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Edge effects on epiphytic lichens in remnant stands of managed landscapes in the eastern boreal forest of Canada

Catherine Boudreault [*], Yves Bergeron,
Pierre Drapeau, Liliana Mascarúa López

Centre d'Étude de la Forêt and the Natural Sciences and Engineering Research Council,
UQAM-UQAT Industrial Chair in Sustainable Forest Management, Université du Québec à Montréal,
C.P. 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada

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Abstract

In the managed boreal landscapes of Quebec (eastern Canada), corridors of riparian buffers and upland strips are often the only remnants of productive mature and overmature forests left in the harvested landscape. Because corridors are narrow and have multiple edges, edge effects on forest structure and on epiphytic lichens may be proportionally stronger in these linear remnant habitats than in patchy forest remnants. In this study, we compared the overall biomass of different epiphytic lichen taxa (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) in four different forest types (linear cutblock separators, riparian buffers, large forest remnants, and control interior forests). We also examined whether edge effects on lichen biomass were present in two types of forest remnants (linear cutblock separators and large forest remnants). Epiphytic lichens were sampled along one transect perpendicular to clear-cut edge in 10 sites within each forest type. We used nested ANCOVA to compare lichen biomass among distance from edge classes and remnant forest types. *Bryoria* biomass was higher in large forest remnants and interior forests than in riparian buffers and cutblock separators, whereas *Evernia* biomass was higher in riparian buffers than in other forest types. *Usnea* biomass did not vary among forest types. On a transect into the forest, *Bryoria* biomass at 0 and 15 m from the edge was significantly lower than at 30 m. The biomass of *Evernia* and *Usnea* was significantly lower at the edge of the clear-cut (0 m) compared to interior plots (30 m). Our results suggest that a landscape where only cutblock separators and riparian buffers are left as remnant mature and overmature forests will not maintain epiphytic lichen communities of mature and overmature interior forests anywhere in the landscape, especially the high biomass of *Bryoria* observed in interior forests. Wider cutblock separators would be required to maintain core habitat conditions for species associated with late seral stages.

Keywords: Linear cutblock separators; Riparian buffers; Large forest patches; Corridors; Fragmentation; Upland strips; Lichen biomass

1. Introduction

Landscape fragmentation is of major concern for the conservation of biodiversity in forested landscapes. Habitat fragmentation is defined as the conversion of a formerly continuous habitat into small and isolated remnant patches (Meffe and Carroll, 1994), which results in the creation of biologically relevant edge effects (Franklin and Forman, 1987; Donovan et al., 1997; Sillett, 1994; Esseen and Renhorn, 1998). At the edge between two units with high structural contrast, a forested zone where the microclimatic conditions are modified from the closed forest is often observed (e.g., increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity; Matlack, 1993; Chen et al., 1993, 1995). The proportion of habitats in this edge zone is related to the shape and size of the remnant fragment; for example, small and linear fragments have proportionally more edge than large and round fragments (Saunders et al., 1991). The presence of an edge zone leads to a decrease in core habitat size (Öhman and Eriksson, 1998), thus making species associated with core habitats particularly impacted by edge effects, as their habitat area is reduced (Saunders et al., 1991; Meffe and Carroll, 1994).

An increased rate of tree mortality due to windthrow is a major consequence of edge effects (Esseen, 1994; Jönsson et al., 2007). Trees along the edges are more susceptible to uprooting or breakage of their bole or branches than trees found within a stand (Dewalle, 1983). The loss of dominant trees from the canopy can lead to serious modifications of forest structure

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[*] Corresponding author.
E-mail address: boudreault.catherine@courrier.uqam.ca (C. Boudreault).

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and the light environment, and may alter species composition of communities (Saunders et al., 1991). As clear-cut stands that are adjacent to remnant forests regenerate, edge effects usually decrease (Harper et al., 2005); however, in some cases effects are still detected long after edge creation (Matlack, 1993; Rheault et al., 2003).

Many studies report that epiphytic lichens are affected by edge effects (Sillett, 1994; Esseen and Renhorn, 1998; Kivistö and Kuusinen, 2000; Hilmo and Holien, 2002; Rheault et al., 2003; Esseen, 2006; Belinchón et al., 2007). Lichens are exposed to new gradients of light, humidity, and wind after edge creation. Epiphytic lichens may be particularly sensitive to microclimatic modifications, because their metabolic activity varies passively with environmental conditions (poikilohydric organisms) (Nash, 1996), particularly with the availability of light and water (Campbell and Coxson, 2001). For instance, shade-adapted species such as *Lobaria oregana* and *Pseudocyphellaria rainierensis* in Douglas–fir forests (Sillett, 1994), and *Lobaria pulmonaria* in deciduous stands (Gauslaa and Solhaug, 1996) were affected by light intensity increases at the forest edge. Other studies have shown that fruticose lichens (pendant growth form) accumulate less biomass at forest edges (Esseen and Renhorn, 1998; Rheault et al., 2003) and are prone to fragmentation by wind (Esseen, 1985), which is particularly relevant as they are the dominant epiphyte in boreal forests. A decline in available substrates (i.e., number of trees, number of branches per tree, and branch length) due to wind damage (Saunders et al., 1991) may also explain the decrease in epiphytic biomass at the edge of forest remnants (Rheault et al., 2003).

In the managed boreal landscapes of Quebec (eastern Canada), corridors of riparian buffer strips and upland strips are often the only remnants of productive mature and overmature forests left in the harvested landscape. Riparian buffer strips are widely used to minimize the impacts of logging on riparian habitats, which are key habitats for the maintenance of biodiversity and for ecosystem processes at the landscape level (Naiman et al., 1993; Lamb et al., 2003). Recently, upland strips (cutblock separators) were implemented in Quebec in order to reduce the maximum size of two adjacent cutblocks (Gouvernement du Québec, 2005). These linear habitats may act as refugia in harvested landscapes for species associated with mature and old-growth forest. By linking unharvested forest patches to one another, such corridors may also increase the probability of survival of local populations by promoting movement of individuals among patches (Bennett, 1990, 2003). In contrast, because corridors have multiple edges, edge influences on forest structure may be stronger in these linear remnant habitats than in patchy forest remnants (Mascarúa López et al., 2006).

As linear habitats may act as biodiversity reservoirs in boreal forests, it becomes critical to evaluate the capacity of these corridors to maintain the integrity of communities of sessile organisms, such as lichens. Research efforts regarding sessile organisms have been mainly conducted in riparian buffers (e.g., Lamb et al., 2003; Hylander et al., 2002, 2005), while the effectiveness of upland strips in maintaining the integrity of these organisms has been barely studied (but see Rheault et al., 2003). In the current study, we address three questions: (1) are there differences in the biomass of fruticose lichens (*Bryoria* spp., *Usnea* spp., and *Evernia mesomorpha*) between forest types (cutblock separators, riparian buffers, large forest remnants adjacent to a single clear-cut, and interior forests), (2) are edge effects present in cutblock separators and large forest remnants, and (3) are edge effects stronger in narrow linear corridors (cutblock separators) compared to large patchy forest remnants?

2. Methods

2.1. Study area

The study was conducted in the western part of the bioclimatic domain of *Picea mariana*-feather moss forest in Quebec (49°00′–49°45′N, 76°00′–77°30′W) (Saucier and Robitaille, 1998). The area was located in the eastern part of the Abitibi region, near the municipality of Lebel-sur-Quévillon. This region forms part of the northern Clay Belt (Rowe, 1972), a broad physiographic unit characterized by lacustrine deposits from proglacial lakes Barlow and Ojibway (Vincent and Hardy, 1977). Clay soils predominate, the topography is relatively flat, and the forest mosaic is dominated by black spruce (*P. mariana*) stands. Black spruce is occasionally interspersed with balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and eastern larch (*Larix laricina*). Jack pine stands dominate drier sites such as outwash deposits, old beaches, and eskers (Rowe, 1972). Clear-cuts adjacent to remnant forests were dominated by either naturally regenerated or planted black spruce or jack pine 1- and 5-m tall. From 1971 to 2001, a mean annual temperature of −0.7 °C and a mean annual precipitation of 905 mm were recorded at Matagami, located at approximately 100 km from our study sites (Anon., 2004).

Mechanized-industrial logging, mainly clearcutting, began in the early 1970s. Since 1996, the Quebec government forest regulations require that clear-cuts do not exceed 150 ha (Gouvernement du Québec, 2005), and that between two contiguous cut overs, cutblock separators dominated by trees >7 m in height must be retained. The width of the separators varies with the size of adjacent clear-cut areas. When adjacent clear-cuts are smaller than 100 ha, the width of cutblock separators is 60 m. If the size of one of the adjacent clear-cut areas is over 100 ha, the width of the separator must be at least 100-m wide. The trees in the separators may be cut when the regenerating trees in the cut block reach 3 m. The riparian banks on both sides of permanent streams, lakes, or other surface water bodies must be protected by riparian buffers with a minimum width of 20 m.

2.2. Lichen species in the study

We studied fruticose epiphytic lichens because they are the dominant epiphytic group in boreal forests. The three genera of fruticose lichens that we studied are *Bryoria*, *Usnea*, and *Evernia*, the only taxa of fruticose lichens present in the study sites. The most common and abundant *Bryoria* and *Usnea* species in our study area were *B. trichodes* ssp. *trichodes* and *U. filipendula*. *B. nadvornikiana*, *B. furcellata*, *B. lanestris*, *U. hirta*, and *U. subfloridana* were also frequently observed (unpublished data). Although present in the study area, *U. longissima* was encountered infrequently. *Evenia mesomorpha* is the only species of the genus that was present in our study area. Finally, *Hypogymnia physodes*, *Tuckermannopsis americana*, *Parmeliopsis ambigua*, *P. hyperopta*, *Mycoblastus sanguinarius*, and *Japewia tornoensis* were common epiphytic lichens in the forest stands that we sampled.

2.3. Sampling design

We studied epiphytic lichens in four types of forest: (1) 60-m wide cutblock separators; (2) 45–70-m wide riparian buffers surrounding streams; (3) large forest remnant patches adjacent to a single clear-cut that was at least 300-m wide; and (4) interior forests. Site selection was based on information gathered from digital forest inventory maps. Emphasis was placed on stands that were dominated by black spruce over 12 m in height and between 70 and 120 years of age. Edges between the remnants and the clear-cuts were straight. The sites were located near young edges that were between 5 and 11 years old, as this period was considered long enough to accumulate logging generated forest structure changes along edges (Ruel et al., 2001). Because available stands that fulfilled our criteria were limited, we did not control for edge orientation, although we recognize the importance of this factor (see Hylander, 2005). We preferred to maximize the number of stands within each forest type (riparian buffers, cutblock separators, large patches, and interior forests) to better understand within-forest type variability.

For each type of forest, we sampled 10 sites, for a total of 40 sites. In each site, we sampled epiphytic lichens along one transect perpendicular to the clear-cut edge. Transects were 60-m long in cutblock separators and in large forest remnants, and varied between 45- and 75-m long in riparian buffers due to the variability of the buffer width. In interior forests, epiphytic lichens were collected along 100-m long transects located nearby the large forest remnant transects, but deeper within the same forest stand; they were located at least 100 m away from any edge. Large forest remnants, cutblock separators, and interior forests were chosen in a way to maximize similarity in soil features, slope, and tree species composition. None of these three forest types contained riparian habitats.

Epiphytic lichens were sampled in rectangular plots of 5 m × 20 m (long axis parallel to the forest edge) located at 15-m intervals along each transect in the cutblock separators, riparian buffers, and in the large forest remnants. Interior forests were sampled with three plots spaced 50 m apart from one another along transects. Data on forest structure variables were collected in the plots. All live trees, standing dead trees (snags), and fallen trees (logs) ≥ 5 cm dbh (diameter at breast-height) were inventoried. Only logs with intact bark (classes 1 and 2, Thomas et al., 1979) were sampled, because the objective was to detect forest damage due to recent harvesting (for more detail, see Mascarúa López et al., 2006). In each plot, we randomly selected 10 black spruce trees. For each tree, we sampled one branch (length >100 cm) at a randomly selected height (between 1.5 and 5 m) and orientation. We then measured the branch length and branch width and we assessed its vitality (dead/live). The distal 100 cm of these branches were pruned and the branch diameter at the cutting point was measured. Branches were brought back in the laboratory and we sorted thalli of *E. mesomorpha*, *Bryoria* spp., and *Usnea* spp. Lichens were dried at 60 °C for 24 h before being weighed (0.0000 g).

2.4. Data analyses

Simple linear regression was used to detect significant relationships between tree and branch characteristics (independent variables), and lichen biomass (dependent variables) for the three taxa on branches collected across all forest types. Variables selected were branch length, branch diameter, tree dbh, stem density and basal area. Regressions were conducted with mean values calculated at the plot level.

Differences in epiphytic lichen biomass among forest types (i.e., cutblock separators, riparian buffers, large forest remnants, and interior forests; $n = 40$) were tested at the transect level (calculated over all sampled branches in each transect) by using one-way ANOVA (PROC GLM, SAS Institute, 2002). Forest type was the main effect. Stand (stem density, basal area, mortality, and windthrow) and branch characteristics (branch diameter, branch length, and proportion of live branches) were also compared among forest types with one-way ANOVA. Mortality was calculated as the ratio of logs plus snags to the number of all trees (live and dead), and windthrow was calculated as the ratio of logs to the number of all trees (live and dead) that were recorded in each transect. The response variables were mean lichen biomass and branch characteristics calculated over all sampled branches in each transect. Stand structure variables were estimated by averaging all plots in each transect. Biomass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$), branch length data were log-transformed ($\log x$), and mortality and windthrow data were arcsine-transformed ($\text{arcsine}(x/100)^{0.5}$) to conform to the normality and homoscedasticity assumptions of ANOVA. We used post hoc Tukey HSD tests to detect significant differences ($p \leq 0.05$) among forest types. Chi-squared tests were used to compare lichen frequencies between forest types for the three taxa. Pearson chi-square components (χ^2: $[O - E]^2/E$) were used to measure the difference between observed (O) and expected (E) values. The response variables were presence or absence of the taxa on each collected branch.

Nested two-way ANCOVA models were used to compare lichen biomass and stand and branch characteristics among distance classes (for the first 30 m) and remnant forest types. Forest type (cutblock separators and large forest remnants) and distance from the edge (0, 15, and 30 m) were fixed factors, sampling site was a random factor nested within the forest type, and stem density and stand age were added as covariates in the analyses (except for variables of stand structure). Nested ANOVA was used to account for site variability within-forest type. Analyses were performed with the MIXED procedure of SAS (SAS Institute, 2002). Response variables were mean lichen biomass and mean branch characteristics calculated over the 10 branches that were collected in each $5\ \text{m} \times 20\ \text{m}$ plot, and stand characteristics for each $5\ \text{m} \times 20\ \text{m}$ plot. Since cutblock separators had two plots for some distances (i.e., the transects crossed their entire width), these plots were averaged prior to the analyses. Biomass data were square-root transformed ($x^{0.5} + (x + 1)^{0.5}$), branch length data were log-transformed ($\log x$), and mortality and windthrow data were arcsine-transformed (arcsine$(x/100)^{0.5}$) to fulfill basic assumptions of parametric procedures. Denominator degrees-of-freedom were calculated using Satterthwaite's approximation (Littell et al., 1996). Since the MIXED procedure does not compute an F-test for the variance component of random effects, the significance of the random effect was calculated with the likelihood ratio statistic, which was computed by taking the difference between the -2 REML log-likelihood (Restricted Maximum Likelihood estimator) of the model containing the random effect and the model without the random effect, as suggested by Littell et al. (1996). Significant differences ($p \leq 0.05$) between distance and forest type classes were detected with Tukey HSD tests. No attempt was made to evaluate edge effects in riparian buffers because edge effects in this forest type are a combination of a natural gradient changing with increasing distance to the water and an anthropogenic gradient at the edge of the clear-cut; thus, it is difficult to detect edge effects in this type of habitat without an appropriate control of riparian habitats imbedded within continuous forests.

The importance of edge aspect on lichen biomass in cutblock separator transects was also assessed. As all linear cutblocks separators had similar orientation, the difference between their south-south-east (SSE) and north-north-west (NNW) facing edge plots (0 m from the edge) was tested with one-way ANOVA. Response variables were mean lichen biomass calculated over the 10 sampled branches collected within a plot. Lichen biomass values were square-root transformed. No attempt was made to evaluate the edge aspect in large forest patches because most of them were SSE-oriented (7 out of 10).

3. Results

3.1. Relationships between lichen biomass and stand and branch characteristics

Branch length was significantly correlated with branch diameter ($r = 0.438$, $p < 0.001$). The biomass of *Bryoria* increased significantly with branch diameter and branch length, but r^2 values are low, indicating relatively weak relationships (Fig. 1). The biomass of *Evernia* and *Usnea* was unrelated to any branch characteristics ($p > 0.05$). Live branches had 3.8 times more biomass of *Bryoria* than dead ones, but approximately the same amount of *Usnea* and *Evernia*. No significant relationship between stand variables (tree dbh, basal area, and stem density) and lichen biomass was found (results not presented).

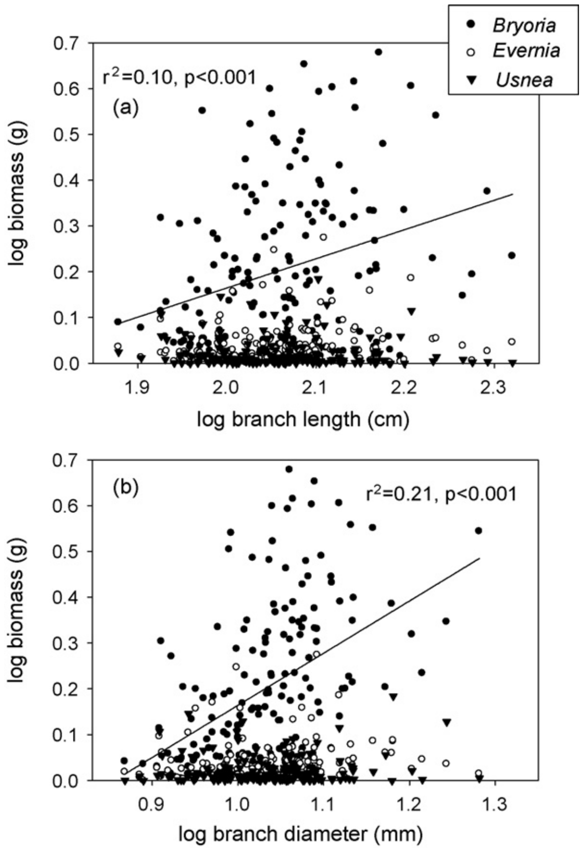

Fig. 1. Relationships between lichen biomass and branch characteristics: (a) branch length (*Bryoria* spp.: $r^2 = 0.10$, $p < 0.001$; *Evernia mesomorpha*: $r^2 = 0.02$, $p = 0.06$; *Usnea* spp.: $r^2 = 0.001$, $p = 0.68$) and (b) branch diameter (*Bryoria* spp.: $r^2 = 0.21$, $p < 0.001$; *E. mesomorpha*: $r^2 = 0.006$, $p = 0.30$; *Usnea* spp.: $r^2 = 0.02$, $p = 0.08$) ($n = 167$). Lines are shown only for significant relationships.

3.2. Among forest types comparison

Basal area was significantly lower, and mortality and windthrow were significantly higher in cutblock separators compared to interior forests (Table 1). Branches were significantly shorter in riparian buffers compared to large forest remnants. Stem density, branch diameter, and number of live branches did not differ among forest types (Table 1).

Species of the genus *Bryoria* dominated lower tree canopies in interior forests. *Bryoria* was almost 8 times more abundant than *Usnea* and 30 times more abundant than *Evernia* (Fig. 2). *Usnea* was four times more abundant than *Evernia* (Fig. 2). *Bryoria* was also the most frequent taxa: it occurred on all sampled branch sections. In cutblock separators and in large forest remnants, *Bryoria* was again much more abundant in terms of biomass than *Usnea* and *Evernia*, but in riparian buffers, its biomass was only twice that of *Usnea* and *Evernia* (Fig. 2). *Usnea* and *Evernia* had a similar biomass in cutblock separators and in riparian buffers, but the biomass of *Usnea* was higher than that of *Evernia* in large forest remnants.

Bryoria biomass was significantly lower in cutblock separators and in riparian buffers than in interior forests and large forest remnants (Fig. 2; $F_{3,36} = 13.09$, $p < 0.001$). *Evernia* biomass was significantly greater in riparian buffers

Table 1
Mean ± S.E. of stand and branch characteristics among forest types[a], together with *F*-statistics and *p*-values from one-way ANOVAs used on forest types ($n = 40$)

Characteristic	Cutblock separators	Riparian buffers	Large forest remnants	Interior forests	$F_{3,36}$	p
Basal area (m^2/ha)	15.5 ± 2.1 b	22.3 ± 2.2 ab	23.2 ± 1.5 ab	25.0 ± 2.7 a	3.58	0.023
Stand density (stems/ha)	1076.7 ± 143.7 a	1457.8 ± 195.2 a	1324.5 ± 170.1 a	1730.0 ± 194.7 a	2.36	0.088
Mortality (%)	37.3 ± 4.9 a	22.6 ± 3.2 ab	31.7 ± 4.6 ab	21.3 ± 3.6 b	3.48	0.026
Windthrow (%)	12.0 ± 3.2 a	7.5 ± 2.2 ab	8.6 ± 3.7 ab	2.6 ± 1.0 b	2.92	0.047
Branch diameter (mm)	11.1 ± 0.3 a	10.3 ± 0.4 a	11.6 ± 0.2 a	10.9 ± 0.4 a	2.27	0.097
Branch length (cm)	117.3 ± 3.4 ab	109.1 ± 4.6 b	127.8 ± 5.9 a	113.3 ± 4.6 ab	2.91	0.048
Live branches (%)	0.3 ± 0.1 a	0.3 ± 0.1 a	0.4 ± 0.1 a	0.4 ± 0.2 a	0.54	0.656

Within each row, means with different letters differ significantly at $p = 0.05$.

[a] Means were calculated with three distance classes for cutblock separators, riparian buffers, and interior forests and with five distance classes in large forest remnants.

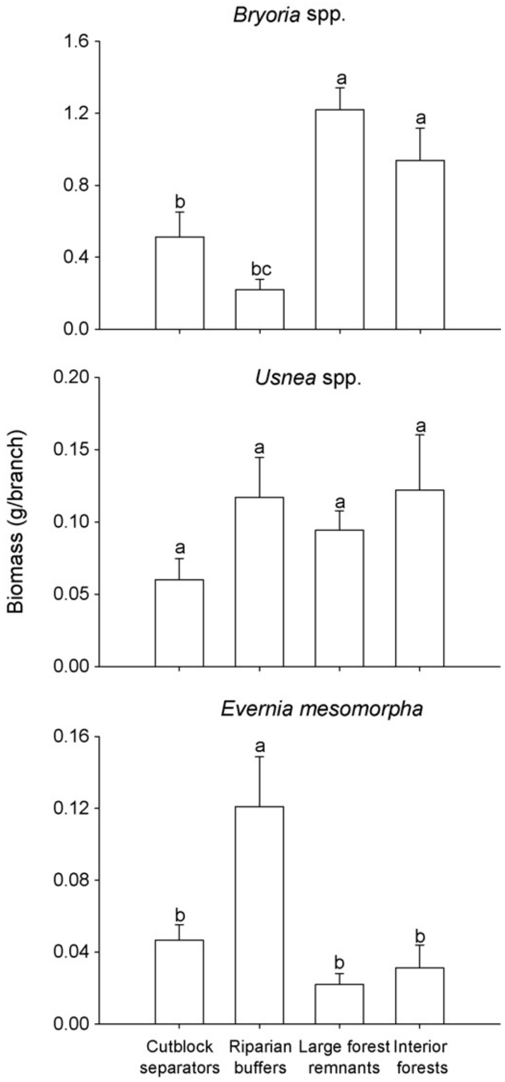

Fig. 2. Comparison of biomass (mean ± S.E.) among forest types (cutblock separators, riparian buffers, large forest remnants with only one edge, and interior forests) for *Bryoria* spp., *Usnea* spp., and *E. mesomorpha*. Means with different letters differed significantly ($p \leq 0.05$) based on LSmeans Tukey HSD tests. Means were calculated with three distance classes for cutblock separators, riparian buffers, and interior forests and with five distance classes in large forest remnants. Note that scales are different in each graph.

than in other forest types (Fig. 2; $F_{3,36} = 8.45$, $p < 0.001$), and *Usnea* biomass did not differ significantly across the different forest types (Fig. 2; $F_{3,36} = 1.32$, $p = 0.282$). There were no significant differences between large forest remnants and interior forests for these three lichen taxa (Fig. 2).

Evernia was more frequently found on branches in riparian buffers (60.2%) compared to cutblock separators (54.7%), interior forests (48.6%) and large forest remnants (42.5%) ($\chi^2 = 26.43$, $p < 0.001$). *Usnea* was less frequent in cutblock separators (66.2%) than in large forest remnants (76.8%), riparian buffers (78.6%), and interior forests (78.8%) ($\chi^2 = 19.38$, $p < 0.001$). *Bryoria* was frequent in all forest types (>95%), but its frequency in interior forests (99.8%) was significantly higher ($\chi^2 = 10.89$, $p = 0.012$).

3.3. Influence of distance from forest edge

Basal area, stem density, mortality, windthrow, and branch diameter differed significantly with distance to forest edge, but not between cutblock separators and large forest remnants (forest type) (Tables 2 and 3). At the edge, stem density and basal area were lower, and windthrow and mortality was higher than at 30 m, but the differences between 0 and 15 m were not significant for stem density and windthrow (Tukey HSD tests; Fig. 3). Branches had a smaller diameter at 0 and 15 m from the edge than at 30 m (Tukey HSD tests; Fig. 3). The interaction term was not significant for any stand or branch variables, whereas site variability was significant for all variables except branch diameter (Tables 2 and 3).

After taking into account the influence of stand age and stem density, the difference in lichen biomass among distance classes was significant for *Bryoria* and *Usnea* and nearly significant for *Evernia* ($p = 0.055$) (Table 3). Lichen biomass differed significantly among remnant forest types for *Bryoria* and *Evernia*, and among sites for *Evernia* and *Usnea* (Table 3). Since the interaction term was not significant for *Bryoria*, *Evernia*, or *Usnea* (Table 3), the effect of distance was consistent across forest types. *Bryoria* biomass was significantly greater in large forest remnants than in cutblock separators, whereas the reverse was found for *Evernia* (Tukey HSD tests). *Bryoria* biomass at 0 and 15 m was significantly

Table 2

Nested ANCOVA summaries for effects of forest type (large forest remnants and cutblock separators) and distance from the edge (three distance classes in each forest type: 0, 15 and 30 m) on stand characteristics ($n = 60$)

Source	d.f.	Basal area (m^2/ha)		Stem density (stems/ha)		Mortality (%)		Windthrow (%)	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Forest type	1	2.34	0.143	1.45	0.244	0.49	0.492	0.01	0.924
Distance	2	**8.85**	**<0.001**	**7.44**	**0.002**	**6.79**	**0.003**	**4.34**	**0.028**
Forest type × distance	2	0.54	0.586	0.81	0.453	2.3	0.115	2.01	0.161

Significant effects are shown in bold type. The random effect site (forest type) was tested with the likelihood ratio statistic. The likelihood values for stem density, basal area, mortality, and windthrow were, respectively, 10.5, $p < 0.05$; 20.4, $p < 0.05$; 19.1, $p < 0.05$; and 9.4, $p < 0.05$.

Table 3

Nested ANCOVA summaries for effects of forest type (large forest remnants and cutblock separators) and distance from the edge (three distance classes in each forest type: 0, 15 and 30 m) on biomass of *Bryoria*, *Evernia*, and *Usnea*, and branch characteristics ($n = 56$)

Source	d.f.	Branch length (cm)		Branch diameter (mm)		Live branches (%)		*Bryoria* (g)		*Evernia* (g)		*Usnea* (g)	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Forest type	1	1.67	0.214	0.01	0.917	0.03	0.855	**6.55**	**0.021**	**5.62**	**0.030**	0.32	0.582
Distance	2	1.53	0.232	4.55	**0.017**	0.54	0.589	**4.39**	**0.020**	3.15	0.055	**3.59**	**0.039**
Forest type × distance	2	0.29	0.751	0.41	0.667	0.46	0.633	0.03	0.973	0.65	0.530	0.18	0.835
Stem density	1	4.01	0.052	0.34	0.564	1.86	0.181	0.10	0.751	0.11	0.745	0.37	0.546
Stand age	1	0.20	0.658	1.43	0.250	0.24	0.629	1.21	0.289	1.62	0.222	1.16	0.301

Significant effects are shown in bold type. Stem density and stand age were treated as covariates and site was nested within-forest type (random factor). The random effect site (forest type) was tested with the likelihood ratio statistic. The likelihood values for *Bryoria*, *Evernia*, *Usnea*, branch length, branch diameter, and proportion of live branches were, respectively, 3.0, $p > 0.05$; 4.5, $p < 0.05$; 4.1, $p < 0.05$; 5.9, $p < 0.05$; 1.3, $p > 0.05$; and 7.1, $p < 0.05$.

lower compared to 30 m (Tukey HSD tests), and was 2.3 times higher in large forest remnants than in cutblock separators (Fig. 4). *Usnea* biomass at 0 m was half of that at 30 m, whereas biomass at 15 m was not significantly different from those at 0 and 30 m (Tukey HSD tests). *Evernia* biomass was smaller at the edge compared to that at 30 m (Tukey HSD tests), and the mean value at the edge of cutblock separators was 3.6 larger than at the edge of large forest remnants (Fig. 4).

The magnitude of edge influence computed as the ratio between edge and interior values in cutblock separators and large forest remnants for *Bryoria* was, respectively, 0.38 and 0.57, for *Usnea* 0.32 and 0.51, and for *Evernia* 0.59 and 0.29.

No significant effect of edge aspect in cutblock separators was detected with ANOVA for *Bryoria* ($F_{1,16} = 1.99$, $p = 0.180$), *Evernia* ($F_{1,16} = 2.93$, $p = 0.106$), or *Usnea* ($F_{1,16} = 1.69$, $p = 0.212$).

4. Discussion

4.1. Comparisons among forest types

In theory, larger remnants support larger populations and have a bigger core area unaffected by edge effects than smaller remnants (Saunders et al., 1991). In this study, *Bryoria* biomass at the transect level was similar in large forest remnants and interior forests, but biomass was much lower in the relatively small cutblock separators. This pattern suggests that large forest patches are better habitats for *Bryoria* than cutblock separators. The overall higher biomass of *Bryoria* in large forest remnants compared to cutblock separators may also be an effect of continuous immigration of lichens from forest interiors (source populations) in large forest remnants. In fact, large forest remnants were situated in the edges of interior forests, while the distances between interior forests and cutblock separators were much larger. Differences between large forest remnants and cutblock separators that are likely related to edge effects are discussed in more detail in Section 4.2.

Riparian buffers were characterized by a relatively high biomass of *Evernia* and a relatively low biomass of *Bryoria*. In general, riparian zones are characterized by a naturally open forest structure with trees adapted to a greater penetration of light and wind stress, which results in the root stimulation necessary to develop root stability (Mitchell, 1995). For the same study sites, Mascarúa López et al. (2006) found that the edge influence on forest structure was lower in riparian buffers compared to cutblock separators and that stem density near streams was low even if little damage (mortality or windthrow) was observed. It is likely that the species composition of lichen epiphyte communities in the riparian zone is adapted to light, wind, and microhabitat conditions of the pre-existing edge near a stream. *E. mesomorpha* is a frequent and abundant species in sites exposed to full sunlight (Brodo et al., 2001), which may explain its high biomass in riparian forests. In contrast, fragmentation of lichen thalli or high light intensity in these open forests might have been too high to promote *Bryoria* biomass accumulation.

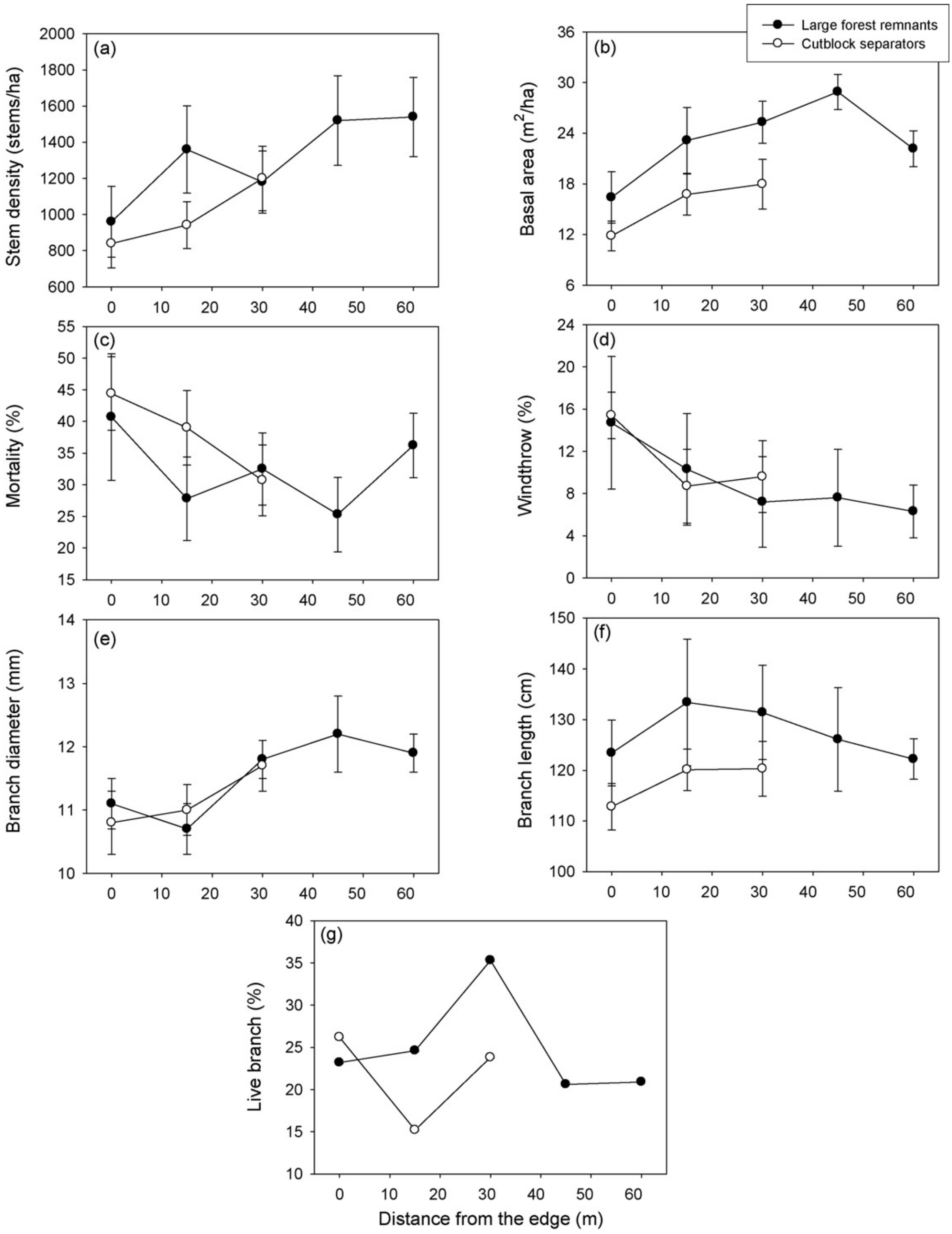

Fig. 3. Mean values ± S.E. of stand and branch characteristics along the clear-cut edge-to-interior gradient in cutblock separators (0 m: $n = 10$; 15 m: $n = 9$; 30 m: $n = 10$) and in large forest remnants (0 m: $n = 8$; 15 m: $n = 9$; 30 m: $n = 10$; 45 m: $n = 10$; 60 m: $n = 10$): (a) stem density, (b) basal area, (c) mortality, (d) windthrow, (e) branch diameter, (f) branch length, and (g) proportion of live branches. Data from the two clear-cut edges were combined for cutblock separators.

4.2. *Edge influence*

Edge effects on biomass per branch were detected for all lichen taxa and in both types of forest edge (cutblock separators and large forest remnants). However, the distance and the magnitude (ratio between edge and interior values) of edge influence vary with taxa and forest type. The distance of edge influence toward the forest interior was greater for *Bryoria*, the dominant group of lichens, than for *Usnea* and *Evernia*; however, the magnitude of edge effect was similar for *Usnea* and *Bryoria*. We documented stronger edge effects on *Bryoria* in cutblock separators, which are exposed to two close anthropogenic edges, than for large forest remnants, exposed to only one edge. For instance, edge and mid-distance *Bryoria* biomass values were less than half the ones found in large forest remnants. Similarly, Mascarúa López et al. (2006) found that

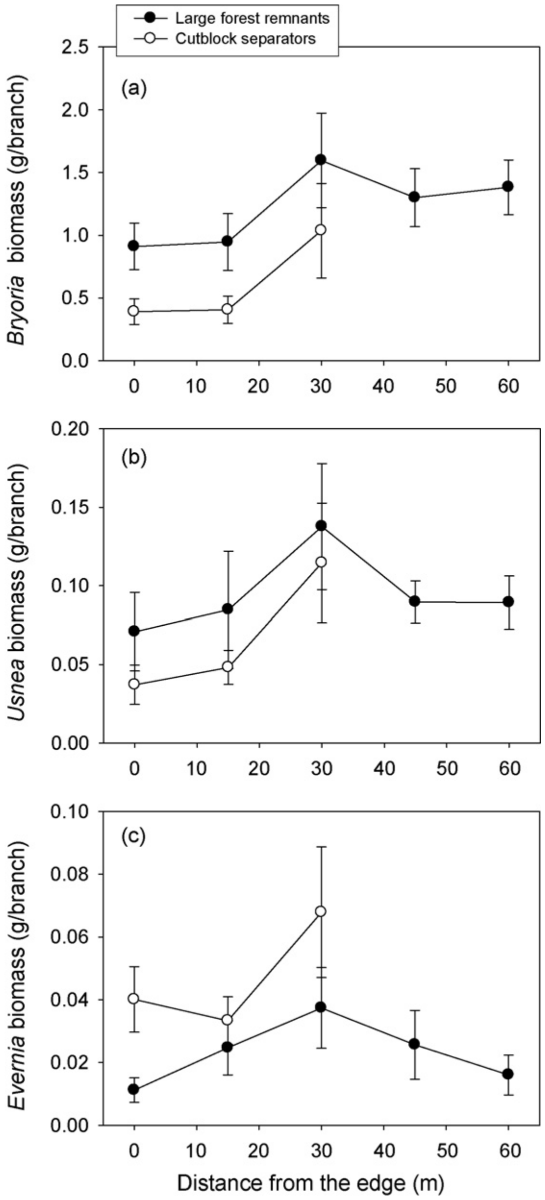

Fig. 4. Mean values ± S.E. of lichen biomass along the clear-cut edge-to-interior gradient in cutblock separators (0 m: $n = 10$; 15 m: $n = 9$; 30 m: $n = 10$), and in large forest remnants (0 m: $n = 8$; 15 m: $n = 9$; 30 m: $n = 10$; 45 m: $n = 10$; 60 m: $n = 10$): (a) *Bryoria* spp., (b) *Usnea* spp., and (c) *E. mesomorpha*. Data from the two clear-cut edges were combined for cutblock separators.

distance of edge influence on forest structure extends 10–25 m from the clear-cut edge into large forest remnants, and across the entire width of cutblock separators. These results align with the general theory that predicts that long and narrow habitats are more affected by edge effects than larger habitats with a more regular shape (Saunders et al., 1991). Multiple edges seem to increase the magnitude and extent of edge effects (Fletcher, 2005; Mascarúa López et al., 2006). In this study, the core area of interior conditions for *Bryoria* in 60-m wide cutblock separators was considerably reduced: at least 50% of these habitats were affected by edge effects.

Biomass accumulation of epiphytic lichens depends on successful colonization of propagules (dispersal and establishment) and subsequent growth and fragmentation of lichen thalli. Edge effects can affect any of these different processes. Moreover, substrate characteristics are important for lichen establishment (Armstrong, 1990). In our study, the lower biomass of *Bryoria*, *Usnea*, and *Evernia* at the edge of forest remnants may reflect the lower quality of substrates at forest edge. For instance, at the edges of clear-cuts and remnant forests, branches had a smaller diameter. Our results and those of other studies (e.g., Esseen et al., 1996) showed that lichen biomass increased with branch diameter. Branches at the edges were also more exposed, without bark or with exfoliating bark and thus seemed more dry (C. Boudreault, personal observation). For tree species that have a bark with a tendency to exfoliate, thalli may be entirely dislodged from the branches during windy conditions. The establishment success of diaspores on branches may also be diminished by windy conditions at the edge, as suggested by Hilmo and Holien (2002) to explain the low number of juvenile thalli of *Bryoria* spp. found at forest edges in spruce stands in Norway. Substrate losses by windthrow at the edge of remnant forests will directly affect the biomass of epiphytic lichens found in remnant stands, but it will also have an indirect effect by decreasing the amount of propagules present in forests for subsequent colonization (Hilmo and Holien, 2002).

Lichen growth under relatively closed forest canopies may be limited because lichen photosynthesis is rarely at its maximum rate at low light level (Green et al., 1995; Esseen, 2006). Higher light levels following edge creation and windthrows may thus favor the growth of lichen thalli. For instance, Esseen and Renhorn (1998) proposed that the increase in biomass of *Alectoria sarmentosa* observed 11–16 years after cut at mid-distance from the edge was a result of an increase in light intensity. Similarly, higher growth rates of two foliose lichens (*L. pulmonaria* and *Platismatia glauca*) were found at 12 m from the edge (Renhorn et al., 1997). In our study, it is not impossible that the growth rate of at least some thalli might have increased after edge creation, but no significantly higher biomass values were found at mid-distances from the edge. However, the growth rate of species that are more frequent and abundant in dense and closed canopy forests, such as *B. nadvornikiana* (Brodo and Hawksworth, 1977; Brodo et al., 2001), may not increase following edge creation. An ongoing study showed that canopy opening following partial cutting has negative impacts on the growth of *B. nadvornikiana* in the western part of the boreal forest of Quebec (Boudreault et al., in preparation). Furthermore, increased evaporation at edges may lead to shorter hydration event time and thus reduce the time for photosynthetic activity as suggested by Esseen (2006). The effect of environmental modifications might be particularly pronounced for small thalli (Gauslaa and Solhaug, 1998), as proposed for *Bryoria* spp. by Hilmo and Holien (2002), because they may desiccate more rapidly than large ones.

Epiphytic lichens only accumulate biomass if growth rates are superior to thallus fragmentation rates. The lower biomass of *Bryoria* in cutblock separators and riparian buffers and the significant decrease in biomass of *Bryoria*, *Usnea*, and

Evernia at the edge of cutblock separators and large forest remnants suggest that fragmentation could have eliminated the positive effects due to increased light levels induced by edge creation. Although thallus fragmentation is an efficient and natural way of dispersal for many *Bryoria* species (Esseen, 1985; Stevenson, 1988; Dettki, 1998), thalli are not adapted to strong winds since they developed in relatively closed stands (Esseen and Renhorn, 1998). Thus, strong winds can have a negative impact on lichen biomass accumulation by causing excessive thallus fragmentation at forest edges (Esseen and Renhorn, 1998; Rheault et al., 2003). Thalli that have subpendant or pendant growth form and filamentous species with highly dissected thalli, like *B. trichodes* and *B. nadvornikiana*, can be easily fragmented by wind (Esseen, 1985). High lichen mortality is mainly associated with extreme climatic events such as storms, particularly during autumn and winter, or heavy snow load on branches (Esseen, 1985). However, species of *Bryoria* that grow rolled up around branches such as *B. furcellata* would be less affected by thallus fragmentation (Rheault et al., 2003). In managed landscapes of northwestern Quebec, Rheault et al. (2003) suggested that the dominance of *B. furcellata* in their study may explain the weak influence of edges on the biomass of this species of *Bryoria*. The presence of a central axis in *Usnea* (Esseen, 1985; Renhorn, 1997) and the robustness of *E. mesomorpha* thalli make these species (except for *U. longissima*) less prone to fragmentation compared with *Bryoria*, and may explain the lower edge influence found for *Usnea* and *Evernia* in our study.

Edge effects on poikilohydric organisms can vary according to edge aspect (Kivistö and Kuusinen, 2000; Hylander, 2005). For instance, Hylander et al. (2005) showed that exposure to sunlight between north-north-east and south-south-west facing edges modify the growth of two mosses at the edge. On the other hand, Renhorn et al. (1997) found no influence of edge aspect on the growth rates of *L. pulmonaria* and *P. glauca*, but in this case, only one east facing edge was investigated. East aspect might represent the most favorable edge for epiphytic lichens, with intermediate light levels and a moister microclimate (Chen et al., 1993). No difference in lichen biomass between our SSE and NNW facing edges of cutblock separators was detected in our study. Since the study was not designed specifically to address this question, it is impossible to determine precisely whether this is due to an absence of effect, or to multiple effects that cancel each other (thalli fragmentation due to wind exposure, desiccation due to solar radiation, etc.).

4.3. Management implications

Epiphytic lichens are more abundant in mature and old-growth forests than in regenerating forests because biomass accumulation is a slow process that occurs as the forests age (Lesica et al., 1991; McCune, 1993; Esseen et al., 1996; Dettki and Esseen, 1998). Consequently, in landscapes harvested by clear-cuts, epiphytic lichens are mainly restricted to remnant habitats of mature and old forests. Because these remnants are mostly of linear shape, edge effects become an important component particularly in cutblock separators that are likely to experience changes in the composition of the lichen communities.

Since lichens were not identified at the species level, it is not possible to tell if some species are more affected by edge effects than others. Hence, conclusions at species level may eventually differ from those at genus level. However, our results suggest that a managed forest where the only mature and overmature stands remaining are cutblock separators and riparian buffers will not maintain the integrity of epiphytic lichen communities at the landscape scale, notably the high biomass of *Bryoria* observed in interior forests. Such a management approach is also likely to jeopardize lichen recolonization of regenerating areas, lichen metapopulation dynamics (Snäll et al., 2005), and other organisms that are associated with epiphytic lichens such as invertebrates and forest birds (Pettersson et al., 1995).

Within a managed forest, some measures must be adopted to reduce edge effects by diminishing the contrast between remnant habitats and the regenerating matrix (Esseen, 2006), while increasing connectivity between remnant habitats and favor epiphytic lichens recolonization. For upland corridors such as cutblock separators our results reemphasize Mascarúa López et al. (2006) conclusions that 60-m wide strips are not large enough to maintain core habitat conditions for species associated to late seral stages. Therefore, the width of linear habitats should be increased. Partial cuts could be used at the interface between clear-cuts and remnant forests to compensate for the economic losses associated with the widening of corridors, while decreasing the risk of windthrow, increasing the size of the core habitats, and generating a more gradual transition between edge and interior conditions. Because the decrease in edge effects over time is dependent on the trees in regenerating areas, it is also important to insure that regenerating areas near edges are well stocked. Riparian buffers might be adequate for maintaining epiphytic lichen communities living at the interface of aquatic and terrestrial ecosystems since little damage to forest structure was detected by Mascarúa López et al. (2006). However, further research that compares continuous forests with a riparian zone to riparian buffers are needed to evaluate edge effects in this type of habitat.

Finally, because biomass accumulation of epiphytic lichens is a slow process that requires forest continuity, forest management units need to maintain large tracts of mature and overmature forests between cutover areas that offer adequate interior conditions and reduce edge effects. Even if cutblock separators and riparian buffers could not maintain by themselves the integrity of interior mature or overmature forest epiphytic lichen community in a forestry-dominated landscape, they could act as ‘‘life-boats’’ by providing refuge for lichen species and increase connectivity between large tracks of residual forests. When large forests are linked with linear and patchy remnant habitats in cutover landscapes, they could be functional ‘‘source’’ habitats in a context of metapopulation dynamics (Sillett et al., 2000).

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