



Differential impact of clearcut and insect outbreak on boreal lichens and bryophytes 50 years after disturbance

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ABSTRACT

Lichens and bryophytes are ubiquitous in terrestrial habitats, sensitive to environmental changes, and they contribute to ecosystem functions and biogeochemical cycles. Intact forest ecosystems host distinct biotic communities that are associated with microhabitat and structural diversity at stand and landscape scales. In the boreal region of eastern Canada, insect outbreaks and clearcutting (the dominant timber harvesting method) are common disturbances. However, while insect outbreaks from native species can maintain ecological continuity, clearcutting disrupts it and homogenizes forest structure. We compared lichen and bryophyte communities between old-growth forest stands and 50 years-old stands regenerated from clearcuts and insect outbreaks. From these communities, liverwort and deadwood specialist species richness was higher in insect outbreak and old-growth than in clearcut forest stands. Stand type explained 10.3 % and 7.0 % of the variability observed in liverwort and deadwood specialist community composition, respectively. Clearcut stands were responsible for most of this variability since communities had less unique species and lacked some of the most common species found in old-growth and insect outbreak stands. Indeed, many species associated with deadwood and ecological continuity appeared unable to recolonize forest stands between planned intervals of clearcut rotations (i.e. ~50 to 60 years in our study area). However, deadwood volume did not differ between stand types and could not explain any part of the observed variability in the composition of communities. We suggest that forests regenerating from insect outbreaks are a suitable alternative for biological conservation in regions where old-growth forests are rare, especially for liverworts and deadwood specialists.

1. Introduction

Recent reviews indicate that species extinction rate is higher than it would be in the absence of anthropogenic disturbances (Cowie et al., 2022). There is an opportunity to reduce this biodiversity crisis through conservation actions undertaken in threatened ecosystems, from establishing protected areas to improving land-use policies (Allan et al., 2022). Intact forest ecosystems and wilderness areas are paramount to long-term sustainability of biological diversity, ecological processes, ecosystem services, and indigenous cultures (Di Marco et al., 2019; Watson et al., 2018). Lichens and bryophytes can be found in almost any terrestrial ecosystem on Earth; they are especially abundant at higher

latitudes, where they have major impacts on biogeochemical cycles and ecosystem functions (Asplund and Wardle, 2017; Porada et al., 2014). Moreover, lichen and bryophyte communities are sensitive to environmental changes (Hawksworth and Rose, 1970; Lang et al., 2012; Nas-cimbene and Spitale, 2017) and can be useful to monitor the current biodiversity crisis and the efficiency of policies intended to avert it (Miller et al., 2020; Outhwaite et al., 2019; Pakeman et al., 2019).

The boreal forest includes some of the largest remaining areas on Earth with very low anthropogenic impact (Gauthier et al., 2015), where lichens and bryophytes are conspicuous features of the ecosystem (Asplund and Wardle, 2017; Turetsky et al., 2012). Forests that have been historically exempt of severe anthropogenic activities, such as

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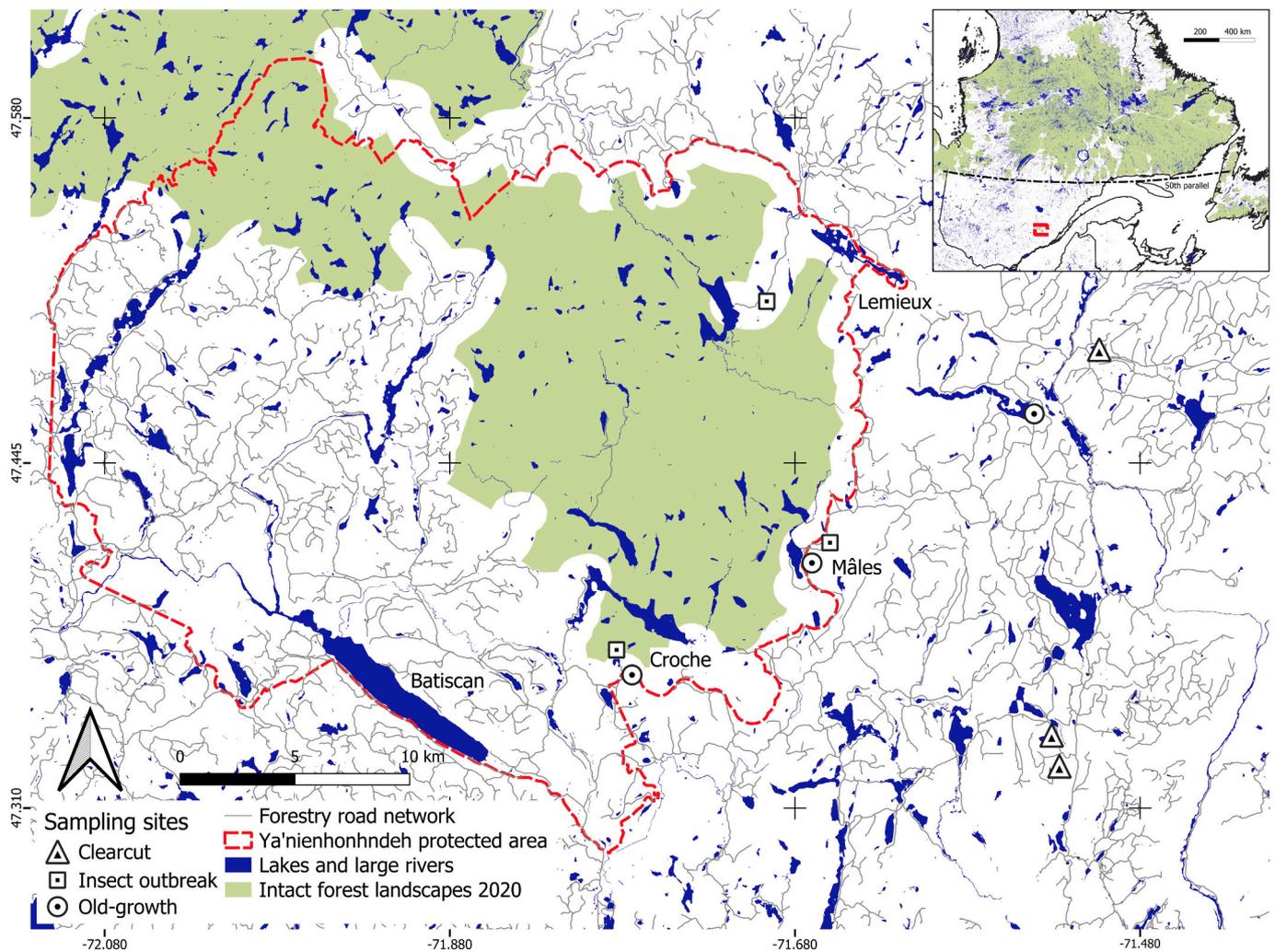


Fig. 1. Location of selected balsam fir forest stands to sample lichens, bryophytes, and liverworts in eastern Canada in 2019. Lemieux, Mâles, and Croche are the sectors, each including one forest stand per stand type. Batiscan is the largest lake in the area. Gray lines represent the forestry road network. The inset map locates the study area (in red) in eastern Canada, where the dotted line represents the 50th parallel. The data on intact forest landscapes are from Potapov et al. (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

industrial timber harvesting or mining, have a high degree of ecological continuity and often host unusual sets of specialist species (Fritz et al., 2008; Selva, 2003; Wiersma and McMullin, 2019). In the boreal forest of eastern Canada, insect outbreaks and windthrows are the dominant natural disturbances and they tend to develop irregular stand structures where diverse communities thrive (Despouts et al., 2004; McCarthy and Weetman, 2007; McMullin et al., 2010). Meanwhile, clearcuts are the dominant timber harvesting method and they homogenize forest structure, hence influencing biotic communities (Boucher et al., 2015; García-Tejero et al., 2018). Asexually reproducing deadwood specialist species that have limited dispersal capabilities are among the most sensitive to forest management and fragmentation (Boudreault et al., 2018; Sillett et al., 2000; Söderström, 1988). Unavailability of microhabitats associated with old-growth forest also impedes the establishment of specialist species (Fenton and Bergeron, 2008; Löhmus and Löhmus, 2011; Rheault et al., 2009). Reducing gaps between managed and natural forests is a cornerstone of natural disturbance-based forest management, a strategy to balance human resource needs with biodiversity goals through a mixture of land sparing and sharing at different spatial scales (De Grandpré et al., 2018; Kuuluvainen et al., 2021).

Many studies interested in the long-term response of boreal lichen and bryophyte communities to disturbances involve a comparison between harvesting methods and old-growth or wildfires (e.g.,

Nascimbene et al., 2010; Paquette et al., 2016). Investigations on the effect of insect outbreaks compared to clearcuts rarely involve both bryophytes and lichens, or focus on the first decades of succession (Fourrier et al., 2015; Schmalholz et al., 2011). In a boreal landscape which includes a large area of unmanaged forest, we investigated whether lichen and bryophyte communities at the stand level converge to a similar state 50 years after a clearcut and an insect outbreak. We hypothesized that the disruption in ecological continuity caused by the mass removal of logs (i.e. future deadwood habitat) during clearcuts compared to insect outbreaks will influence bryophyte and lichen community composition, and that differences can still be detected 50 years later.

2. Material and methods

2.1. Study area

The study area is located in the Ya'nienhonhndeh territory of the Huron-Wendat First Nation, northwest of Québec City in eastern Canada (47°27'N, 71°45'W). According to Potapov et al. (2017), it is part of the southernmost intact forest landscape in the province of Québec, and it has a rich cultural heritage (Lesage et al., 2018). Sampling was conducted in the highest elevation zone between 650 and 750 m above sea

level where forests are dominated by balsam fir (*Abies balsamea* (L.) Mill.), mostly co-occurring with white birch (*Betula papyrifera* Marshall) and white spruce (*Picea glauca* (Moench) Voss). Mean annual temperature in the region is 0.5 °C and mean annual rainfall and snowfall are 963 mm and 620 cm, respectively (Environment Canada, 2023). Forest succession is driven mainly by spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks (Blais, 1983), as naturally occurring forest fires ceased more or less abruptly 4500 years ago (Couillard et al., 2013). This part of the Ya'nienhonhndeh territory has historically been left unharvested by pulp and paper companies due to successive severe insect outbreaks (Blouin, 1981).

2.2. Sampling and forest structure variables

We collected lichen and bryophyte samples in June and July 2019 in a stratified sampling design with three sectors and three stand types (nine stands in total). The stand types are: 1. stands regenerated from clearcuts 50 years ago; 2. stands regenerated from a severe insect outbreak 50 years ago; 3. stands >80 year-old affected by a mild insect outbreak 50 years ago, hereafter referred to as old-growth (Fig. 1). We selected stands in ArcGIS 10.8 (ESRI, 2020) based on the 5th decennial forest inventory, where the threshold to differentiate a mild from a severe insect outbreak is 75 % of basal area lost (Government of Québec, 2023), and the stands were groundtruthed for suitability. Selection criteria were accessibility, absence of silvicultural treatments, balsam fir cover >50 %, white birch cover >15 %, moderate drainage, thick glacial till surface deposit, and a podzol soil type. In each forest stand, we measured forest structure variables in three circular plots of 400 m² following standard Canadian methodology (National Forest Inventory, 2008) to compare forest structure between stand types and sectors (Table A1).

In addition to the stand structure sampling, we sampled lichens and bryophytes in eight cubic plots of 8 m³ (2 × 2 × 2 m) per forest stand, hence 24 plots of 8 m³ per stand type and 72 in total (Fig. A1). The location of the 8 m³ plots was predetermined in studied stands at regular intervals of 50 to 80 m to represent the variability present within the stand and to avoid spatial autocorrelation. In the field, we established the center of the 8 m³ plots at the middle of the largest piece of deadwood almost entirely covered by bryophytes within a 5 m radius around the observer at the predetermined location. Within each plot of 8 m³, we measured and identified every tree to species. We also measured the diameter of snags and the volume of deadwood, but their identification to species was not possible when in an advanced state of decomposition. We used a prism plot radius factor 2 to acquire forest structure variables linked to each lichen and bryophyte plot of 8 m³ to evaluate how forest structure influenced community composition. The forest structure variables acquired from the prism plots were: basal area of trees and snags, mean diameter at breast height (DBH) of trees and snags, percentage of *Abies balsamea*, *Betula papyrifera*, *Picea* spp., and snags, as well as age of the largest tree.

Within each plot of 8 m³, we collected at least one sample of every species of lichen and bryophyte colony found occurring on soil, deadwood, trees, and snags, sampling systematically from the soil up towards deadwood, and then to trees to avoid trampling. Mixed colonies of liverworts were also gathered for later observation to detect inconspicuous species. Samples were dried at 40 °C for 48 h then frozen at -20 °C for 72 h prior to identification. For our analyses, we grouped the liverwort species *Calypogeia neesiana* and *C. integristipula* into a complex and we did the same for a second complex composed of *Lophozia ventricosa* and *L. silvicola*. All other individuals were identified to species and used in the analyses. We used stereo- and compound microscopes to identify moss, liverwort and lichen species with reference books and keys (Brodo, 2016; Brodo et al., 2001; Faubert, 2012, 2013, 2014; Lendemer, 2013; McCune, 2017a, 2017b; Selva, 2013, 2014). We performed spot tests on lichens with sodium hypochlorite, potassium hydroxide 10 %, and *p*-phenylenediamine in 70 % ethanol (Brodo et al., 2001). Thin layer

chromatography was systematically performed in toluene/acetic acid 200:30 (Orange et al., 2010) for specimens of the genera *Bryoria*, *Leptra*, *Lepraria*, *Micarea*, *Mycoblastus*, *Ochrolechia*, *Ropalospora*, *Trapeliopsis*, *Usnea*, and the *Cladonia chlorophaea* group. We deposited 403 vouchers in the public collection at the Louis-Marie Herbarium (QFA), including at least one from most species identified.

2.3. Data analyses

Statistical analyses were performed in R software version 4.2.3 (R Core Team, 2023). We checked species accumulation curves to evaluate if our sampling effort was sufficient to capture most species occurring in the targeted habitats (Colwell et al., 2004). The data we collected would have ideally been analyzed using a model that included random effects of stand or sector to reflect the nested structure of the data (Pinheiro and Bates, 2000). Unfortunately, the variance of these random effects could not be estimated in these models, as the estimate was too close to 0. Due to model instability, we used Poisson regressions to determine the influence of stand type, sector, and their interactions on the species richness of liverworts, lichens, mosses, and deadwood specialists. Here, deadwood specialists refer to species of liverworts, lichens, and mosses that occurred exclusively on deadwood, and for which our experience and the literature concurred with this observed substrate restriction (Table A2). We used type I analysis of deviance based on log-likelihood ratio tests to evaluate the contribution of each term in the model (Fox, 2002; McCullagh and Nelder, 1989). We used Tukey-type multiple comparisons for factors identified as having an effect in the analysis of deviance. We used residual diagnostics to check assumptions and estimated potential overdispersion based on the Pearson chi-square (McCullagh and Nelder, 1989). We used Venn diagrams to evaluate the overall number of species shared between stand types, but also unique to stand types. Furthermore, we investigated species and pairs of species associated with stand types and pairs of stand types through indicator species analyses (De Cáceres and Legendre, 2009; De Cáceres et al., 2010, 2012).

We assessed the influence of stand type and sector on liverwort, lichen, moss, and deadwood specialist community composition with permutational analyses of variance (PERMANOVA) based on Euclidean distances implemented in the *vegan* package (Oksanen et al., 2022). We used Euclidean distances instead of Bray-Curtis to meet the assumption of homogeneous multivariate dispersions (Anderson, 2001, 2006). We then visualized results through a non-metric multidimensional scaling (NMDS) ordination with Bray-Curtis dissimilarity matrices. We also carried out distance-based redundancy analyses (dbRDA) to evaluate how much of the variability observed in community composition could be explained by forest structure variables (Legendre and Anderson, 1999). The explanatory variables considered in the dbRDA were: volume of deadwood and number of trees in 8 m³ plots, and mean DBH of trees, age of the largest tree, and percentage of snags and *Betula papyrifera* in the corresponding prism plots. We ensured that these variables were not strongly correlated (Pearson correlation $|r| < 0.4$).

Finally, we compared forest structure variables from the circular 400 m² plots between stand types and sectors with two-way ANOVAs and Tukey HSD post-hoc tests to ascertain that stands were similar. Assumptions were checked with residual diagnostics. When variances were heterogeneous or when residuals were not normally distributed, we log-transformed the response variable, but sometimes this was not sufficient to meet assumptions. In such cases, we used a generalized least square model that included a term to explicitly model heteroscedasticity (Pinheiro and Bates, 2000). Data and annotated scripts are available upon request to the corresponding author.

3. Results

We report 91 species of lichens and allied fungi from 2613 determinations, 21 species of liverwort from 2789 determinations, and 33

Table 1

Analysis of deviance table (type I effects) based on log-likelihood ratio tests from Poisson regression models comparing liverwort, lichen, moss, and deadwood specialist species richness, including the effect of stand type, sector, and their interaction from a balanced sampling design in eastern Canada. There were 63 residual degrees of freedom in the analyses. Model coefficients, standard errors, and 95 % confidence intervals of the Poisson models are detailed in Table A4.

	Source					
	Stand type		Sector		Stand type × sector	
Response community	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Liverworts	18.81	<0.001	0.27	0.876	2.52	0.642
Lichens	8.24	0.016	3.35	0.187	5.46	0.243
Mosses	1.79	0.408	0.89	0.639	3.10	0.541
Deadwood specialists	19.96	<0.001	0.01	0.996	0.94	0.918

species of moss from 2219 determinations. A determination is defined as the identification of any one species in any one sample. The 25 most common species represented 72 % of the total number of specimens while 29 species were only found in a single plot of 8 m³ (Table A2). >60 % of all species were collected at least once in each of the three stand types, but old-growth stands had more unique species ($N = 22$) than stands in clearcuts ($N = 11$) and insect outbreaks ($N = 3$, Fig. A2). Species unique to old-growth stands include seven calicioid lichens and fungi, and another seven species of bryophytes and lichens that are deadwood specialists. Accumulation curves showed that most bryophytes occurring in the selected stands were likely to have been sampled, but more lichen species would probably have been found with additional sampling effort (Fig. A3). Mean plot species richness of liverworts, lichens, and deadwood specialists varied with stand type, but not with sector or their interaction (Table 1). Insect outbreak and old-growth stands hosted significantly more species of liverworts and deadwood specialists per plot of 8 m³ than clearcut stands (Fig. 2), even if the species richness at stand-level was very similar among stand types (Table A3). In contrast, there was no evidence of variation in moss

species richness with either stand type, sector, or their interaction (Table 1).

The best indicator species of old-growth, insect outbreak, and clearcut stands were the bryophyte pairs *Calypogeia neesiana/integristipula* + *Brotherella recurvans*, *Bazzania trilobata* + *Nowellia curvifolia*, and *Polytrichum commune* + *Ptilium crista-castensis*, respectively (Table 2). Naturally-disturbed forests (i.e. combination of old-growth + insect outbreak stands) had both the most ($n = 69$) and the best (Indicator Value Index (IndVal) > 0.800) indicator species while clearcut stands had only three indicator species. When calicioid fungi and lichens (i.e. genera *Calicium*, *Chaenotheca*, *Mycocalicium*, *Phaeocalicium*, and *Sclerophora*) were analyzed as a group, their presence became an indicator of old-growth stands (IndVal = 0.433, $p = 0.042$), which performed better when coupled with the deadwood specialist liverwort *Syzygiella autumnalis* (IndVal = 0.500, $p = 0.001$).

PERMANOVA revealed that stand type explained 10.3 % and 7.0 % of the variability observed in liverwort and deadwood specialist community composition, respectively, with no effect of sectors (Table 3). Clearcut stands were responsible for most of this variability since communities had less exclusive species and often lacked some of the most common species found in naturally-disturbed stands such as *Brotherella recurvans*, *Lepidozia reptans*, and *Nowellia curvifolia*. Meanwhile, old-growth and insect outbreak stands consistently hosted highly similar liverwort and deadwood specialist communities (Fig. 3). Lichen and moss communities were also influenced by both stand type and sector, although each factor explained no >5.0 % of the observed variability (Table 3, Fig. A4).

Distance-based redundancy analyses showed that lichen community composition varied with the number of trees per plot of 8 m³ and the percentage of white birch cover, whereas moss communities varied with mean tree diameter at breast height (DBH) and the age of the largest tree (Fig. 4). Liverwort community composition did not vary with any of the measured forest structure variables ($F < 2.000$, $p > 0.105$). Deadwood specialist community composition varied with the age of the largest tree

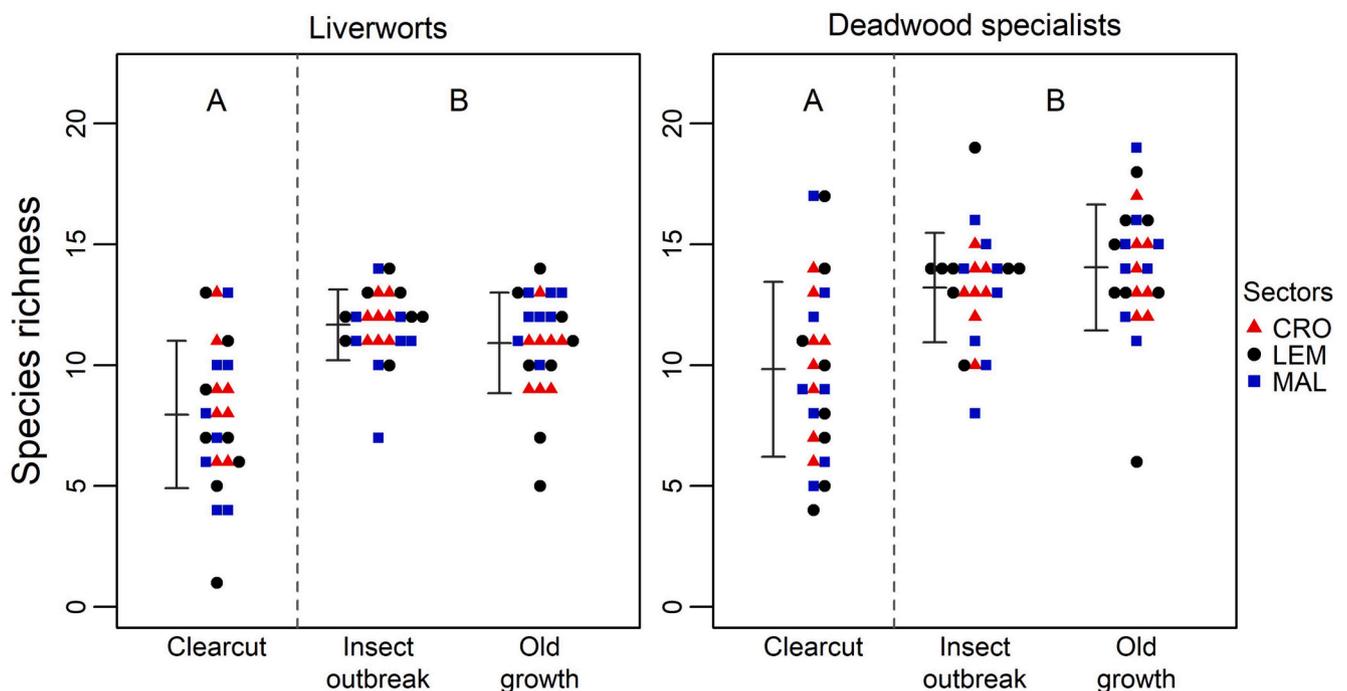


Fig. 2. Species richness by stand type for deadwood specialists (left) and liverworts (right) from a balanced sampling design of 72 plots of 8 m³ in eastern Canada. Letters A and B represent significantly different groups based on Tukey-type post-hoc multiple comparisons performed when the analysis of deviance detected an effect of stand type (Table 1). Whiskers show the standard deviation around the observed mean. Abbreviations: CRO = Croche Lake (red triangles); LEM = Lemieux Lake (black circles); MAL = Males Lake (blue squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Indicator species analysis measuring the association between species and stand types from a balanced sampling design of 72 plots of 8 m³ in eastern Canada. Only the three best indicators of each stand type are shown. “N” is the total number of indicators per stand type (Table A6). “A” is the probability that a plot belongs to the target stand type if the species are found. “B” is the probability of finding the species in a plot belonging to the target stand type. The Indicator Value Index (IndVal) is the square-root of the product of A and B.

Stand type	Indicators	A	B	IndVal	p
Old-growth N = 21	<i>Calypogeia neesiana/integristipula</i> + <i>Brotherella recurvans</i>	0.688	0.458	0.561	0.004
	<i>Calypogeia neesiana/integristipula</i> + <i>Parmeliopsis hyperopta</i>	0.647	0.458	0.545	0.026
	<i>Calypogeia neesiana/integristipula</i> + <i>Vulpicida pinastri</i>	0.625	0.417	0.510	0.044
Insect outbreak N = 50	<i>Bazzania trilobata</i> + <i>Nowellia curvifolia</i>	0.654	0.708	0.681	0.001
	<i>Bazzania trilobata</i> + <i>Biatora vernalis</i>	0.682	0.625	0.653	0.001
	<i>Neorthocaulis attenuata</i> + <i>Loxospora elatina</i>	0.600	0.625	0.612	0.012
Clearcut N = 3	<i>Polytrichum commune</i> + <i>Ptilium crista-castensis</i>	0.750	0.250	0.433	0.034
	<i>Cladonia rangiferina</i> + <i>Imshaugia aleurites</i>	1.000	0.167	0.408	0.023
	<i>Cladonia rangiferina</i> + <i>Ropalospora viridis</i>	1.000	0.167	0.408	0.023
Young (=insect outbreak + clearcut) N = 2	<i>Ptilium crista-castensis</i> + <i>Ropalospora viridis</i>	0.806	0.604	0.698	0.032
	<i>Nowellia curvifolia</i> + <i>Parmelia saxatilis</i>	1.000	0.208	0.456	0.037
Naturally-disturbed (=old-growth + insect outbreak) N = 69	<i>Lepidozia reptans</i>	0.706	1.000	0.840	0.028
	<i>Platismatia glauca</i> + <i>Blepharostoma trichophyllum</i>	0.706	1.000	0.840	0.028
	<i>Nowellia curvifolia</i>	0.804	0.854	0.829	0.001
Old-growth + clearcut N = 2	<i>Polytrichum commune</i>	1.000	0.229	0.479	0.026
	<i>Tetraphis pellucida</i> + <i>Hypogymnia tubulosa</i>	1.000	0.208	0.456	0.038

($F = 2.670, p = 0.012$), although the overall model did not explain much of the observed variability ($R^2 = 0.037$) and is therefore not represented. Deadwood and stump density was similar between stand types, and deadwood volume in 8 m³ did not influence the composition of any community. Forest structure variables showed that old-growth stands had higher white birch tree cover, insect outbreak stands had smaller mean tree DBH and higher sapling density, and clearcut stands had larger sapling mean DBH and higher percentage of dead saplings (Table A5).

4. Discussion

In accordance with our hypothesis, we observed that lichen and bryophyte community composition differs between clearcuts and insect outbreaks, and that differences can still be detected and attributed to the type of stand-replacing disturbance 50 years later. We previously unveiled similar patterns in soil microbial communities within the same research design (Bell-Doyon et al., 2022). Our results concur with a study in New Brunswick where insect outbreaks had a different impact on bryophyte communities than wildfires and clearcuts 40 years after disturbance (Schmalholz et al., 2011). These combined observations indicate that clearcuts impact boreal forest biodiversity in a way that deviates from insect outbreaks, and that this gap is not overcome by

secondary growth between planned intervals of clearcut rotations (i.e. ~50 to 60 years in our study area). However, it must be kept in mind that these studies are observational, and they did not characterize the surrounding landscape which can influence the composition of lichen and bryophyte communities at stand level (Caruso et al., 2010; Löhmus et al., 2007; Ruete et al., 2014).

Concurrent with the literature (e.g. Boudreault et al., 2018; Söderström, 1988), we observed that liverwort and deadwood specialist communities were the most sensitive to clearcuts. This result could be explained by a discontinuity in deadwood supply combined with low dispersal capability of mainly asexually reproducing species (Sillett et al., 2000). Indeed, while trees overwhelmed by insects eventually become suitable habitat for deadwood specialist communities, only stumps remain in clearcuts. Unlike fallen trees, we observed that rotten stumps were overgrown by large and common mosses such as *Pleurozium schreberi* and *Hylocomium splendens*, which outcompete tiny deadwood specialist liverworts. Moreover, other studies in the boreal forest have shown that there is a gap in deadwood availability in the first decades following clearcuts (Nirhamo et al., 2023; Paquette et al., 2016). However, 50 years after disturbance, we detected no significant difference in deadwood and stump density between stand types (Table A5), and the volume of deadwood within plots of 8 m³ sampled for lichens and bryophytes did not influence the composition of any community. This

Table 3

Results from PERMANOVA (type I effects) with 10,000 permutations on Euclidean distances of liverwort, lichen, moss, and deadwood specialist communities from a balanced sampling design of 72 plots of 8 m³ in eastern Canada. Abbreviations: df, degrees of freedom; SS, sum of squares; MS, mean sum of squares. Multivariate dispersions were homogeneous in all groups ($F < 1.761, p > 0.100$).

Community	Source	df	SS	MS	F	R ²	p
Liverworts	Stand Type	2	19.31	9.66	4.064	0.103	<0.001
	Sector	2	5.97	2.99	1.257	0.032	0.187
	Stand type × Sector	4	13.11	3.28	1.380	0.070	0.059
	Residuals	63	149.63	2.38			
Lichens	Stand Type	2	25.42	12.71	1.562	0.042	0.001
	Sector	2	29.50	14.75	1.813	0.049	<0.001
	Stand type × Sector	4	37.50	9.38	1.152	0.062	0.081
	Residuals	63	512.62	8.14			
Mosses	Stand Type	2	10.56	5.28	1.583	0.042	0.014
	Sector	2	12.56	6.28	1.883	0.050	0.001
	Stand type × Sector	4	19.03	4.76	1.427	0.075	0.009
	Residuals	63	210.00	3.33			
Deadwood specialists	Stand type	2	21.50	10.75	2.648	0.070	<0.001
	Sector	2	9.58	4.79	1.180	0.031	0.193
	Stand type × Sector	4	20.83	5.21	1.283	0.068	0.050
	Residuals	63	255.75	4.06			

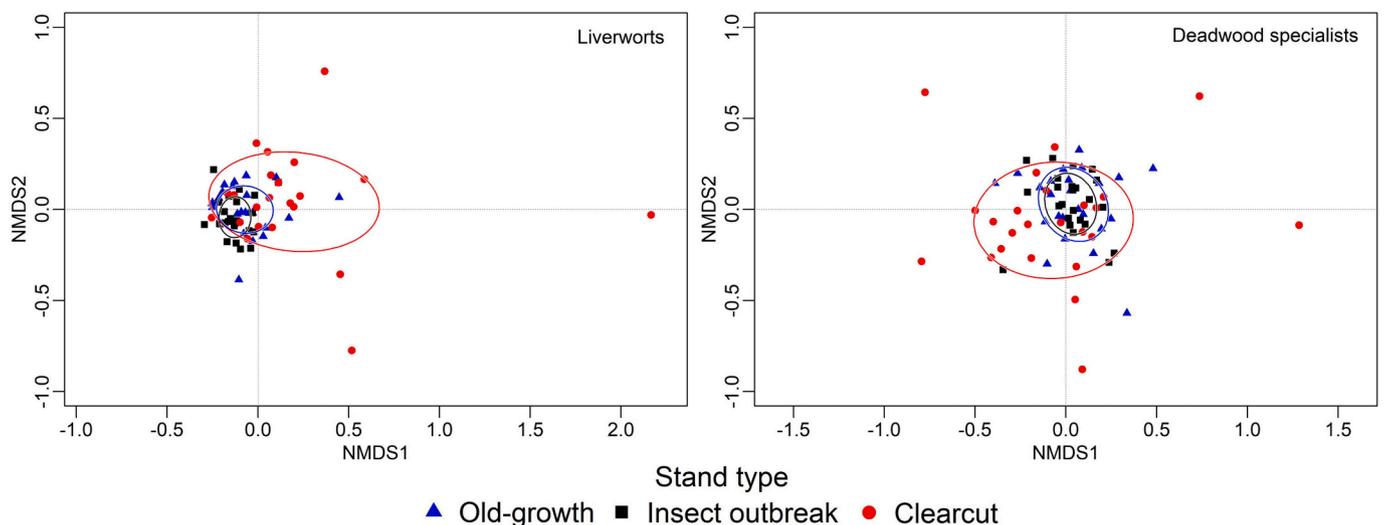


Fig. 3. Ordination plots based on a non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity matrices showing the variability in liverwort (left) and deadwood specialist (right) community composition across stand types from a balanced sampling design of 72 plots of 8 m³ in eastern Canada. Ellipses indicate the standard deviation of points around their group's respective centroid. Sectors are not represented since they did not have a significant impact on liverwort and deadwood specialist community composition ($F < 1.258$, $p > 0.186$).

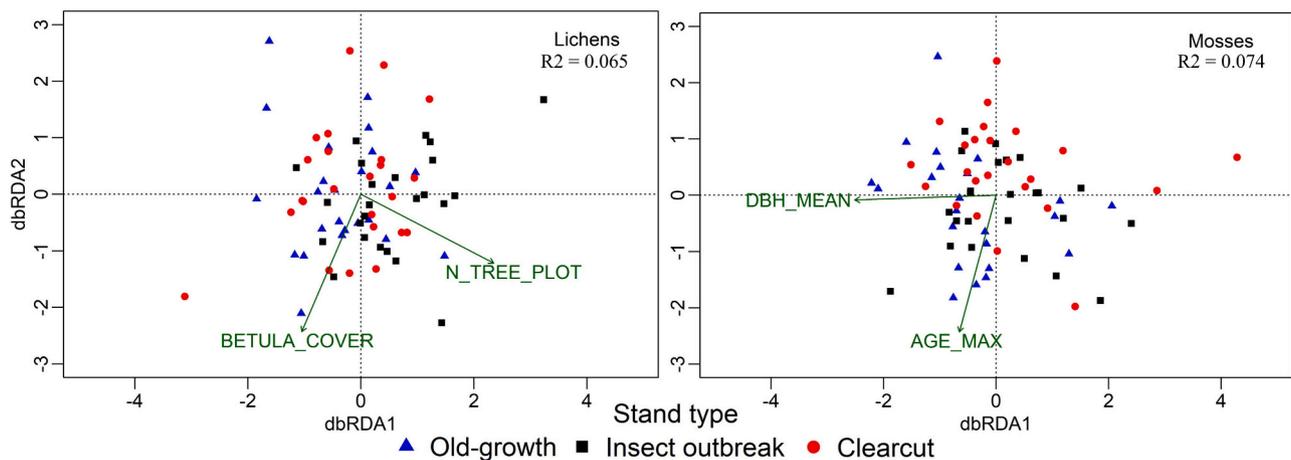


Fig. 4. Ordination plots based on distance-based redundancy analysis showing the influence of forest structure variables on lichen (left) and moss (right) community composition from a balanced sampling design of 72 plots of 8 m³ in eastern Canada. Both axes are statistically significant in both graphs ($F > 2.165$, $P < 0.050$). N_TREE_PLOT = Number of trees per bryophyte and lichen plot of 8 m³; DBH_MEAN = Mean diameter of trees at breast height; BETULA_COVER = Percent cover of *Betula papyrifera*; AGE_MAX = Age of the largest tree. The last three variables are from the prism plot radius factor 2 associated with each plot of 8 m³ where bryophytes and lichens were sampled.

implies that the higher variability in community composition and lower species richness highlighted in 50 year-old stands regenerated from clearcuts cannot be explained by a higher deadwood sampling effort in naturally-disturbed stands. Thus, we can argue that continuity of deadwood supply appears critical to maintain deadwood specialist diversity in boreal forests.

Calicioid lichens and fungi have been proposed as indicators of old-growth forests and ecological continuity (Selva, 2003; Tibell, 1992; Wiersma and McMullin, 2022), and our indicator species analysis supports their reliability as such. However, the use of indicator species to evaluate forest continuity is restricted by regional variability, meaning that indicators in one place are not necessarily valid elsewhere (Sætersdal et al., 2005; Whittet and Ellis, 2013). Thus, indicator species from our study may not be useful across the broad spectrum of boreal forest integrity (Martin et al., 2018, 2019, 2021). Calicioids as a community might overcome this regional-specificity issue because their pattern of increased abundance and richness in intact forests seems to hold across regions (Bell-Doyon et al., 2021; Goward and Arsenault,

2018; Selva, 2003; Tibell, 1992), although the availability of specific substrate is also an important factor to consider (Löhms and Löhms, 2011). Besides looking at specific indicators, we suggest that in this case the sheer number of indicator species of naturally-disturbed forest stands ($N = 140$) relative to clearcut stands ($N = 3$) highlights how different their communities are from each other.

5. Conclusions

Considering that many species associated with deadwood and ecological continuity appeared unable to recolonize forest stands between harvesting rotations, we argue that successive clearcuts may lead to long-term biodiversity erosion. Meanwhile, lichen and bryophyte communities from old-growth stands were highly similar to 50 year-old stands regenerated from an insect outbreak. Thus, we suggest that forests regenerating from insect outbreaks are a suitable alternative for biological conservation in regions where old-growth forests are rare, especially for communities of liverworts and deadwood specialist which

are the most sensitive to clearcuts.

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CRedit authorship contribution statement

Philip Bell-Doyon: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marc J. Mazerolle:** Writing – review & editing, Validation, Software, Methodology, Formal analysis, Conceptualization. **Louis Bélanger:** Writing – review & editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Nicole J. Fenton:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis. **Juan Carlos Villarreal A.:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Philip Bell-Doyon reports financial support was provided by Conseil de la Nation Huronne-Wendat. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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