Word count: 5993

Vegetation patterns across edges of bogs and lakes in spruce and hemlock forests of southwestern Nova Scotia

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Abstract

Although forest edges surrounding lakes and wetlands are common in many heterogeneous landscapes, there are few studies on patterns of vegetation across these natural landscape boundaries. We investigated forest structure, understorey composition and bryophytes at bog and lakeshore edges in spruce and old growth hemlock forests. Our objectives were to estimate edge width for vegetation across lake and bog edges, and to examine patterns across the bog forest edge. We sampled canopy cover, trees, deadwood, structural diversity, species diversity, saplings and understorey vegetation along transects across four bog and four lakeshore edges in spruce forests and five lakeshore edges in hemlock forests. We used randomization tests to determine the distance of edge and forest influence into adjacent interior forest and bog, respectively. Patterns were assessed using wavelet analysis to determine locations of abrupt changes. Edge influence extended only 5 m into the forest for most variables with notable results of fewer bryophytes, more shrubs and greater tree and shrub diversity at lakeshore edges in hemlock forests. Forest influence at bog edges resulted in a wider approx. 40 m transition zone within the bog in which tree density, graminoid cover, *Sphagnum* spp. cover and herb diversity were greater than both adjacent bog and forest. Varying edge width and responses to edge influence between forest types emphasizes the need for site specific studies. Lakeshore and bog forest edges harbour greater diversity and unique vegetation structure on heterogeneous landscapes in Nova Scotia, particularly in bog margins, and are key areas to consider for conservation.

Key words Bog-forest gradient, Edge influence, Forest structure, Lakeshore edges, Spatial pattern, Wavelet analysis

Acknowledgements In addition to our funding sources, we thank Christine Angelids, Anna Naylor and Ana Perez for their assistance in the field and Anne Mills for her help with bryophyte identification. We also thank Alain Beliveau, Parks Canada and the Mersey Tobeatic Research Institute for logistical support, and the reviewers for helpful feedback on an earlier version of our manuscript

Introduction

Natural forest edges are common in heterogeneous landscapes and may harbour relatively high species diversity; however, studies of vegetation at natural edges are still relatively scarce (Franklin et al. 2021). Natural inherent edges are gradual transitions with generally lower tree abundance but higher cover of shrubs, herbs and nonvascular plants compared to interior forest (Franklin et al. 2021). These transitions often have greater plant species diversity compared to adjoining ecosystems (Harris 1988; Naiman et al. 1993; Luczaj and Sadowska 1997; Erdos et al. 2013). The variable structure of natural edges creates more complex transition zones (Hanson and Stuart 2005; Harper et al. 2014), often with structural features that can provide important habitat for conservation (e.g., Franklin et al. 2015; Barbé et al. 2017; Dazé Querry and Harper 2017).

Many studies of vegetation at natural edges investigated the edges of water bodies or wetlands; a global synthesis by Franklin et al. (2021) found 35 studies, 15 of which were conducted in temperate ecosystems. Some of their results include greater plant species diversity (Kupfer and Malanson 1993; Coroi et al. 2004; Dieterich et al. 2006), higher tree or sapling density (Kupfer and Malanson 1993; Harper and Macdonald 2001; Komomen 2009), more short trees (Langlois et al. 2015), greater shrub cover (Salek et al. 2013; Paradis et al. 2015) and greater bryophyte cover (Paradis et al. 2015) at edges compared to interior forest. Bog margins have complex vegetation structure with dense trees and higher productivity (Howie and Meerveld 2011; Paradis et al. 2015; Langlois et al. 2015). There is still a need for site-specific studies on vegetation at natural edges to understand patterns of forest structure, composition and diversity across the landscape; even studies on the bog margin rarely extend into the adjacent forest (Howie and Meerdveld 2011).

We investigated forest structure, understorey composition and bryophytes across bog edges in spruce forests and lakeshore edges in spruce and old-growth hemlock forests. We had three specific objectives: 1) to determine the width of bog and lakeshore edges, 2) to examine patterns across the bog forest transition and 3) to compare results among different response variables. We assessed distance of edge influence (DEI) for bog and lakeshore edges as the range of distances over which average values were significantly different from interior forest, and distance of forest influence (DFI, terminology from Baker et al. 2013) for bog edges as the range of distances over which average values were significantly different from the bog. We tested the hypothesis that these natural forest edges are hotspots for biodiversity by determining if species or structural diversity was greater compared to the adjacent forest.

Methods

Site description

We conducted our study in southwest Nova Scotia, Canada, with sites located in Kejimkujik National Park and surrounding areas (Fig. 1). This part of Nova Scotia has an average annual rainfall of 1155 mm, and temperatures averaging -6.1°C in January and 18.4°C in July (Environment Canada 2010). Temperate (Acadian) forests are dominated by *Picea, Abies, Betula* and *Acer*, whereas old growth hemlock forests are dominated by *Tsuga canadensis*. Dominant species in the bogs include bryophytes *Sphagnum* spp. and *Pleurozium schrebrei*, and shrubs *Rhododendron canadense* and *Kalmia angustifolia*.

Data collection

Data were collected along transects set up perpendicular to four ombrotrophic bog edges and four lakeshore edges in *Picea* (spruce) dominated forests June to August 2010, and five lakeshore edges in old-growth hemlock forests May to June 2011. Transects extended from the edge (0 m, defined as the limit of continuous forest canopy) up to 180 m into the forest for lakeshore transects and from 180 m into the bog to 180 m into the forest for bog transects. Thus the sampling design was unbalanced between bog and lakeshore transects since there was no vegetation on the lake side of the forest edge.

We sampled forest structure, bryophytes and soil characteristics at 0, 5, 15, 25, 40, 60, 100, 140 and 180 m from the edge into the forest and bog; for hemlock lakeshore transects a plot was added at 0 m and plots were located at 150 and 200 m instead of 140 and 180 m (Fig. 2). On one transect, 180 m was too close to another edge so we established another sampling point 40 m away also at 140 m. We recorded the species, dbh (diameter at breast height, 1.4 m) and canopy position (i.e., dominant or above the canopy, codominant or at canopy height, intermediate or just below the canopy receiving light from above, suppressed or well below the canopy, Côté 2000) of every live tree with dbh > 5 cm within a 5 × 20 m plot at each distance, length parallel to the edge. Canopy cover was estimated in the centre of the plot as the average of four measurements using a convex densitometer (two measurements facing either end of the transect). We tallied the number of logs intersecting the major axis of the plot (>5 cm diameter at the intersection point).

We set up contiguous 1 × 1 m quadrats from -62.5 to +62.5 m across the bog edges, from -2.5 to +62.5 m across the lakeshore edges, and across 5 m spans along the transect at the interior sampling points (100, 140/150, 180/200 m). Within each quadrat, we estimated the cover of shrubs, herbs, bryophytes, graminoids (except in hemlock forest), lichens and litter (only in hemlock forest), and the cover of individual vascular plant and common bryophyte species. Shrubs were woody non-tree species that can grow more than 50 cm tall. Herbs included short woody species that do not grow more than 50 cm tall. Cover was estimated visually to the nearest 10%, except to the nearest 1% for cover less than 5%.

Data analysis

Forest structure response variables included canopy cover; tree basal area; tree, snag and log density; tree species richness and diversity; and horizontal and vertical tree structural richness and diversity. Tree basal area was calculated from the dbh of all trees within each plot. Species diversity was calculated using the Shannon diversity index. Horizontal richness was the number of dbh size classes (10 cm increments) and vertical richness was the number of canopy positions within a plot; we used the Shannon index to calculate horizontal and vertical diversity using these categories (terminology follows LaRue et al. 2023). Understorey response variables included the cover of shrubs, herbs, bryophytes, graminoids, lichens and litter; sapling density; shrub, herb and bryophyte richness and diversity (calculated using the Shannon index); and cover of individual species with frequency greater than 10%. Because we did not identify many bryophytes to species, bryophyte diversity is more accurately the diversity of bryophyte genera.

We estimated the magniture of edge influence (MEI) and DEI for each response variable using the randomization test of edge influence (RTEI) Add-In in Microsoft Excel (Harper and Macdonald 2011). MEI measures how much the variable differs at a given distance compared to the interior ecosystem: MEI = $(x_d - x_i)/(x_d + x_i)$ where x_d = average of variable x at distance d and x_i = average in the interior forest (Harper et al. 2005). We used three sampling points along each transect at 100, 140/150 and 180/200 m for interior forest. For the magnitude of forest influence (MFI, terminology from Baker et al. 2013), we compared plots along the bog transect to interior bog (100, 140, 180 m into the bog). For understorey variables, values were averaged for each 5 m segment of the transect (e.g., -2.5 to 2.5 m for 0 m).

DEI measures how far from the edge a response variable significantly differs from interior forest. We quantified DEI using RTEI with blocking, which tests the significance of the response variable for each distance using randomization tests (see Harper and Macondald 2011, Harper et al. this issue for details). DEI was estimated as the set of distances with a significant response for structure variables and as the set of two or more consecutive distances (or segments separated by one distance) for understorey variables. We also used RTEI analysis to estimate the DFI by comparing values at different distances to interior bog.

We conducted wavelet analysis in PASSAGE 2.0 (Rosenberg and Anderson 2011) to assess patterns across the bog forest gradient and to determine locations of abrupt change (see Harper et al. this issue for more details). We analyzed understorey response variables (except individual vascular plant species) in the contiguous 1 x 1 m plots within 62.5 m on either side of the bog-forest edge. We used the Haar wavelet template and assessed wavelet position variance (10% maximum scale) with randomization tests (999 permutations, 95% confidence interval) to identify significant abrupt transitions. We estimated the distance of edge change (DEC) by considering significant peaks of at least two consecutive distances on at least two transects or distances that were offset by 1 m.

Results

Lakeshore forest edges

Edge influence on vegetation structure at lakeshore forest edges in Nova Scotia was not very apparent or extensive. Neither canopy cover nor basal area had any discernible trend along the edge to interior forest gradient at lakeshore edges in spruce and hemlock forest (Fig 3). Average canopy cover remained above 70% and basal area was consistent with an average of about 10 m^2 / ha in spruce forests but much greater and more variable in hemlock forests (35-65 m^2 / ha). Tree and snag density in both forest types, and log density in spruce forests, was higher near lakeshore edges (up to 20 and 6 / 100 m^2 within 25 m of the edge, respectively, for tree and snag density), but not significantly. There were significantly fewer logs at lakeshore edges of hemlock forests (0-5 m) but more logs 20 to 40 m from the edge compared to interior forest. The richness of tree species and trees of different sizes did not vary noticeably along the transects except for significantly greater species richness of about three species per plot at lakeshore edges of hemlock forests compared to two in interior forest; horizontal richness was about twice as high in spruce compared to hemlock forests.

The lack of edge influence on vegetation structure at lakeshore edges is reflected in the generally low MEI values and the DEI results (Table 1). In spruce forests, edge influence was only significant at single distances with greater canopy cover at 60 m and tree species richness at 15 m. In hemlock forests, edge influence extended up to 25 or 40 m for greater canopy cover, tree density, tree species richness and log density, although DEI did not always start at 0 m and edge influence on log density was negative 0 to 5 m and positive 25 to 40 m.

More understorey variables experienced edge influence at lakeshore edges such as lower cover of bryophytes, greater cover of shrubs and more litter (hemlock forest only) with DEI up to 60, 20 and 50 m, respectively (Table 1). There was no significant edge influence on graminoid, herb or lichen cover. Greater sapling density extended 35 to 40 m from spruce lakeshore edges compared to interior forest. Edge influence was positive for shrub richness and diversity at hemlock edges, positive for herb diversity at spruce edges but negative for bryophyte richness and diversity at hemlock edges; DEI estimates were variable but usually 0 to 5 m for hemlock edges.

Three and four individual species were affected by edge influence at spruce and hemlock edges, respectively, out of 25 species. Only *Pleurozium schreberi* had lower cover at the edge compared to interior in both forest types with a DEI of at least 10 m.

Bog forest edges

The structure of bog-forest edges was generally similar to interior forest but often different from the bog (Fig. 4). Canopy cover and tree basal area increased gradually from very low values in the bog to the edge of the forest, after which values remained consistent at about 70-80% cover and 20-30 m^2 per ha in the forest, respectively. Canopy cover from -20 to -40 m in the bog was significantly different with intermediate values between both interior ecosystems (hatched area in Fig. 4a). Tree basal area at the edge and within the forest was significantly greater than in interior bog. On the bog side of the edge, there was a zone of significantly greater tree density (approx. 25 per 100 m^2) compared to both forest and bog (10-15 per 100 m^2). Snag density increased from bog to forest with significantly greater amounts 40-60 m frrom the edge compared to the bog. Log density was significantly different throughout most of the bog compared to forest and vice versa with a sharp increase from -15 to -5 m on the bog side of the edge. The richness of tree species and trees of different sizes increased gradually from the bog to forest but trends were not significant except for greater horizontal richness in the forest and at the edge compared to interior bog.

Although there was significant DEI on forest structure at bog edges, distances were almost entirely constrained to the bog side of the edge, meaning that values at the edge were not significantly different from interior forest (Table 2). Exceptions included some measures of diversity that were significantly greater (tree species diversity) or lower (horizontal richness, vertical diversity) at single distances. Similar to vegetation structure, the DEI for plant groups never extended beyond 0 m. Even in the bog, the cover of bryophytes and herbs was not significantly different from interior forest, but there was greater cover of graminoids and shrubs and lower cover of lichens far into the bog compared to the adjacent forest. There was no significant edge influence on bryophyte richness or diversity. Nine out of 23 individual species were affected by edge influence with DEI rarely extending beyond the edge.

In contrast, forest influence usually extended throughout much of the bog to forest gradient, with average values at most distances near the edge significantly different from interior bog for canopy cover, tree basal area, log density and horizontal richness. Forest influence affected all plant groups; bryophytes and herbs had greater cover in the forest compared to the bog, and lichens and shrubs had lower cover. There was no significant forest influence on bryophyte richness or diversity. Fifteen out of 23 individual species were affected by forest influence with DFI usually extending well into the bog.

Positive MEI and MFI indicate a peak in a response variable at the bog-forest transition, as observed for tree density (described above, Fig. 4c) and tree species diversity. The same pattern occurred for graminoids, herb diversity and *Sphagnum* spp. cover, which were greater than both adjacent ecosystems for -30 to 0 m into the bog, 0 to 5 m at the forest side of the edge and -60 to -20 m in the bog, respectively. Sapling density also exhibited both edge and forest influence, but negative MEI and positive MFI indicates a gradual transition from low cover in the bog to high cover in the forest; the zones -15 to -5 m and 10 to 20 m were significantly different from both adjacent ecosystems with intermediate values. Shrub richness and diversity showed the opposite trend decreasing from the bog to the forest with narrow DEI and DFI.

Fine-scale patterns of understorey vegetation along the bog to forest gradient varied substantially for different response variables and rarely coincided (Fig. 5). Shrub and lichen cover decreased gradually from interior bog to the edge and remained low throughout the forest. Abundance of graminoids and herbs was generally low but with peaks on the bog and forest sides of the edge, respectively. Bryophytes had the opposite trend with high cover except near the forest edge. The DEC results generally matched the locations of peaks in abundance or sharp changes with locations in the forest for herbs and bryophytes, near the edge for graminoids and in the bog for lichens and shrubs. Sapling density had a slight peak on the bog side of the edge but increased substantially about 40 m into the forest with a significant DEC at about 45 m. Species richness of shrubs, herbs and bryophytes followed similar trends as their cover with DEC on the forest side of the edge for herbs and at the edge for brypophytes. Of the four common bryophyte species, *Dicranum* spp. and *Hylocomnium splendens* had low cover throughout but slightly higher abundance in the forest, whereas *Sphagnum* spp. and *Pleurozium schreberi* had substantially high cover in the bog and forest, respectively. DEC results indicate abrupt changes near the edge for *Sphagnum* spp. and into the forest for *Hylocomnium splendens* and *Pleurozium schreberi*.

Summary of trends across lakeshore and bog edges

We summarized trends in edge influence by comparing the proportion of variables with significant DEI, DFI and DEC (Fig. 6). More variables exhibited edge influence at lakeshore edges of hemlock forests compared to spruce forests. Overall, there was a DEI of 5 m for a third of understorey variables in hemlock forests; otherwise DEI extended up to 60 m for a few variables. At bog edges DEI extended to 5 m for less than ten percent of variables. In contrast, DFI extended to 40 m into the bog for about a quarter of variables. At the edge, about twice as many variables were significantly different from bog (DFI) than from forest (DEI); the proportion of variables equally different from both interior ecosystems occurred at about -20 m into the bog. DEC occurred throughout the bog to forest gradient for only a few variables.

Discussion

Lakeshore forest edges

Although vegetation at lakeshore forest edges was not very distinct from the surrounding forest there were some notable differences. Fewer logs at hemlock lakeshore edges was probably due to logs being washed away immediately at the edge, but our finding of more logs further from the edge was similar to greater log density found within 20 m of lakeshore edges in boreal forest in Alberta (Harper and Macdonald 2001). Greater tree species richness at hemlock edges was likely due to additional tree species adapted to greater light compared to closed canopy forests away from the edge. Structurally, lakeshore edges of spruce forests were virtually indistinguishable from interior forest. Edge influence was more substantial on the understorey. Lakeshore edges had more shrubs (particularly *Gaylussacia* spp.) than interior forest, likely due to increased exposure to light; increased shrub cover might have led to a reduction in the cover of bryophytes (particularly *Pleurozium schreberi*).

The very short DEI for lakeshore edges (approx. 5 m) was similar to 8 m wide riparian edges in European deciduous forests (Salek et al. 2013) but narrower than 40 m wide lakeshore edges in boreal forest in Alberta (Harper and Macdondald 2001). Our results do not fit the general pattern of more extensive widths of natural edges compared to anthropogenic edges reported by

Franklin et al. (2021). We are uncertain why DEI was not as extensive in our forests; perhaps conifer trees are less affected by wind disturbance along the lakeshore. However, it is clear that site-specific studies are needed even for the same edge type.

Bog forest edges

The forest side of the bog edge was similar to lakeshore edges with a DEI of 0 m into the forest except for a greater abundance of graminoids, saplings and a few species such as *Sphagnum* spp. Most changes in vegetation occurred on the bog side of the edge such as the decrease in canopy cover, tree basal area, snags, logs and structural diversity from the forest to the bog, and the corresponding increase in shrubs and lichens. Our results indicate a much wider transition zone on the bog side of the forest edge with DFI extending 40 m into the bog for most variables. Franklin and Harper (2016) found similar results of a wider transition zone on the non-forested side of natural created forest edges from insect disturbance compared to the forest side. However, our estimate of 40 m is less than 12 m found for the edges of boreal peatlands in Alberta using a different method based on the dissimilarity in plant species composition (Mayner et al. 2018). Our result fits into the general finding of wider, more gradual transition zones at natural edges (Franklin et al. 2021), but only if the transitions include forest influence on the non-forested side of the edge.

Simply reporting the width of the bog forest transition zone conceals more complex patterns of vegetation within the bog. We found zonation evidenced by peaks in graminoid cover, tree density and *Sphagnum* cover into the bog at 0 to -30 m, -15 to -40 m and -20 to -60 m, respectively. These patterns characterize bog margins, which consist of a lagg zone and rand between bog and forest (Howie and Meerveld 2011; Paradis et al. 2015). Trees and shrubs often grow alongside sedges in the rand due to the drop in water table depth (Howie and Meerveld 2011) and can be accompanied by abundant herbs and *Sphagnum* (Paradis et al. 2015). Langlois et al. (2015) refers to the band of black spruce trees as the rand-forest; however, in their study it was accompanied by a lower abundance of *Sphagnum*. In our study, the band of greater tree density overlapped with both greater *Sphagnum* and graminoid (including sedges) cover, suggesting a zonation of both rand and lagg. Paradis et al. (2015) describes lagg plant communities as 'peculiar' because their species are more abundant than in both adjacent communities. We consider the structure and composition of these bog margins as an example of natural forest edges providing unique vegetation structure on heterogeneous landscapes.

We found evidence for greater diversity at bog forest edges only for herb and tree species on the forest and bog side of the edge, respectively. This is likely due to the overlap in tree and herb species that are adapted to growing in bog or forest, a common phenomenon at natural edges or ecotones (Kupfer and Malanson 1993; Naiman et al. 1993; Luczaj and Sadowska 1997; Coroi et al. 2004; Dieterich et al. 2006; Franklin et al. 2021). The lack of a trend in vertical diversity seems surprising given the short stature of trees in bogs; this is likely due to our assessment of relative canopy height, which, in hindsight, should have used the canopy height of the forest side rather than within the bog for comparison. Shrub diversity was much higher in the bog as there were more shrub species in the open non-forested area. Bryophyte diversity remained constant along the gradient, perhaps showing that bryophyte genera are adapted to specific conditions such as soil moisture and do not overlap in their distributions at a fine scale. An example of this is how the decrease in *Sphagnum* coincided with the increase in *Pleurozium*. However, as we did not identify most of the bryophytes to species (especially *Sphagnum*), species diversity may show a different pattern.

Our method of quantifying locations of abrupt changes in response variables across the bog to forest gradient (DEC) did not reveal consistent results. DEC results were scattered, suggesting that abrupt changes can occur anywhere and are not limited to or even focused on the visible forest edge. Harper et al. (2021) found similar inconsistent results for forested wetland – upland forest edges. We suspect that changes occur more gradually, as seen for the decrease in shrub diversity from bog to forest. DEC is not a useful metric as the transition from bog to forest is gradual rather than abrupt. Even locations of DEC near the edge are not intuitive; e.g., the DEC for herb diversity occurred on either side of a small dip within an overall peak at approx. 15 m into the forest. Langlois et al. (2017) also found that gradual patterns of vegetation height can make it difficult to interpret the bog forest boundary. However, Mayner et al. (2018) did find abrupt changes or dissimilarities in plant species composition that coincided with visible boundaries of peatlands, suggesting that species composition may have more discernible patterns at bog edges than measures of structure or diversity. Others have found that abrupt transitions for vegetation structure occur throughout the gradient at locations other than edges, sometimes with no discernible concurrence with the location of the edge (Franklin and Harper 2016; Harper et al. 2018).

Conclusions and significance

Although lakeshore forest edges in Nova Scotia were only 5 m wide, bog forest edges were 40 m wide due to vegetation zonation extending well into the bog. A key conclusion from our study is that forest influence extended further than edge influence at bog forest edges. At lakeshore edges, bryophytes (especially *Pleurozium schreberi*) were negatively affected by edge influence whereas shrubs were more abundant compared to interior forest. At bog edges there were bands of high abundance of *Sphagnum* spp., graminoids and tree density. As we hypothesized, these natural forest edges were locations of greater diversity for tree species and shrubs at lakeshore edges in hemlock forests, and for tree species and herbs on the bog and forest sides of the edge, respectively.

On the landscape level, natural lakeshore and bog forest edges harbour greater diversity and structural habitat features that differ from adjacent ecosystems, particularly within the bog near the forest edges, and therefore are key areas to consider for conservation (see also Franklin et al. 2015; Dazé Querry and Harper 2017). In forested wetlands, shrubs provide important structurally complex habitat for bird species (Brazner and MacKinnon 2020). Paradis et al. (2015) and Langlois et al. (2015) emphasize that conservation of peatland complexes must include the bog margin, which provides important habitat for biodiversity. Although it is clear that natural forest edges provide unique habitat on the landscape, varying edge width and responses to edge influence between different edge and forest types emphasize the need for site specific studies to understand implications of edge influence for conservation.

Author contributions W.B. and K.O. collected the data. K.A.H. supervised the data collection, analyzed the data and wrote the manuscript with feedback from other authors.

Funding Funding was provided by Natural Science and Engineering Research Council of Canada (Discovery Grant to Harper).

Data availability Data are available on the Borealis repository (Harper 2022) at the following DOI: https://doi.org/10.5683/SP3/YO7LE9 as part of a data paper (Harper et al. 2023).

Conflict of interest The authors have no competing interest to disclose.

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Tables and Figures

Table 1. Magnitude and distance of edge influence (MEI and DEI) for response variables at lakeshore forest edges in spruce and old-growth hemlock forests. Edge influence is only reported for individual species if significant. Significant DEI was positive/negative (greater/less at the edge compared to interior forest) when MEI was positive/negative or if indicated.

Response	MEI Spruce	DEI (m) Spruce	MEI Hemlock	DEI (m) Hemlock
Canopy cover	0.02	60	0.04	40
Tree basal area	0.04	ns	-0.16	ns
Tree density	-0.02	ns	0.06	5, 25
Snag density	-0.11	ns	-0.39	ns
Log density	-0.17	ns	-0.45	0 to 5, 25 to 40*
Tree species richness	0.09	15	0.28	0 to 25
Tree species diversity	-0.03	ns	-0.62	ns
Horizontal richness	0.07	ns	-0.04	ns
Horizontal diversity	-0.26	ns	0.02	ns
Vertical richness	0.03	ns	-0.09	ns
Vertical diversity	-0.09	ns	0.12	ns
Bryophytes	-0.71	0 to 15, 40 to 60	-0.71	0 to 55
Graminoids	1.00	ns	N/A	N/A
Herbs	-0.37	ns	-0.37	ns
Lichens	-0.67	ns	0.27	ns
Litter	N/A	N/A	0.52	0 to 50

Shrubs	0.79	0 to 20	0.93	0 to 5
Sapling density	-0.63	35 to 40 (+ve)	-0.61	ns
Shrub richness	0.39	ns	0.92	0 to 5
Shrub diversity	0.31	ns	0.74	0 to 5
Herb richness	-0.09	ns	0.23	ns
Herb diversity	0.05	15 to 20	0.31	ns
Bryophyte richness	-0.36	ns	-0.26	30 to 40
Bryophyte diversity	-0.32	ns	-0.27	0 to 5
Gaylussacia sp.	0.93	0 to 5	0.93	ns
Gaultheria procumbens	0.00	ns	0.79	0 to 5
Maianthemum canadense	-0.37	ns	0.76	40 to 55
Pleurozium schreberi	-0.73	0 to 10, 40 to 55	-0.61	0 to 10
Trientalis borealis	-0.39	35 to 40	-0.30	ns
Vaccinium myrtilloides	-0.67	15 to 20	N/N	N/A

* DEI of 0 to 5 is for negative edge influence whereas other distances are for positive edge influence (greater values compared to interior forest).

Table 2. Magnitude and distance of edge influence (MEI and DEI) and of forest influence (MFI and DFI) at bog forest edges compared to interior forest and bog, respectively. Edge influence was only reported for individual species if significant. Significant DEI/DFI was positive/negative (greater/less at the edge compared to interior forest) when MEI/MFI was positive/negative.

	MEI	DEI (m)	MFI	DFI (m)
Canopy cover	0.01	-60 to -25 (-ve)	0.71	-40 to 60
Tree basal area	-0.08	-60	0.59	-40, -15 to 60
Tree density	0.10	-40 to -15	0.20	-40 to -15
Snag density	-0.06	-40	0.53	-5, 40 to 60
Log density	-0.11	-60 to -15	0.85	-5 to 60
Tree species richness	0.00	-60, -25 (-ve)	0.22	5, 60
Tree species diversity	0.35	-25 to -15, 5	0.10	-25 to -15
Horizontal richness	-0.01	-60 to -25, -5, 60	0.35	-15 to 60
Horizontal diversity	0.09	-15	0.06	-15
Vertical richness	-0.01	ns	0.02	ns
Vertical diversity	-0.08	-60 to -5, 25, 60	-0.02	ns
Bryophytes	0.17	ns	0.21	-60 to -10, 10 to 15, 30 to 60
Graminoids	0.94	-60 to -55, -30 to 0	0.79	-35 to 0
Herbs	0.29	ns	0.86	-40 to 60
Lichens	-0.83	-60 to -35 (+ve)	-1.00	-45 to 60
Shrubs	0.19	-60 to -25	-0.65	-10 to 60

Sapling density	-0.30	-60 to 30	0.72	-15 to -5, 10 to 20, 35 to 60
Shrub richness	0.45	-60 to 5	-0.32	0 to 60
Shrub diversity	0.49	-60 to -5	-0.34	0 to 60
Herb richness	0.26	ns	0.78	-50 to 50
Herb diversity	0.42	0 to 5	0.89	-35 to 60
Bryophyte richness	0.09	ns	0.23	ns
Bryophyte diversity	0.01	ns	0.25	ns
Chamaedaphne calyculata	0.00	-60 to -20 (+ve)	-1.00	-20 to 60
Cornus canadensis	0.45	ns	0.98	-35 to 45
Dicranum sp.	-0.65	-5 to 5	0.06	35 to 60
Gaultheria procumbens	0.20	ns	0.70	-5 to 0
Hylocomium splendens	-0.22	ns	1.00	25 to 40
Kalmia angustifolia	-0.07	-60 to -25 (+ve)	-0.86	-20 to 60
Mitchella repense	-0.40	ns	1.00	10 to 25
Mitella nuda	0.54	ns	1.00	0 to 15
Pleurozium schreberi	-0.14	40 to 50 (+ve)	-0.06	15 to 60 (+ve)
Pteridium aquilinum	-0.71	-50 to -30, -15 to -10	1.00	0 to 45
Rhododendron canadense	1.00	-60 to -15	-0.93	5 to 60
Rhododendron groelandicum	1.00	-60 to 0	-0.87	-10 to 60

Sphagnum spp.	1.00	-60 to 5	0.31	-60 to -20, 15 to 60
Trientalis borealis	0.14	ns	1.00	15 to 25
Vaccinium myrtilloides	-0.59	ns	0.89	-45 to 40
Vaccinium oxycoccus	0.56	-40 to -35	0.00	ns

Figure captions

Fig 1 Map of the study site on Google Earth with locations of lakeshore edges of spruce forests (L), bog edges of spruce forests (B) and lakeshore edges of old-growth hemlock forests (O) in Nova Scotia, Canada. Kejimkujik National Park is outlined on the map

Fig 2 Sampling design showing the locations of forest structure plots along bog and lakeshore edge transects in spruce and old-growth hemlock forests

Fig 3 Trends across lakeshore forest edges for canopy cover (a), basal area (b), tree density (c), snag density (d), log density (e), tree species richness (f), horizontal richness (g) and vertical richness (h). Average values are shown for lakeshore edges in spruce forest (filled circles) and in hemlock forest (open circles). Ref(erence) represents 3 distances along each transect. Large circles show 2 or more consecutive averages that were significantly different from interior forest. Magnitude and distance of edge influence for these trends are reported in Tables 1 and 2

Fig 4 Trends in average values across lakeshore forest edges for canopy cover (a), basal area (b), tree density (c), snag density (d), log density (e), tree species richness (f), horizontal richness (g) and vertical richness (h). Bog and Forest represent averages from 3 distances along each transect. Large circles show 2 or more consecutive averages that were significantly different from interior forest (lines top left to bottom right) or bog (lines top right to bottom left); cross hatching indicates averages significantly different from both adjacent ecosystems. Magnitude and distance of edge influence for these trends are reported in Tables 1 and 2

Fig 5 Trends across bog forest edges for (a) cover of bryophytes (green), graminoids (black), lichens (purple), herbs (dark yellow) and shrubs (blue); (b) sapling density; (c) species richness of bryophytes (green), herbs (dark yellow) and shrubs (blue); and (d) cover of bryophyte species *Dicranum* spp. (dark yellow), *Hylocomnium splendens* (green), *Pleurozium schreberi* (blue) and

Sphagnum spp. (black). Distances range from negative values in the bog to positive values in the forest with 0 m at the edge. Colour coded horizontal lines at the top indicate distance of edge change (DEC, see methods for details) for each variable. There was no significant DEC for shrub richness in (c) or *Dicranum* spp. in (d). Corresponding diversity measures for (c) exhibited similar trends but with no significant DEC

Fig 6 Proportion of response variables with significant edge influence for structure variables at lakeshore edges (a) and bog edges (b), and for understorey variables at lakeshore (c) and bog edges (d). In (a) and (b), circles represent the number of variables with significant edge influence at each distance for lakeshore edges of spruce (filled circles) and hemlock (open circles) forests. In (c) and (d), the number of variables with significant edge and forest influence are represented by Xs and small +, respectively. In (d), the proportion of variables with significant distance of edge change is represented by horizontal lines. Response variables include ones from Tables 1 and 2, and Fig. 5 (including diversity)

Fig 1 Map of the study site on Google Earth with locations of lakeshore edges of spruce forests (L), bog edges of spruce forests (B) and lakeshore edges of old-growth hemlock forests (O) in Nova Scotia, Canada. Kejimkujik National Park is outlined on the map

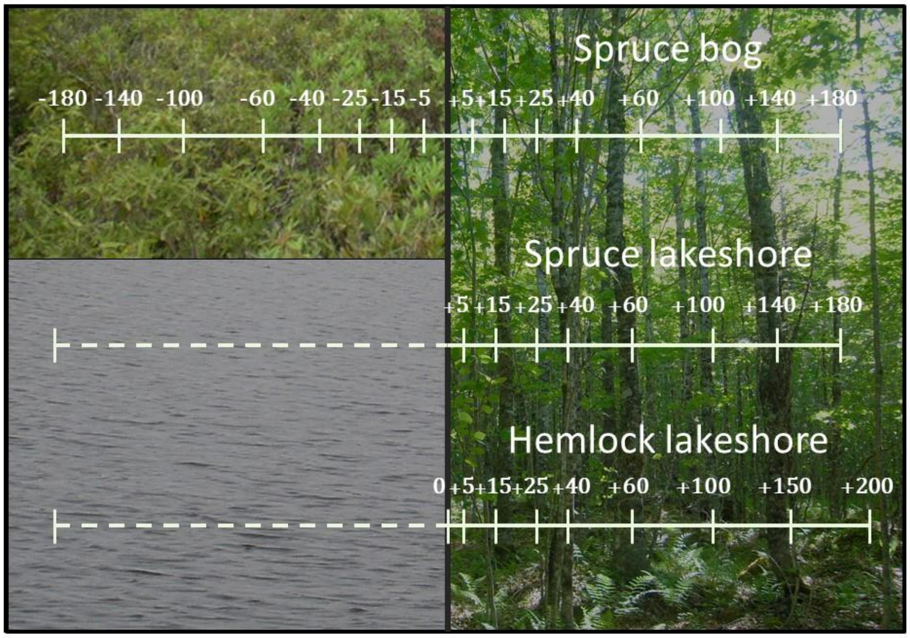
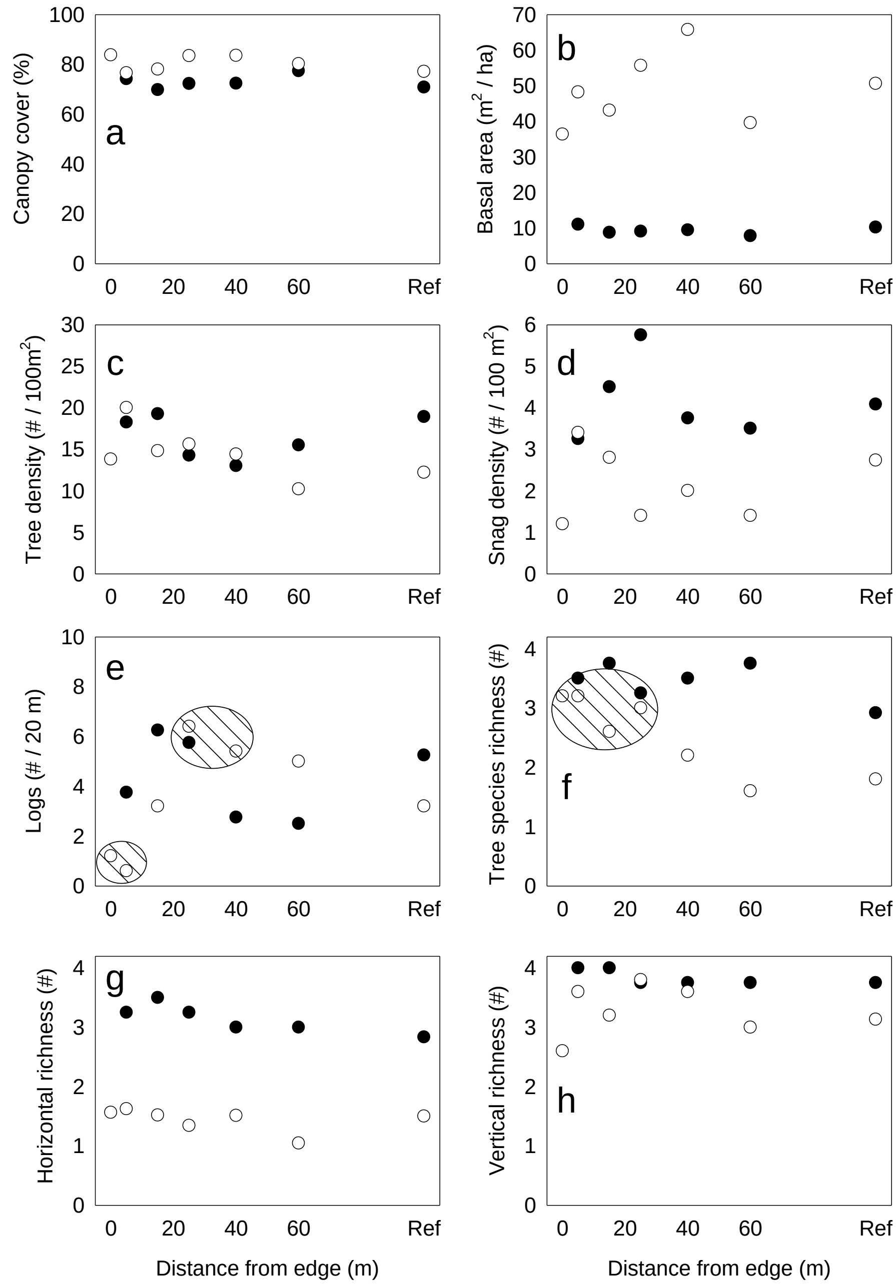
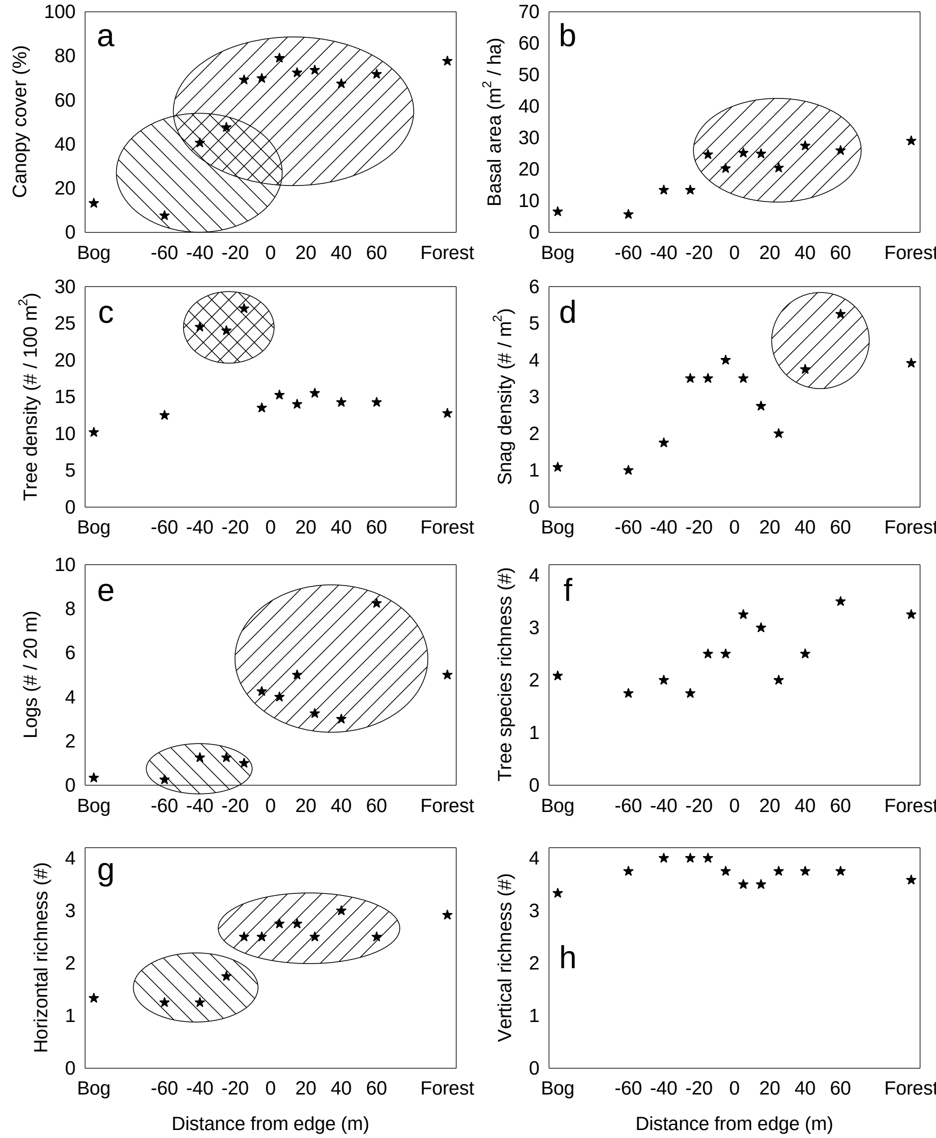


Fig 2 Sampling design showing the locations of forest structure plots along the bog and lakeshore edge transects in spruce and old-growth hemlock forests



100
80
60
40
20
0
Canopy cover (%)
a
0
20
40
60
Ref
70
60
50
40
30
20
10
0
Basal area (m2 / ha)
b
30
25
20
15
10
5
Tree density (# / 100m2)
c
6
5
4
3
2
1
Snag density (# / 100 m2)
d
10
8
6
4
2
Logs (# / 20 m)
e
4
3
2
1
Tree species richness (#)
f
Horizontal richness (#)
g
Vertical richness (#)
h
Distance from edge (m)
Distance from edge (m)

Fig 3 Trends across lakeshore forest edges for canopy cover (a), basal area (b), tree density (c), snag density (d), log density (e), tree species richness (f), horizontal richness (g) and vertical richness (h). Average values are shown for lakeshore edges in spruce forest (filled circles) and in hemlock forest (open circles). Ref(erence) represents 3 distances along each transect. Large circles show 2 or more consecutive averages that are significantly different from interior forest. Magnitude and distance of edge influence for these trends are reported in Tables 1 and 2



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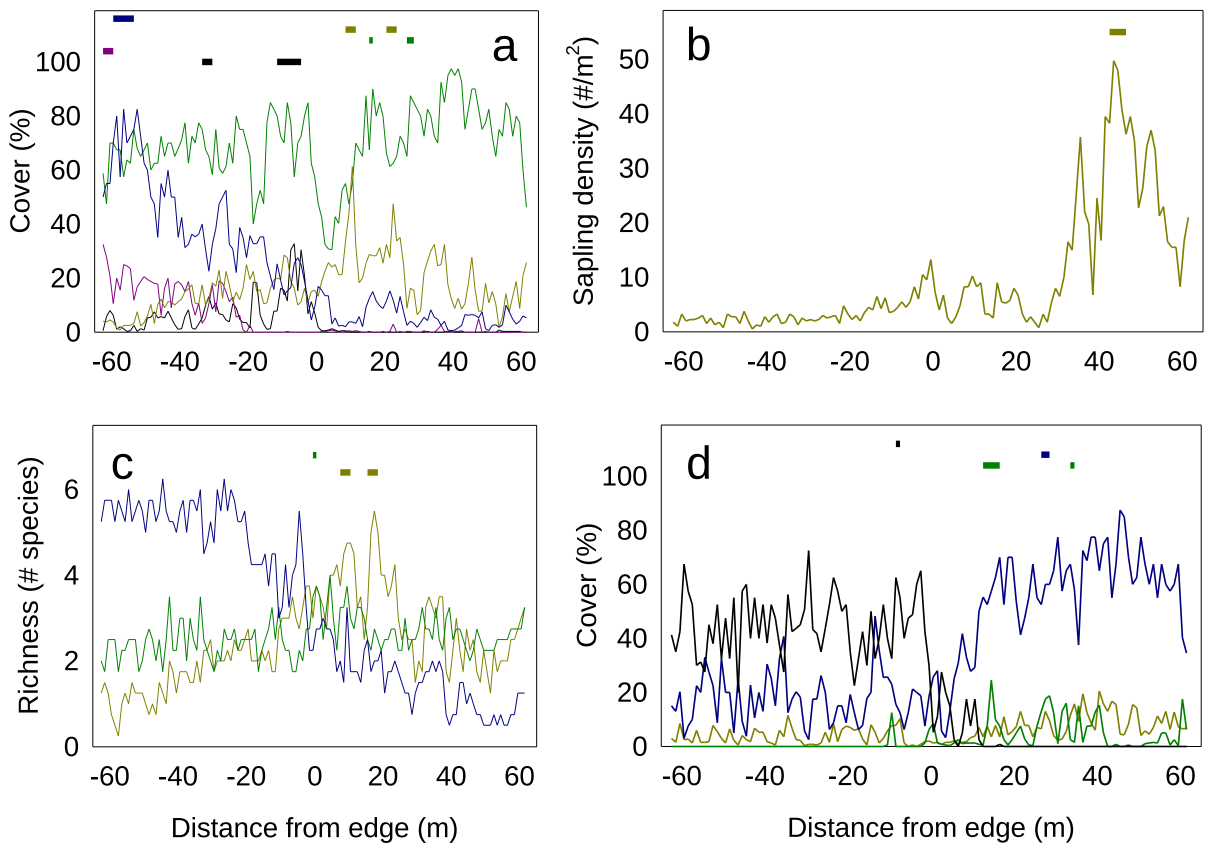
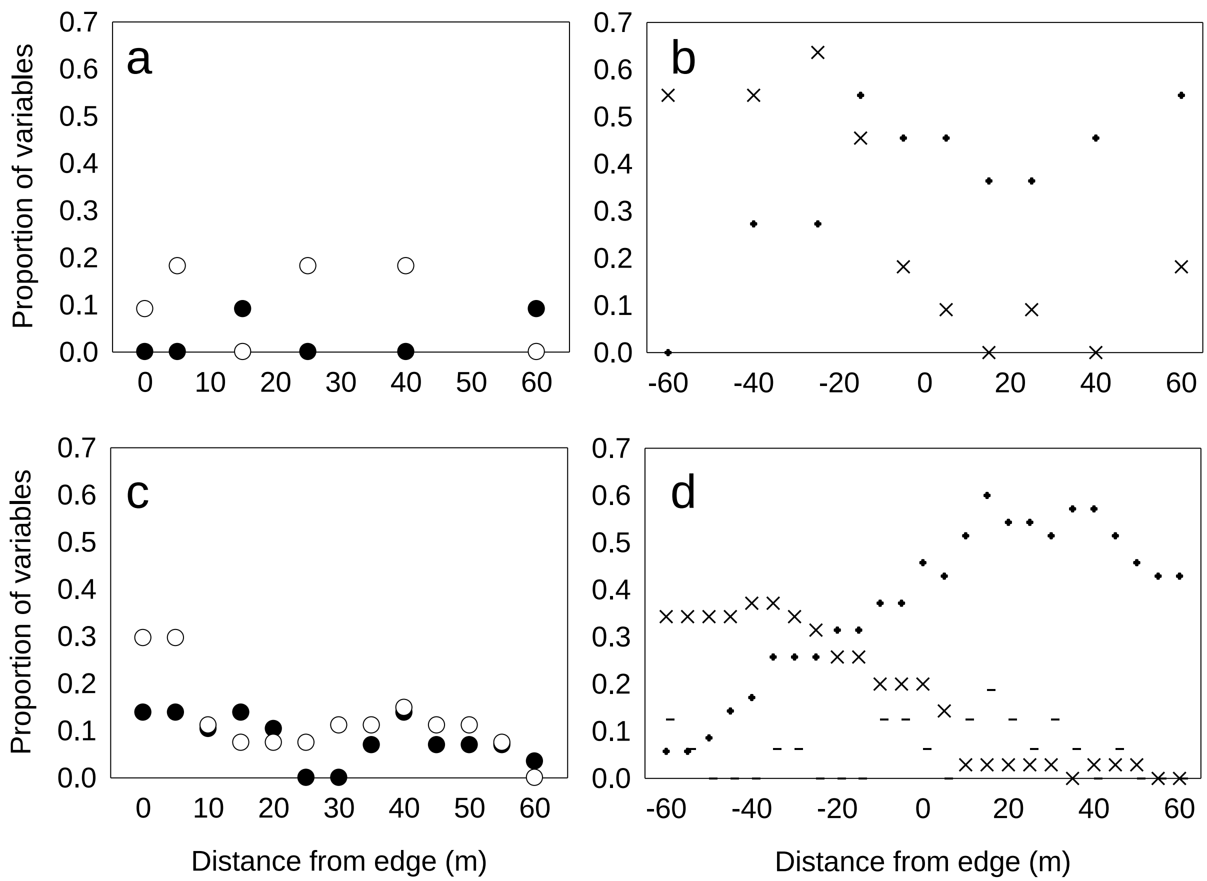


Fig 5 Trends across bog forest edges: (a) cover of bryophytes (green), graminoids (black), lichens (purple), herbs (dark yellow) and shrubs (blue); (b) sapling density; (c) species richness of bryophytes (green), herbs (dark yellow) and shrubs (blue); and (d) cover of bryophyte species *Dicranum* spp. (dark yellow), *Hylocomnium splendens* (green), *Pleurozium schreberi* (blue) and *Sphagnum* spp. (black). Distances range from negative values in the bog to positive values in the forest with 0 m at the edge. Colour coded horizontal lines at the top indicate distance of edge change (DEC, see methods for details) for each variable. There was no significant DEC for shrub richness in (c) or *Dicranum* spp. in (d). Corresponding diversity measures for (c) exhibited similar trends but with no significant DEC



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