consequence of timber harvesting, edges due to natural disturbances or landscape heterogeneity are also common. Forest edges have been well studied in temperate and tropical forests, but less so in less productive, disturbance-adapted boreal forests.
2. We synthesized data on forest vegetation at edges of boreal forests and compared edge influence among edge types (fire, cut, lake/wetland; old vs. young), forest types (broadleaf vs. coniferous) and geographic regions. Our objectives were to quantify vegetation responses at edges of all types and to compare the strength and extent of edge influence among different types of edges and forests.
3. Research was conducted using the same general sampling design in Alberta, Ontario and Quebec in Canada, and in Sweden and Finland. We conducted a meta-analysis for a variety of response variables including forest structure, deadwood abundance, regeneration, understorey abundance and diversity, and non-vascular plant cover. We also determined the magnitude and distance of edge influence (DEI) using randomization tests.
4. Some edge responses (lower tree basal area, tree canopy and bryophyte cover; more logs; higher regeneration) were significant overall across studies. Edge influence on ground vegetation in boreal forests was generally weak, not very extensive (DEI usually < 20 m) and decreased with time. We found more extensive edge influence at natural edges, at younger edges and in broadleaf forests. The comparison among regions revealed weaker edge influence in Fennoscandian forests.
5. *Synthesis.* Edges created by forest harvesting do not appear to have as strong, extensive or persistent influence on vegetation in boreal as in tropical or temperate forested ecosystems. We attribute this apparent resistance to shorter canopy heights, inherent heterogeneity in boreal forests and their adaptation to frequent natural disturbance. Nevertheless, notable differences between forest structure responses to natural (fire) and anthropogenic (cut) edges raise concerns about biodiversity implications of extensive creation of anthropogenic edges. By highlighting universal responses to edge influence in boreal forests that are significant irrespective of edge or forest type, and those which vary by edge type, we provide a context for the conservation of boreal forests.

Key-words: boreal forest, cut edges, edge effects, fire edges, habitat fragmentation, lakeshore edges, meta-analysis, randomization tests, wetland edges

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Introduction

Anthropogenic edges are an important consequence of timber harvesting and deforestation in managed forested landscapes, contributing to forest degradation and the loss of biodiversity (Saunders, Hobbs & Margules 1991; Chen, Franklin & Spies 1992; Gascon, Williamson & da Fonseca 2000; Laurance *et al.* 2002; Harper *et al.* 2005; Broadbent *et al.* 2008). A large portion of the landscape may be experiencing edge influence from forest edges created by human activity (Harper *et al.* 2005). However, edges due to natural disturbances or natural landscape heterogeneity are also common. Adaptation of species and ecosystems to such natural edges will likely affect the magnitude and extent of edge influence at created edges. Because edge influence is affected by the contrast between ecological characteristics of the forest vs. those of the adjacent non-forested ecosystem, landscapes that are naturally heterogeneous might tend to have less dramatic edge effects (Harper *et al.* 2005). In the boreal forest, where large-scale natural disturbances (fire, insect outbreaks, windthrow) are common (Kneeshaw, Bergeron & Kuuluvainen 2011), edge influence from anthropogenic disturbance could be expected to have less ecological impact than in other forested ecosystems. Most studies on the influence of created edges have focused on tropical or temperate forests; however, the boreal forest that comprises 32% of global forests (Burton *et al.* 2003) has received less attention (Harper *et al.* 2005).

The boreal forest biome is characterized by features that might lead to relatively low magnitude and shallow penetration of edge influence at edges created by harvesting: frequent large-scale natural disturbances, short canopy height and natural landscape heterogeneity due to an abundance of water bodies and wetlands. Unmanaged boreal forests are shaped by natural disturbances such as fire, insect outbreaks and windstorms (Bonan & Shugart 1989; Engelmark 1999); therefore, distinct edges are a natural feature of these landscapes. Due to the harsh climate, boreal forests often have more open and shorter canopies with widely spaced trees than is typical in the more productive temperate and tropical forests. Many natural, permanent forest edges adjacent to water bodies or wetlands are found in boreal landscapes with abundant lakes and open wetlands such as bogs and fens in topographic depressions shaped by past glaciations (Brandt 2009). Because of this landscape context, the negative ecological effects of the creation of anthropogenic edges might be less than has been observed in other forest ecosystems.

Responses to edge influence vary among edge types, edge ages and forest types. In the boreal forest, natural fire edges have some characteristics that often differ from those of cut edges (Harper *et al.* 2004; Larrivée, Drapeau & Fahrig 2008; Braithwaite & Mallik 2012). Complex fire boundaries create highly variable edges that may result in a more gradual transition zone extending up to 40–50 m (Harper *et al.* 2004; McIntire & Fortin 2006; Larrivée, Drapeau & Fahrig 2008). Understorey composition can also differ between fire and cut edges or salvage cut fire edges (Harper *et al.* 2004; Hanson & Stuart 2005; Braithwaite & Mallik 2012). Although edge influence is expected to

decrease over time at regenerating fire and cut edges as the contrast between adjacent communities is reduced (Matlack 1994; Harper & Macdonald 2002), Dupuch & Fortin (2013) found evidence of persistent edge influence at cut edges for over 60 years in *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (black spruce) forest. Edges adjacent to water bodies and wetlands are relatively permanent features of the landscape with a well-developed boundary structure that is expected to shelter the adjacent forest from increased light and wind; thus, lake and wetland edges are expected to have stronger but less extensive edge influence (penetrate a shorter distance into the forest) than other edge types (Harper *et al.* 2005).

Regional differences in edge influence depend largely on patch contrast (Harper *et al.* 2005), which partly depends on the dominant tree species. Within Canada, coniferous *P. mariana* forests are often shorter and more sparse than broadleaf forests; they would, therefore, be expected to have less patch contrast (difference between the forest and adjacent non-forested system) leading to weaker edge influence (less difference between the edge and the interior, Harper *et al.* 2005). Edge responses may also differ between edges in Canadian boreal landscapes, which are subject to frequent large-scale stand-replacing natural disturbances, and those in Fennoscandia where the landscape experiences primarily surface fires (Kuuluvainen & Aakala 2011). The latter are expected to have greater effects of edge influence because plant species at these edges are not adapted to a regime of stand-replacing disturbances that would frequently expose forests to edges. In summary, we hypothesize (i) stronger and more extensive edge influence at younger edges, in Fennoscandia and in broadleaf forests; (ii) more extensive but not necessarily stronger edge influence at fire vs. cut edges; and (iii) stronger but less extensive edge influence at natural lakeshore and wetland edges vs. cut edges.

Here we synthesize available data from studies on the influence of natural edges (wildfire, lake/wetland) and those created by forest harvesting on vegetation in coniferous- and broadleaf-dominated boreal forests across Canada and Fennoscandia. Although our study was not initially designed as a global experiment (Borer *et al.* 2014), our set of individual studies combines similar methodology and site-specific designs. Our objectives were (i) to quantify edge responses across all studied types of boreal forest edges; and (ii) to compare the strength and extent of edge responses among fire, cut and lake/wetland edges, between coniferous and broadleaf boreal forests, and among regions (Alberta, Ontario/Quebec, Sweden/Finland). We selected a variety of response variables including forest structure, deadwood abundance, regeneration, understorey vascular plant abundance and diversity and non-vascular plant cover.

Materials and methods

STUDY AREAS AND SAMPLING DESIGN

Research was conducted in several locations in Alberta, Ontario and Quebec in Canada, and in Sweden and Finland (Fig. 1, Table 1). In

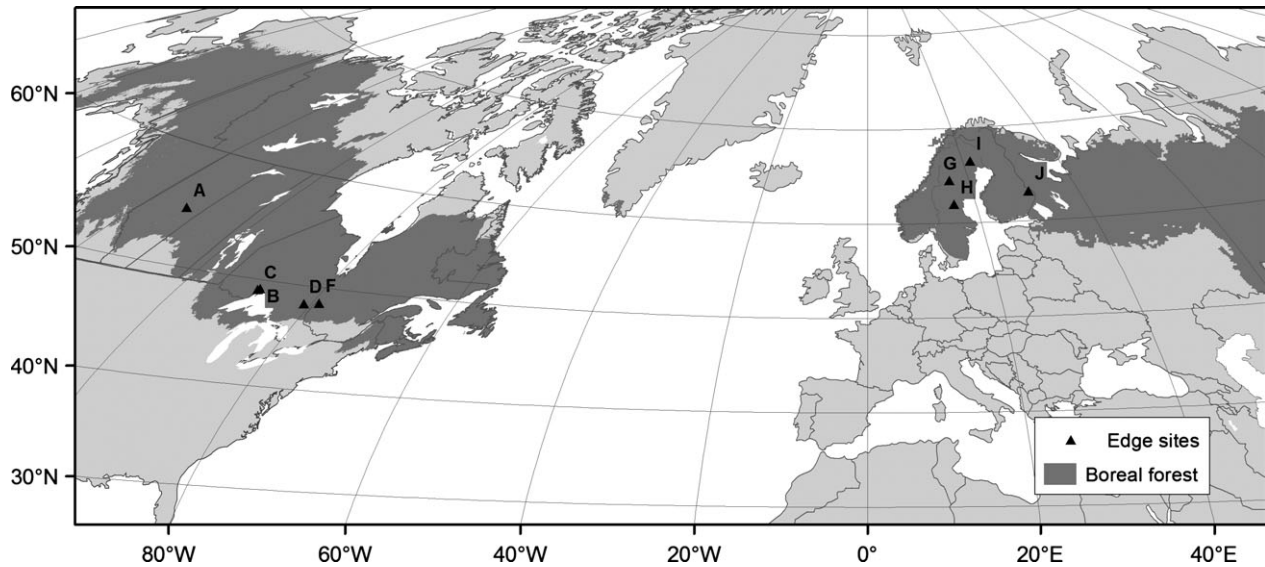


Fig. 1. Map of the study areas. Letters refer to study areas listed in Table 1.

Table 1. Location, forest stand characteristics and types of edges sampled for the study areas in mature coniferous and broadleaf boreal forests

Study area	Location	Lat.	Long.	Elev. (a.s.l.)	Dominant trees	Age (year)	Height (m)	Edges
A*	Alberta, Canada	56°N	113°W	610–670 m	<i>Populus</i> spp.	70–140	12–30	Cut, fire, lake
B*	Ontario, Canada	49°N	89°W	199 m	<i>Populus</i> spp.	60–130	10–25	Cut
C*	Ontario, Canada	49°N	89°W	199 m	<i>Picea mariana</i>	60–170	8–17	Cut, fire
D	Ontario, Canada	48°N	81°W	300 m	<i>Populus</i> spp.	95–105	12–22	Fire
E	Quebec, Canada	50°N	79°W	300 m	<i>P. mariana</i>	80–275	8–12	Cut, fire
F	Quebec, Canada	48°N	79°W	275 m	<i>Populus</i> spp.	130	20–25	Cut, partial cut
G*	North-west Sweden	64°N	16°E	200–550 m	<i>Picea abies</i>	90–200	20–28	Cut
H	Northern Sweden	62°N	16°E	100–475 m	<i>P. abies</i> , <i>Pinus sylvestris</i>	60–159	13–28	Cut
I	Northern Sweden	66°N	22°E	300–325 m	<i>P. abies</i>	150–200	17–23	Wetland
J	Eastern Finland	62°N	31°E	170 m	<i>P. sylvestris</i>	100–150	15–25	Cut, wetland

Data are from the studies listed in Table 2.

*Edge aspects were limited to south or south-west; other studies included edges with a variety of aspects.

Canada, broadleaf forests were dominated by *Populus tremuloides* Michx. or *Populus balsamifera* L. and coniferous forests were dominated by *P. mariana*. Coniferous forests in Sweden and Finland were dominated by *Picea abies* (L.) Karst or *Pinus sylvestris* L. Although most studied forests are of natural origin with minimal anthropogenic disturbance (apart from the studied edges), forests in study area H had been selectively logged and fallen logs were removed. Stand age (or age of the dominant trees) ranged from 60 to 275 year and canopy height from 8 to 30 m. Edges include 1- to 70-yr-old cut edges, 1- to 38-yr-old fire edges and lake/wetland forest edges (Table 2). Edge aspects spanned a range of orientations in most studies, but were limited to south- and south-west-facing edges in four study areas (A, B, C, H). In all studies except one, sampling was conducted along transects (4–23 per study) established perpendicular to edges with sample points located at different distances from the edge. The exception was study I2 where sampling was conducted in forest islands with plots located at different distances from wetland edges but not arranged along transects. All transects were at least 100 m apart except for studies in study areas B and C where data for two transects approx. 50 m apart were averaged. Although the details of sampling differed among studies (see Table S1 in Supporting Information), the

overall sampling design was consistent, allowing for calculation of metrics of edge influence that could be compared.

RESPONSE VARIABLES

We selected 14 response variables that summarize key aspects of forest vegetation: tree basal area and canopy cover; snag and log abundance; snag and log structural diversity; regeneration of conifer and broadleaf tree species; shrub and herb abundance and species richness; and terricolous bryophyte and lichen cover. Not all variables were available from all studies.

Live tree basal area was calculated as $\Sigma(\pi r^2)$ where r = radius (diameter at breast height (dbh)/2) for all live trees with dbh ≥ 5 cm in 5×20 m plots (long axis parallel to the edge) or using a relascope from the plot centre. Canopy cover was estimated using a convex spherical densiometer or visually. Snag abundance was quantified as density or basal area, and downed log abundance was measured as the number of logs along a 20-m transect or within a plot. Structural diversity of snags and logs was calculated using the Shannon index ($-\Sigma[p_i \ln(p_i)]$), where p_i is the proportion of snags or logs in

Table 2. Details on sampling design for each study

Study	Data source	Edge age (year)	Number of transects	Plot locations (m from edge)
Cut edges				
A1	Harper & Macdonald (2002)	1, 2, 5	10 + 10 + 10 = 30	0, 5, 10, 20, 40, 60, 100, 150, 200
A2	Harper & Macdonald (2002)	16	8	0, 5, 10, 20, 40, 60, 100, 150, 200
B*	Stewart (2004)	3–7	20	0, 5, 10, 15, 20, 25, 30, 35, 40, 9 plots at > 100 m for each transect
C1*	Stewart (2004)	3–6	20	0, 5, 10, 15, 20, 25, 30, 35, 40, 9 plots at > 100 m for each transect
E1	Harper <i>et al.</i> (2004)	2–5	10	0, 5, 15, 25, 40, 60, 100, 150, 200
E2	Harper <i>et al.</i> (2014)	16	10	0, 5, 15, 25, 40, 60, 100, 150, 200
F1†	S. E. Macdonald, Y. Bergeron, D. Lesieur & K. A. Harper, unpubl. data	5	7	0, 5, 15, 25, 40, 60, 100, 150, 200
F2 (partial cut)	S. E. Macdonald, Y. Bergeron, D. Lesieur & K. A. Harper, unpubl. data	7	4	0, 5, 15, 25, 40, 7 plots at ≥ 80 m in total
G1	Esseen & Renhorn (1998)	1–3	5	5, 25, 50, 100
G2	Esseen & Renhorn (1998)	8–16	5	5, 25, 50, 100
H1	Hylland (2005)	2–5	16	1, 2, 3, 4, 6, 8, 10, 13, 16, 20, 25, 30, 35, 40, 45, 50, 60, 70, 80
H2	Hylland (2009) and K. Hylander, unpubl. data	40–70	23	10, 20, 40, 80
J1	J. Kouki, unpubl. data	1–10	10	10, 30, 50
Fire edges				
A3	S. E. Macdonald, Y. Bergeron, K. A. Harper, unpubl. data	1	8	0, 5, 15, 30, 60, 100, 150, 200
C2*	Stewart (2004)	4–5	20	0, 5, 10, 15, 20, 25, 30, 35, 40, 9 plots at > 100 m for each transect
D	S. E. Macdonald, Y. Bergeron, D. Lesieur, K. A. Harper, unpubl. data	5	4	0, 5, 15, 30, 60, 100, 150, 200
E3	Harper <i>et al.</i> (2004)	3–4	8	0, 5, 15, 25, 40, 60, 100, 150, 200
E4‡	Harper <i>et al.</i> (2014)	13, 25, 38	4 + 4 + 4 = 12	0, 5, 15, 25, 40, 60, 100, 150, 200
A4§	Lake (A) and wetland (I, J) edges	N/A	12	0, 5, 10, 20, 40, 60, 100, 150, 200
I1	Esseen (2006)	N/A	10	5, 25, 50, 100
I2¶	Moen & Jonsson (2003)	N/A	N/A	16–20, 21–25, 26–30, 31–35, 36–40, 41–45, 46–60, 61–76, 80–293
J2	J. Kouki, unpubl. data	N/A	10	10, 30, 50

*Data for two transects approx. 50 m apart were averaged for 10 sites. Tree basal area, log abundance and snag diversity were sampled at 0, 20, 40 m and in three of the nine interior plots.

†Plots at 100, 150 and 200 m were available on 4, 2 and 1 transects only and were in different forest stands than the edge plots.

‡Two and four plots at 100 and 200 m, respectively, were not available. Canopy cover data are missing for 0–40 m at one 25-yr fire edge.

§Canopy cover, understorey diversity and regeneration were sampled at 10 transects.

¶Plots were located in different forest islands but were not aligned along transects.

different size classes and decay stages. Regeneration was determined as either the average density of seedlings (< 1 m height) in quadrats or as the cover of saplings (< 5 cm dbh) at each sampling point. Shrub abundance was the total cover (estimated visually) of all woody species, usually between 0.5 and 3 m tall, or density measured using the point-quarter-centred method. Herb abundance was the cover of herbaceous plant species plus woody species that are usually < 0.5 m tall. Shrub and herb species richness values were the average number of shrub or herb species per quadrat at each sample point. Bryophyte and lichen cover included the total cover of all ground bryophytes and lichens on the forest floor, estimated visually in quadrats.

ANALYSIS

We conducted meta-analyses to determine the significance of edge influence for each response variable including all studies (except study F2 on partial cut edges) and to examine the influence of several independent factors on edge influence: edge type (fire, cut, lake/wetland), edge age (young ≤ 7 year, old ≥ 8 year), forest type (broadleaf, coniferous) and region (Alberta, Ontario/Quebec, Sweden/Finland). For the meta-analyses, we chose the distance from the edge at which maximum edge influence was observed in each study. To determine this, the average value of a variable in interior forest (\bar{X}_i) was calculated from values in all plots > 60 m from the edge except for studies in study area J where we used the furthest distance from the edge (50 m, see Table 2 for locations and numbers of interior forest plots). For the average response at the edge (\bar{X}_e), we selected the distance at which the average was most different from the average in interior forest. For each response variable, we calculated the standardized effect size Hedge's d using parametric variance:

$$d = \frac{(\bar{X}_e - \bar{X}_i)}{S} \left(1 - \frac{3}{4(N_e + N_i - 2)} \right)$$

where N is the sample size and S is the pooled standard deviation,

$$S = \sqrt{\frac{(N_e - 1)(S_e)^2 + (N_i - 1)(S_i)^2}{N_e + N_i - 2}}$$

and the variance of Hedge's d (v_d) is

$$v_d = \frac{N_e + N_i}{N_e N_i} + \frac{d^2}{2(N_e + N_i)}$$

We then calculated an overall effect size for each response variable using the Hedge's d of each individual study. We considered a response as significant (positive or negative edge influence) when the effect size was greater or less than zero (i.e. confidence interval did not overlap zero). We performed further analyses to determine whether edge influence was affected by our various independent factors. We partitioned effect sizes based on the categories within a factor, estimated the overall effect size for each individual category and tested for significant differences among categories using randomization tests. All analyses were conducted in MetaWin (Rosenberg, Adams & Gurevitch 2000).

In addition to the meta-analysis, we determined the magnitude of edge influence (MEI) and distance of edge influence (DEI) for each response variable; this facilitated comparisons among studies as different methods of analysis for edge influence can produce different results for the same data sets (Harper & Macdonald 2011). MEI is a

measure of the strength of edge influence, which we calculated as $MEI = (\bar{x}_d - \bar{x}_i) / (\bar{x}_d + \bar{x}_i)$ 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 (Harper *et al.* 2005). This metric ranges from -1 (negative edge influence) to $+1$ (positive edge influence). We report MEI at the distance where the absolute value of MEI was greatest; MEI at other distances was used to determine DEI as follows.

To quantify DEI, we used the randomization test of edge influence (RTEI, Harper & Macdonald 2011), a standard method that can be used for all data sets, even those with low sample size, and has been found to be generally invariable to sampling design while being sensitive to variation in the interior ecosystem but not at the edge (Harper & Macdonald 2011). RTEI tests the significance of MEI (i.e. is it significantly different from zero) for different distances from the edge using randomization tests of the data at a given distance from the edge and in the interior forest. RTEI can be used with blocking (e.g. when interior forest plots are along the same transects as the edge plots) or without blocking. We used RTEI with blocking for studies in study areas A, B, C and E, and RTEI without blocking for studies in study areas D, F, G, H, I and J.

The RTEI analysis was done separately for each response variable and for each distance from the edge using the following steps (Harper & Macdonald 2011). (1a) For RTEI with blocking, we randomly selected one value from a data set including the value at a given distance from the edge and all interior forest values for that transect and assigned it as the 'edge' value. (1b) For RTEI without blocking, we randomly selected x 'edge' values ($x = \#$ transects) from a data set including all values at a given distance from the edge and all interior forest values and assigned them as 'edge' values. (2) Randomized MEI values were calculated using the randomly selected 'edge' values with all the remaining values as 'interior' values. (3) These first two steps were repeated for a total of 5000 permutations to create a distribution of randomized MEIs. (4) The percentile of the observed MEI within the distribution of the randomized MEIs was compared to half the P -value for a two-tailed test at $\alpha = 0.05$. DEI was defined as either 0 m (or the closest distance to the edge) if MEI was significant only at that position or as the set of two or more consecutive distances where MEI was significant. If MEI was not significant at the closest distance from the edge or at two consecutive distances, DEI was reported as not significant and was excluded from averages of DEI. We used this definition of DEI in order to counteract effects of multiple testing while still adopting a more liberal, exploratory approach to find possible trends. We used exact permutation (all possible permutations) when the number of possible permutations was < 5000 (i.e. for studies in study areas D, F and G). Missing values in the interior forest data plots were replaced with average values of interior forest for that study.

Results

Our meta-analysis showed significant negative edge influence (i.e. lower values at the edge compared to interior forest) on tree basal area, canopy cover and bryophyte cover, and significant positive edge influence on log abundance and broadleaf regeneration in boreal forests (Fig. 2a). Edge influence was, overall, not significant for snag abundance and diversity, log diversity, shrub and herb abundance and richness, coniferous regeneration or lichen cover, as illustrated by confidence intervals of mean effect sizes that included zero.

Analyses examining the influence of our independent factors revealed significant negative edge influence on canopy

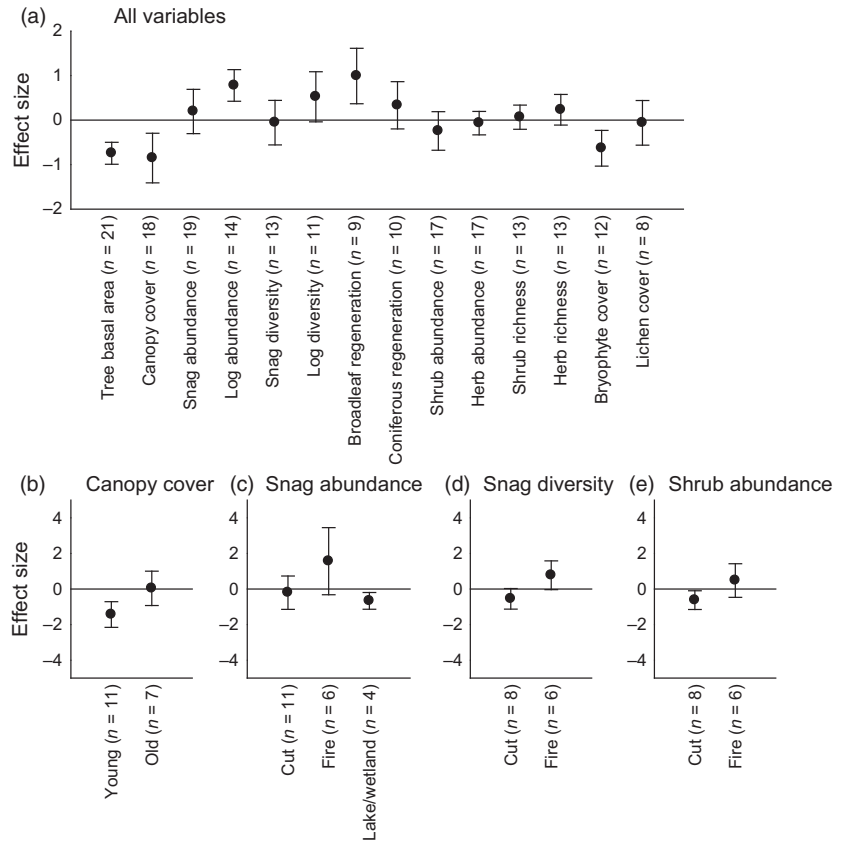


Fig. 2. Effect sizes and 95% confidence intervals from the results of the meta-analyses of edge influence for (a) each response variable for all edges combined; (b) canopy cover for different edge ages; and (c) snag abundance, (d) snag diversity and (e) shrub cover for different edge types. Only significant comparisons are shown (see Table S5 in Supporting Information). Sample sizes are indicated on the x-axis. Note the different scale for the y-axis in (a). Results for individual edge studies are found in Table S2 in Supporting Information.

cover for younger but not older edges (Fig. 2b), on snag abundance only for lake/wetland edges (Fig. 2c) and on shrub abundance at cut edges (Fig. 2d,e). There was also a significant effect of edge type for snag diversity; edge influence was negative for cut edges but this was not statistically significant (for details, see Table S5 in Supporting Information). The effect size for positive edge influence on snag abundance at fire edges was high, but it was quite variable and therefore also not significant (Fig. 2c).

Average edge influence on tree basal area and canopy cover was negative with moderate MEI (Fig. 3, Table S3 in Supporting Information). MEI for snag abundance and diversity was low with high variability among studies, whereas average MEIs for log abundance and diversity were positive with less variation. Edge influence on regeneration was positive for both types of trees but with much higher MEI for broadleaved trees, and very high variability in MEI for coniferous regeneration. MEI on abundance and species richness

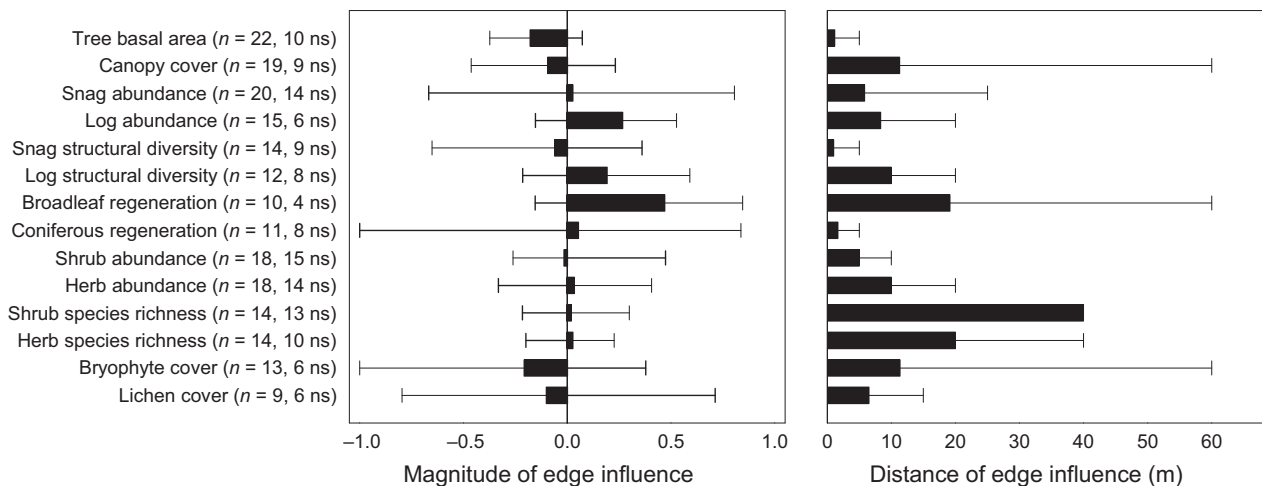


Fig. 3. Magnitude and distance of edge influence (DEI) for each response variable in all studies. Bars and whiskers represent the mean and maximum absolute values across all studies. The total number of studies and the number of studies with non-significant DEI results are indicated by n and ns, respectively. See methods for details on studies and calculations. Results for individual studies are found in Tables S3 and S4.

of shrubs and herbs was much lower than for bryophyte and lichen cover, which both had negative MEI but with a wide range among studies.

Overall, edge influence on forest structure and composition did not extend very deep into the forest; DEI rarely exceeded 20 m (Fig. 3, Table S4 in Supporting Information). DEI was particularly shallow for forest structure variables with averages always 12 m or less. Edge influence extended further for canopy cover than for tree basal area, for regeneration of broadleaf trees as compared to conifers, for shrub and herb richness as compared to abundance and for bryophyte cover than for lichen cover.

In general, natural fire and lake/wetland edges showed similar MEI as cut edges with some notable exceptions (Fig. 4). Lakeshore and wetland edges had positive MEI (greater canopy cover at the edge than in interior forest), whereas MEI was negative at other edge types (lower canopy cover at the edge). Edge influence on snag abundance and diversity was negative at young cut edges and lakeshore edges, but positive or weakly negative at other edge types. Young fire edges differed from other edge types by having negative MEI for conifer regeneration and lichen cover (lower at edge as compared to interior forest). Older cut edges generally had weaker edge influence (lower absolute values of MEI) than younger cut edges for canopy cover, snag diversity, broadleaf regeneration, herb abundance and especially bryophyte cover. Older fire edges had lower MEI than young fire edges for snag abundance and bryophyte cover but higher MEI for herb abundance and richness. The one partial cut site included in our study had the strongest MEI (Table S3).

There were few differences in MEI among different forest types with the notable exception that MEI was often weaker in Fennoscandian than in Canadian forests (Fig. 5). For log abundance and structural diversity, MEI was negative in Fennoscandian forests but positive for Canadian forests; however, there was only one Fennoscandian study with data on logs. Considering only forests in Ontario and Quebec, MEI was stronger for log abundance and diversity in conifer forests (positive edge influence), and for coniferous regeneration and bryophytes in broadleaf forests (negative edge influence).

In general, fire edges showed more extensive edge influence (higher DEI) than cut edges for canopy cover, snag abundance, shrub abundance, and bryophyte and lichen cover (Fig. 6). In contrast, cut edges had greater DEI for log abundance and broadleaf regeneration than did fire edges. We found some evidence of a decrease in DEI with edge age for canopy cover, log diversity and herb species richness at cut edges, and for canopy cover at fire edges. DEI at lake edges, when significant, was similar to or less than other edge types. Overall, the lack of significant edge influence in these forests limited the possibilities for comparing edge influence among edge types.

In the regional comparisons, the highest DEI values were most often found for Alberta broadleaf forests, except for snag, shrub and herb abundance, for which DEI was greater in Ontario/Quebec forests (Fig. 7). DEI was never more than 6 m for conifer forests in Sweden or Finland in our studies.

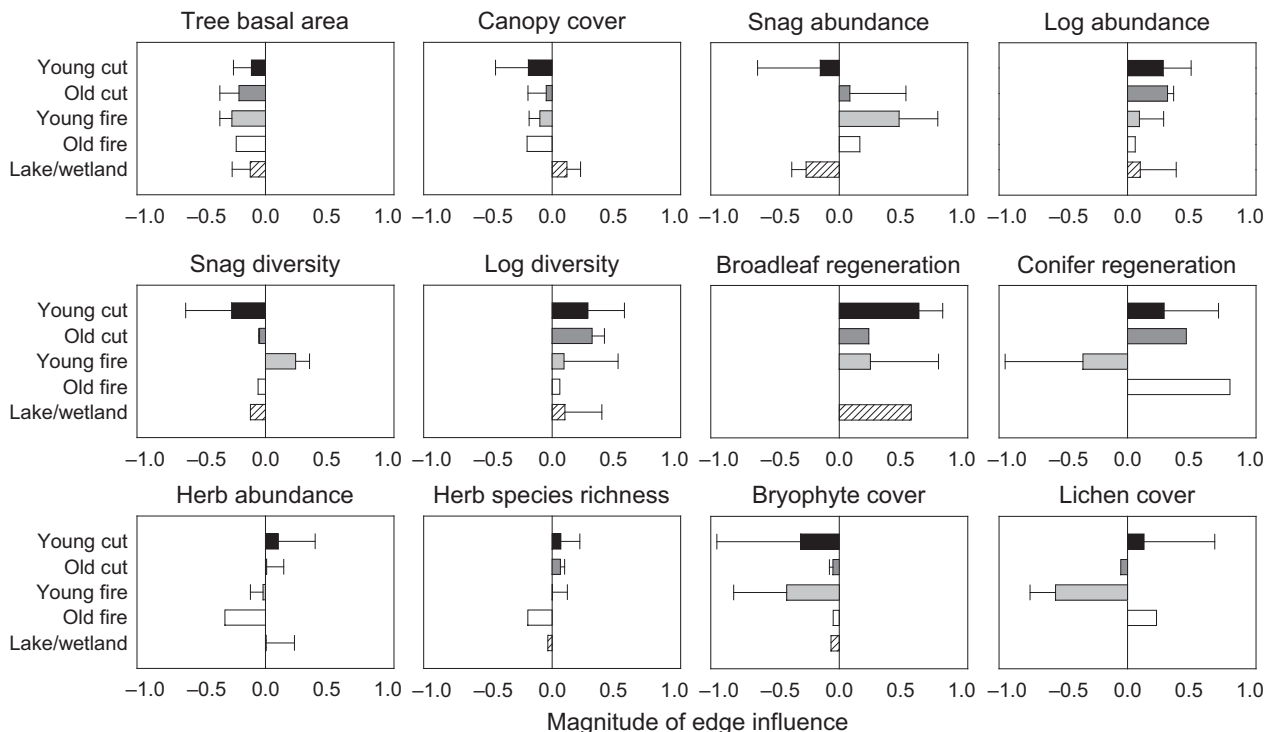


Fig. 4. Magnitude of edge influence (MEI) by edge type for selected response variables. Only variables for which at least one average absolute value of MEI was >0.2 are shown. Bars and whiskers represent the mean and maximum values among all studies. Response/edge type combinations without bars mean that there were no data; MEI was never zero. Results for individual studies are found in Table S3.

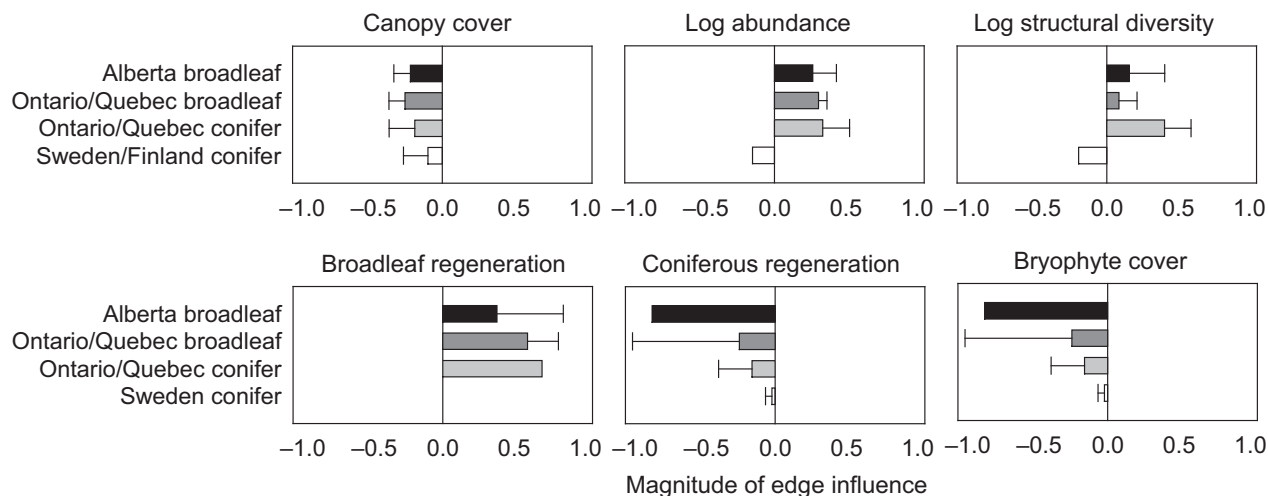


Fig. 5. Magnitude of edge influence (MEI) by forest type and region for selected response variables. Only variables for which at least one average absolute value of MEI > 0.2 are shown. Bars and whiskers represent the mean and maximum values among all studies. Response/forest type combinations without bars mean that there were no data; MEI was never zero. Results for individual studies are found in Table S3.

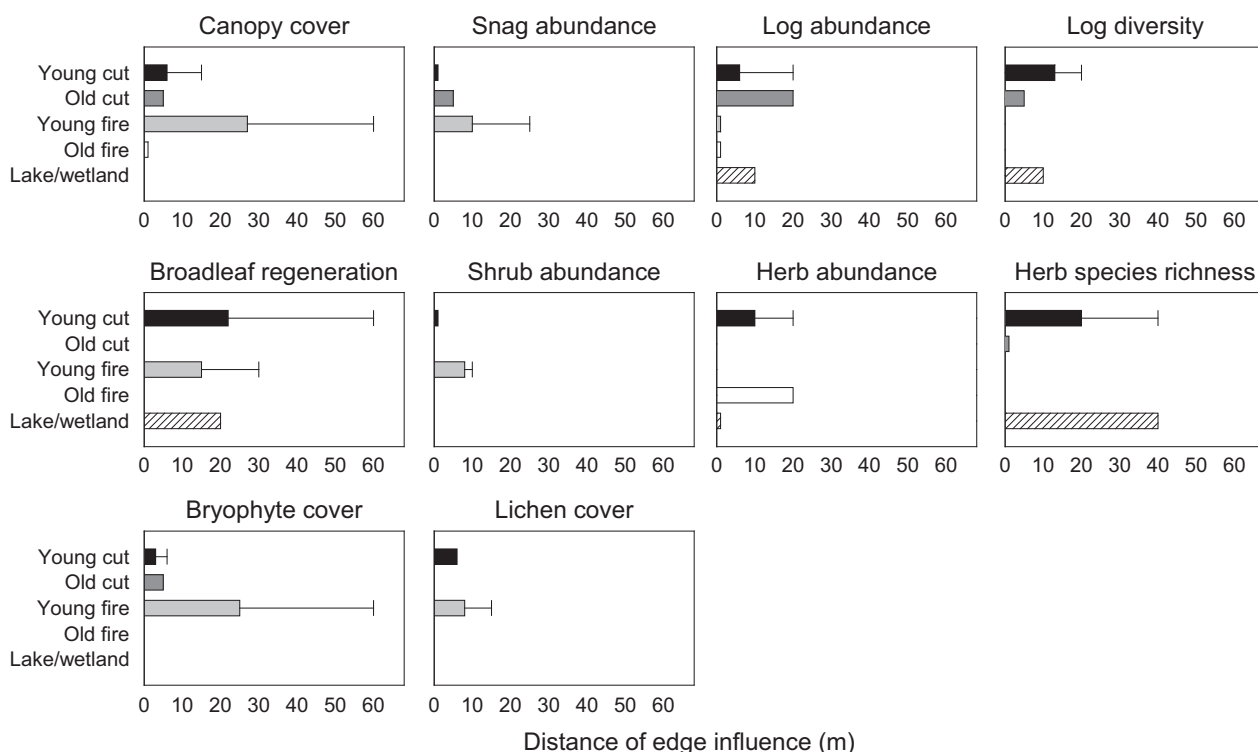


Fig. 6. Distance of edge influence (DEI) by edge type for selected response variables. Only response variables for which DEI was > 5 m and was significant in more than one study are shown. Bars and whiskers represent the mean and maximum values among all studies. Note that a value of 1 was used for DEI = 0 m for clarity. Response/edge type combinations without bars mean that there were no data or DEI was not significant. Results for individual studies are found in Table S4.

Discussion

We present the first comprehensive evidence for the prevalence of edge influence on forest structure and vegetation in disturbance-adapted boreal forests in Canada and Fennoscandia. Edge influence included a reduced tree canopy layer, more downed logs, greater broadleaf regeneration and lower bryophyte cover. Our results show that edge influence on

vegetation in boreal forests is generally weak, not very extensive and decreases with time. In accordance with our hypotheses, we found more extensive edge influence at fire edges compared to cut edges. Surprisingly, fire edges also had more extensive edge influence than lake/wetland edges, which we had not predicted. Our results comparing edge influence among forest types and across regions only partially supported our hypotheses with more extensive edge influence in

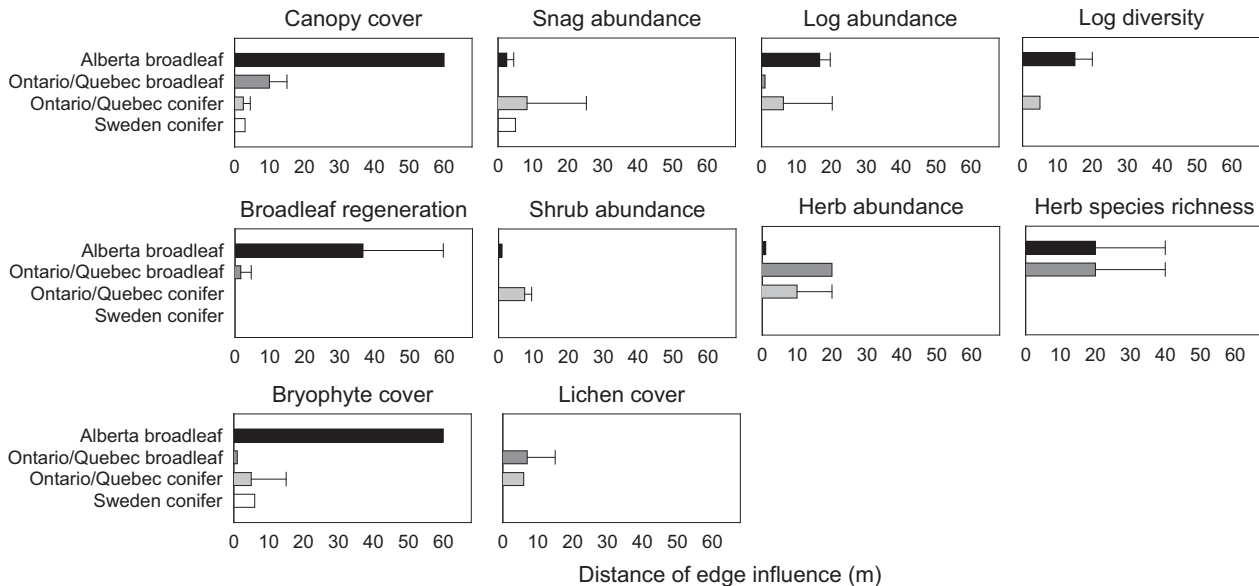


Fig. 7. Distance of edge influence (DEI) by forest type and region for selected response variables. Only response variables for which DEI was > 5 m and was significant in more than one study are shown. DEI could not be determined for the studies in Finland. Bars and whiskers represent the mean and maximum values among all studies. Note that a value of 1 was used for DEI = 0 m for clarity. Response/forest type combinations without bars mean that there were no data or DEI was not significant. Results for individual studies are found in Table S4.

broadleaf forests as we predicted, but weaker edge influence in Fennoscandian forests, which we had not predicted.

To our knowledge, this is the first meta-analysis of edge influence on vegetation and provides evidence that some vegetation response variables show consistent edge influence across much of the boreal forest. We chose variables that were common among studies and that provide a broad picture of edge influence on forest structure and vegetation. Because our studies were conducted independently, we did not control for location or environmental variables. Rather we sought all known studies of vegetation at edges in boreal forests with a similar sampling design of transects with edge and forest interior plots. However, we could not find any such studies in Russia where logging and fire are the main drivers of change in forest cover (Achar *et al.* 2006; Kukavskaya *et al.* 2013). The inclusion of similar studies in Russia would enable a meta-analysis of edge influence that is truly circumboreal. Although we cannot make a quantitative comparison of the effects of edge type, edge age and forest type in boreal forests vs. other forest types, we discuss more general comparisons and offer explanations for the significant trends we observed in boreal forests. A global meta-analysis would be challenging but very informative for edge theory.

EDGE INFLUENCE ON BOREAL FORESTS

Structural damage, as measured by lower tree basal area and canopy cover, and greater log abundance were significant edge responses among all edge and forest types in our studies (with some exceptions for log abundance and diversity, see next section). Such structural changes are common at forest edges due to tree mortality and windthrow (Laurance *et al.*

1998; Burton 2002) and are often documented as being quite severe (e.g. average MEI = 0.4 for canopy cover among various forest types, Harper *et al.* 2005). In boreal forests, however, these edge effects were of moderate strength (MEI approx. 0.2). The structure of these forests, which are relatively short and often have discontinuous canopies, probably results in them being less susceptible to mortality from windthrow. However, severe structural damage has been found in experimentally isolated forest patches at a wind-exposed site in the Scandinavian mountains (Esseen 1994; Jönsson *et al.* 2007), suggesting that edges of mature boreal forests can be highly susceptible to windthrow following severe storms (Valinger & Fridman 2011). Edge influence on snag abundance and diversity was not consistent among studies, likely due to counteracting effects of tree mortality and blowdown of snags. Moreover, in managed forests in Fennoscandia, much of the deadwood, including snags, had been removed by landowners.

Similar to structural damage, edge influence on tree regeneration was also strong and significant among all studies (except for conifer regeneration at younger edges, see next section). There was positive edge influence on regeneration of broadleaf trees, with average MEI similar to what has been found for temperate and tropical forests (MEI = 0.5 for all forests, Harper *et al.* 2005). Many broadleaf boreal forests in Canada, including those in our study, are dominated by *Populus* spp., for which rapid and profuse suckering from a well-developed root system is initiated by the removal of trees in the harvested area (Harper & Macdonald 2002). Edge influence on regeneration of conifers was weaker with lower MEI and DEI than for broadleaf regeneration. Disturbance at the edge exposes mineral soil creating new microsites for seedling recruitment (e.g. for *Picea glauca* (Moench) Voss,

Gärtner, Lieffers & Macdonald 2011), but this effect may not extend far into the forest.

Unlike studies in temperate or tropical forests (Laurance *et al.* 1998; Baker & Dillon 2000; Harper *et al.* 2005), overall edge influence in boreal forests was not significant for understorey vascular plant cover or diversity; our results from individual studies only showed weak edge influence. Boreal forest vascular plant communities are dominated by species adapted to harsh climate and disturbances and therefore may be relatively resistant to different conditions at edges (Harper & Macdonald 2002; Harper *et al.* 2004). Edge influence on the cover of ground lichens was also not significant overall, and this contrasts with the sensitivity of pendulous epiphytic lichens in the forest canopy to negative edge influence in boreal forests (Kruys & Jonsson 1997; Dettki *et al.* 1998; Esseen & Renhorn 1998; Rheault, Drapeau & Bergeron 2003). In contrast, our results suggest that ground layer bryophytes may be particularly sensitive to edge effects, which is likely due to desiccation associated with greater solar radiation, higher temperatures, lower relative humidity and wind (Stewart & Mallik 2006). Negative edge influence on bryophyte cover was significant in all studies and values of MEI and DEI were relatively high. This conforms to what has been found in other boreal forest studies (Fenton, Frego & Sims 2003; Moen & Jonsson 2003; Hylander 2005).

In addition to displaying generally weaker edge influence, edge effects did not extend very far in boreal forests. Our estimates for DEI (generally up to 20 m) are much lower than those reported for other forest types (Harper *et al.* 2005) including sub-boreal (40–120 m, Burton 2002), temperate (16–137 m, Chen, Franklin & Spies 1992) and tropical (85–335 m, Laurance *et al.* 1998). Low solar angles at high latitudes should result in light penetration farther into interior forest, resulting in greater DEI for microclimate changes at edges (Burton 2002; Harper & Macdonald 2002). However, DEI was lowest for forests in our most northern studies in Sweden. The limited extent of edge influence is more likely a function of less lateral penetration of light beyond edges under the short canopy in boreal forests, as compared to taller temperate and tropical forests (Burton 2002; Harper & Macdonald 2002). Further, patch contrast between the shorter, heterogeneous canopy of boreal forests and adjacent openings may be relatively milder than in other forest regions and this would result in shorter DEI (Harper *et al.* 2005). Weak and narrow edge influence in boreal forests may also be attributed to inherent heterogeneity of the interior forest, against which the significance of DEI is assessed, as well as to the high proportion of boreal plant species that are adapted to frequent natural disturbance (Burton 2002; Harper & Macdonald 2002).

Differences in DEI estimates among studies can also be due strictly to the method of analysis (Harper & Macdonald 2011). It is interesting to note that analyses used to calculate most of the temperate and tropical DEI estimates listed above (e.g. curve-fitting methods used by Chen, Franklin & Spies 1992 and Laurance *et al.* 1998) were found to be less conservative than our method (Harper & Macdonald 2011).

Although it remains unclear to what extent differences in DEI estimates are due to region rather than the method of analysis, the large differences in DEI between biomes suggest that edge influence does not extend as far in boreal forests as in other regions. Nonetheless, a larger meta-analysis among studies in different biomes could be revealing.

EFFECT OF EDGE TYPE, EDGE AGE AND FOREST TYPE

Our analyses have demonstrated that in boreal forests, natural edges were often more extensive with greater DEI than anthropogenically created edges, which supports previous findings for lakeshore forest edges (Harper & Macdonald 2001), fire edges (Harper *et al.* 2004) and wetland edges (Moen & Jonsson 2003; Esseen 2006). A prominent difference among edge types was greater abundance and diversity of snags at fire edges compared to interior forest, but the opposite response at cut edges. The obvious explanation is the removal of live and dead stems during harvesting would reduce abundance, whereas partial burning at fire edges would create a higher abundance and diversity of snags (Harper *et al.* 2004; Larrivé, Drapeau & Fahrig 2008). Diversity of deadwood is important for biodiversity in boreal forests (Ohlson *et al.* 1997; Similä, Kouki & Martikainen 2003; Stokland, Sittonen & Jonsson 2012) as organisms differ in their requirements with respect to species, decay stages or sizes of deadwood (Jonsell, Weslien & Ehnstrom 1998; Mills & Macdonald 2004; Saint-Germain, Drapeau & Buddle 2007; Drapeau *et al.* 2009). Edge influence on snag and log abundance and diversity at lake/wetland edges is more difficult to compare to other edge types due to low sample sizes and combining lake and wetland edges.

We detected only minor differences in edge influence with age, but our results do suggest that edge influence weakens with time. We found weaker edge influence at older cut edges and less extensive edge influence at older fire edges, as compared to younger ones. This contrasts with observations of increasing DEI with age at cut edges in a boreal forest (Dupuch & Fortin 2013) and extensive edge degradation (Gascon, Williamson & da Fonseca 2000; Laurance *et al.* 2004) or edge sealing (Camargo & Kapos 1995; Didham & Lawton 1999) at anthropogenic edges in tropical forests. Although greater forest productivity in tropical regions should lead to much faster responses to edge creation and therefore recovery of edge forests, tropical forests are not adapted to frequent disturbances that are prevalent in boreal forests. However, tropical forests also have abundant vines and lianas that grow rapidly to seal the edge (Laurance *et al.* 2001). Rapid regeneration in the adjacent disturbed area in boreal forests, particularly of broadleaf trees, may act to rapidly weaken edge influence such that edge sealing does not occur. A larger sample of edges of different ages in boreal forests would enable further exploration of changes in edge influence over time, which may be nonlinear. Edge influence may also vary with age of the forest, which we did not consider; it is possible that edge influence on old-growth forests is stronger and more extensive than in younger forests.

In general, edge influence was weakest in Fennoscandian coniferous forests and most extensive in Canadian broadleaf forests. Weaker MEI in Fennoscandia was surprising as *P. abies* forests are often relatively tall and more productive than North American boreal forests; they were thus expected to be more sensitive to effects of increased wind. Also, northern European forests are controlled mainly by gap dynamics and surface fires rather than stand-replacing fires or insect outbreaks as in North America (Kneeshaw, Bergeron & Kuuluvainen 2011); we hypothesized this would make them more sensitive to edge influence. However, extensive management of Fennoscandian forests including the removal of deadwood likely affects edge influence in these forests, particularly positive edge influence on logs and snags.

We found support for our hypothesis of stronger and more extensive edge influence in broadleaf compared to conifer forests for some response variables. Greater DEI in broadleaf forests might be a function of the extensive edge influence on regeneration of *Populus* spp., as was found by Harper & Macdonald (2002). Greater herb richness at edges in broadleaf forests may be due to more opportunities for species establishment on ground that is not covered by moss. However, we found greater log diversity at edges in conifer forests, but there was no such edge influence in broadleaf forests; tree size distribution or the processes of tree mortality and decomposition appear to differ between the edge and interior in conifer forests but not in broadleaf forests.

Conclusions and implications

Edges arising from forest harvesting do not appear to have strong, extensive or persistent effects on forest structure and vegetation in boreal forest ecosystems in Canada and Fennoscandia. We hypothesize that edge influence at cut edges is not as extensive or dramatic in boreal forests, as compared to temperate and tropical forests, because: 1) boreal forest species have evolved in landscapes with abundant natural edges, and 2) there is greater inherent variability in forest structure within these forests (Harper & Macdonald 2002; Harper *et al.* 2004). Although boreal forests appear to be relatively resistant to created edge effects on forest structure and composition, edge influence is still of concern in large areas of the boreal forest where anthropogenic edges are abundant. Cut edges can be very detrimental to biodiversity in boreal forests, especially in areas such as Sweden and Finland that are strongly fragmented by clear-cuts and forest roads (Löfman & Kouki 2001; Jansson, Nilsson & Esseen 2011; Anonymous 2013). The opposing edge influence on deadwood between fire (positive edge influence) and cut (negative edge influence) edges is of particular concern.

Consideration of the change in quality, rather than simply the quantity, of natural vs. created edges is also necessary for conservation and forest management. Changing the dominant disturbance regime from wildfire to clear-cut harvesting reduces edge complexity while increasing edge abundance in the boreal forest (Jansson, Nilsson & Esseen 2011). This is particularly true in large parts of the boreal forest where

harvest rotations are significantly shorter than fire cycles (Kuuluvainen 2009; Bergeron & Fenton 2012). In Alberta, for example, extensive forest fragmentation has led to the replacement of natural fire edges by anthropogenic edges such that much of the forest is in close proximity to harvested or agricultural edges (Schneider *et al.* 2003; Komers & Stanojevic 2013).

Our study focused on selected variables describing general vegetation structure, composition and diversity. Edge influence might be different for other organisms ranging from being a lot more extensive for predator–prey interactions between large carnivores and herbivores (e.g. Houle *et al.* 2010) to not more elevated than in the interior forest for nest predation risk of boreal birds breeding at edges (Andrén 1995; Schmiegelow & Mönkkönen 2002). However, woodpeckers may be less prone to forage on snags at < 40 m near an edge even though foraging trees may be more available at edges (Gagné, Imbeau & Drapeau 2007). Some of these ecosystem responses may have long-term secondary edge influence on vegetation. In Fennoscandia, the species that are most at risk are saproxylic beetles, fungi and epiphytic lichens (Tikkanen *et al.* 2006), none of which were directly assessed in our study. Other studies have found more extensive edge influence for liverworts on deadwood (50 m, Moen & Jonsson 2003), bryophytes (Hylander 2005; Stewart & Mallik 2006) and pendulous lichens (Esseen & Renhorn 1998). We caution that these and other responses that we did not measure (e.g. wildlife usage and predation) may show stronger, more extensive or long-lived edge influence. Consequently, edge influence remains a key issue in the conservation of boreal forests.

Natural disturbance emulation silviculture advocates the development of forest harvesting practices that emulate fire (McRae *et al.* 2001). Although it may be thought that making cut edges wider using partial cutting can mimic the greater width of fire edges, this may not be true – we found less extensive but stronger edge influence at partial cut edges at our single study of this edge type. More studies are needed, but it is doubtful that cut edges will ever be able to emulate structural features such as the high abundance of snags found at fire edges. Because forest management is unlikely to completely emulate fire edges, we agree with others that recently burned habitat should be conserved and salvage logging should not be implemented extensively in such habitat (Kouki *et al.* 2001; Lindenmayer *et al.* 2004; Nappi, Drapeau & Savard 2004), particularly at edges of fires.

Our findings are important in that we highlight responses that do not depend on edge or forest type but could be considered universal responses to edge influence, at least in boreal forests. Notably, universal responses to edges include lower tree basal area, canopy cover and bryophyte cover, and greater abundance of logs and regeneration of broadleaved trees. If validated by a similar meta-analysis in temperate and tropical forests or studies specifically designed to compare edge influence among regions, our findings provide an empirical basis for further development of edge theory.

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Data accessibility

Readers can access data used in this study in the Dryad Digital Repository (Harper *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Details on data collected for the response variables for all edge studies.

Table S2. Standardized effect size for different response variables for each study.

Table S3. Magnitude of edge influence for different response variables for each study.

Table S4. Distance of edge influence for different response variables for each study.

Table S5. Results of meta-analysis comparisons among different edge types, edge ages, forest types, and regions for different response variables.