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Patch level boreal bryophyte diversity driven by landscape heterogeneity



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ABSTRACT

While the influence of boreal landscapes on plants has been investigated in the drastically altered landscapes of Europe, we are lacking the knowledge on how the relatively intact landscapes of North America influence local bryophyte communities. Using a patch-landscape approach, we evaluated the effects of landscape composition (considering age and forest type of patches) and configuration (patch density) on bryophyte diversity (richness, common and dominant species) in old forest target patches. The effects of landscape composition and configuration (in 92 landscapes of 10 km radii) were evaluated both for all bryophytes and by guild (mosses, liverworts and Sphagna). The richness of mosses exhibited a negative correlation with the expanding area of young forests in the landscape. Furthermore, liverwort richness and its common species, experienced a significant decline when young forests comprised more than 40% of the landscape area. Response to mixed forest percent area influence differed among guilds, but diversity of liverworts and Sphagna were negatively related to increasing coniferous patch density. Even within the relatively undisturbed boreal forest of North America, young forests within managed forest regions, we suggest that the young forest area not exceed 40% of the surrounding landscape and that aggregation of these stands is avoided. The species loss thresholds detected here can be used in landscape planning to mitigate the negative effects of land-use change on boreal biodiversity.

1. Introduction

Understanding the response of local diversity to landscape composition and configuration (LCC) has become urgent due to the increase in human-modified landscapes (Farigh, 2019; Wen et al., 2023). Research focus to date has been in heavily modified landscapes, such as Europe (Kolb and Diekmann, 2004; Hartel et al., 2010; Gallé et al., 2022), which cannot provide answers on how species respond to a primeval landscape, and how future landscape modifications may change their response. Unlike European boreal forests, North American counterparts are still to a large extent commercially unexploited and, therefore, house a better preserved native biotic community (Ellis, 2013). For these reasons, firstly, we cannot rely exclusively on the effects found in European boreal forests when extrapolating to their North American counterparts. Secondly, it is urgent to fill this knowledge gap to conserve the diversity and ecological processes of one of the relatively well-preserved areas of the planet, before it is over-developed.

North American boreal forests face increasing land transformation

by natural (e.g., wildfires, insect outbreaks) and anthropogenic disturbances (e.g., harvesting, urban development) (Bradshaw et al. 2009; Erb et al. 2018), which are exacerbated by climate change (Macias and Johnson, 2008). These disturbances put at risk one of the planet's largest and most important carbon sinks and its biodiversity (Olson et al. 2001; Bradshaw et al. 2009; Velasco Hererra et al. 2022). Also, natural and anthropogenic disturbances have combined effects that impact ecological processes related to biogeochemical cycles and the structure of the forest community (Artaxo et al., 2022; Shao et al., 2022). In addition, climate change-mediated landscape fragmentation is predicted to reduce suitable niches and lead to the extinction of characteristic trees, birds, and mammals of the North American boreal forests (Murray et al., 2017). Despite these advances, little is known about the response of various plants and animals in these forests to landscape-level changes (Brandt et al. 2013; Venier et al. 2014), particularly of the understory species that are the main diversity driver in these environments (Hart and Chen, 2006). A clear example of one of these least understood groups of the understory concerning landscape effects is the bryophytes.

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Bryophytes (here, mosses, liverworts, and sphagna guilds) are a conspicuous group in boreal forests due to their diversity and biomass (Longton, 1992). Their dominance makes them the primary plants driving ecosystem functions such as primary productivity, water relations, carbon and nitrogen cycles, and as habitat for small invertebrates and a wide diversity of microorganisms (Williams and Rastetter, 1999; DeLuca et al. 2002; Turetsky et al. 2010). In old boreal forests, bryophyte diversity is characterized primarily by the presence of specialist species that are susceptible to off-site disturbances (Barbé et al. 2017). Bryophytes in general, but particularly liverworts, are sensitive to environmental changes because they depend on specific microhabitats conditions (humidity and substrate) (Frego, 2007; Cole et al. 2008). These microhabitat conditions are related to the local habitat characteristics, such as the type of vegetation cover and the patch size (Gignac and Dale, 2005; Barbé et al. 2017). Thus, bryophytes can be influenced by landscape disturbances that modify and fragment their habitat. In addition, these changes may affect the maintenance of their populations in the long term, since some species are dispersal limited and might not be able to reach the next suitable habitat after disturbance (Lönnell and Hylander, 2018; Yin et al. 2019).

The effects of different site-scale disturbances on bryophytes are increasingly better understood in boreal forests (Boudreault et al. 2018; Bartels et al. 2019; Gustafsson et al. 2020; Tullus et al. 2022). However, given the historic and current disturbances of boreal forests on large scales, the dynamics of their bryological richness cannot be understood and conserved by only studying them at the site-scale. Thus, it is necessary to consider the environmental context in which species are living (Hansson, 1992). Unfortunately, patch-landscape studies, analyzing the effects of landscape features on bryophyte diversity of a target site at the center of each study landscape (McGarigal and Cushman, 2002; Arasa-Gisbert et al. 2021) are lacking. The patch-landscape approach is advantageous because it analyzes how ecological variables measured in forest patches at the center of each study landscape are affected by LCC features assessed around each patch (McGarigal and Cushman, 2002). Although Paltto et al. (2006) revealed the influence of the landscape scale amount of habitat on endangered species, studies based on heterogeneous landscapes (mosaic models; Zonneveld, 1995; Antrop, 2022) that are used to explain the local diversity of bryophytes have not yet been developed. The present study aims to address those knowledge gaps by studying bryophyte communities in well-preserved North American landscapes (Turner, 2005). Knowledge about how species respond to landscape heterogeneity could be applied to the territorial planning of boreal forests experiencing habitat loss or undergoing forest management (Molina et al. 2022). For forest management, this would be a step towards implementing optimal human-modified landscapes that integrate management processes at a regional scale while conserving biodiversity (Arroyo-Rodríguez et al., 2020).

Studying bryophyte diversity in 92 old forest target patches, we address three main hypotheses: because landscape configuration patterns such as patch proximity do not seem to be an explanatory driver in bryophyte meta-community dynamics (Barbé et al. 2017), we hypothesize (H1) that landscape composition (variation of percentage of area of different ages and forest types) is the primary driver of bryophyte taxonomic diversity at patch scale. Furthermore, due to the remarkable specialist bryophyte richness in old forests (Barbé et al. 2017, 2020), we expect (H2) that the landscape composition based on the age of its forests influences more the patch bryophyte diversity than landscape composition based on forest type. Also, because liverworts are more vulnerable to local habitat features and disturbances (Fenton et al. 2003; Dynesius and Hylander, 2007), we expect (H3) that this bryophyte guild will be also more affected by landscape spatial patterns. Finally, because land cover dominance (defined by its age or forest type) influences the dynamics of bryophyte population distribution in the landscape (Holt, 1985; Pulliam, 1988; Barbé et al. 2020), we hypothesize (H4) that bryophyte community composition in old forest target patches will

experience species turnover according to LCC changes around the patch.

2. Materials and methods

2.1. Study area

This study was conducted in the western boreal forest in the province of Quebec, Canada (48 $^{\circ}$ N to 61 $^{\circ}$ N and 80 $^{\circ}$ W to 75 $^{\circ}$ W) (Fig. 1). The region has a gradient of spatial heterogeneity represented by forest patches of different ages and dominant tree species, lakes and rivers, and areas altered by natural and anthropogenic disturbances. The topography is generally flat, and soils are characterized by organic and clay deposits (Bergeron et al. 2004). The vegetation is dominated by black spruce forests (Picea mariana Mill). Other species found in the region are white birch (Betula papyrifera Marsh.), and pioneer species such as jack pine (Pinus banksiana Lamb.) and trembling aspen (Populus tremuloides Michx.) after wildfires (Dansereau and Bergeron, 1993). In addition to wildfire, natural disturbances include insect epidemics such as spruce budworm outbreaks (Choristoneura fumiferana Clemens) (Navarro et al. 2018). Organic matter accumulation on poorly drained clay soils, and flat topographies in humid and cold climates (paludification: Lavoie et al. 2005), is also predominant across the region. Human disturbances are characterized by logging activities developed in the last 50 years (Lavoie et al. 2005). Both wildfires and logging have led to landscape fragmentation and an increase in forest cover heterogeneity (Rayfield et al. 2020; Augustin et al. 2022).

2.2. Study design

To determine the LCC effects on local bryophyte communities, we used the patch-landscape approach, measuring the response variables (bryophytes taxonomic diversity indices and composition) in old forest target patches, using explanatory variables (landscape metrics) within the surrounding landscape (Andresen et al. 2018; McGarigal and Cushman, 2002).

We used an extensive existing database of bryophyte community composition collected during previous studies in the region (Chaieb et al. 2015; Castonguay, 2016; Barbé et al. 2020; Barbé et al. 2017). Species nomenclature was reviewed and updated according to the updated bryophyte checklist of the Société Quebecoise de Bryologie (2023). This database includes the community composition (species frequency) of bryophytes in 92 target patches. These target patches are old coniferous forests with age > 80 years old and size between 0.04 ha and 17,000 ha. We selected these target patches because they vary in size and are surrounded by landscapes that vary in the proportion of forest with different ages and tree species dominance. Thus, it was possible to assess the effects of landscape heterogeneity on bryophyte diversity at the patch level. For bryophyte sampling, between one and three rectangular sampling plots (5 \times 10 m) were established in the center of the target patches. The number of plots depended on the size of the target patch. The sampling method used is a modified version of Newmaster et al. (2005) and consisted of collecting all the bryophytes in all microhabitats present in the plots, for example, tree bases, large woody debris, rotten logs, peat mounds, and soil. Thus, we obtained a measure of frequency of each species in each plot.

2.3. Bryophyte taxonomic diversity

First, we used the number of occurrences per target patch as an abundance measure for our analyses. In the case of patches with two or three plots, we combined the data per patch to avoid pseudoreplication (Arasa-Gisbert et al. 2021). We then evaluated the bryophyte sampling completeness of each target patch using the sample coverage estimator where values close to one means complete data (Chao and Jost, 2012). Thus, we ensured that our target patches had equally complete species communities, representing all the species in the patch, and avoided the



b) Landscape classification based on forest patches age



c) Landscape classification based on the forest type of forest patches



Fig. 1. a) Study area in Western Quebec, Canada, showing 92 old forest target patches (black dots) around which, we circumscribe landscapes with a 10 km radius. The landscapes can be classified based on the b) age and c) forest type of their forest patches, which show a gradient in the percentage of their land covers across the study area.

risk of assuming landscape influence based on communities with incomplete sampling. Two of 92 target patches had sample coverage values below 0.70, and we removed these two patches from the subsequent analyses. Also, because our bryophyte sample coverage varied among patches from 0.77 to 0.99, we estimated species diversity using observed and expected data based on the extrapolation approach to ensure target patches were equivalent in sampling effort for the analyses (Chao and Jost, 2012).

Second, for the diversity metrics we calculated the effective number of species (richness, common, and dominant species, hereafter, diversity) for all bryophytes species and by bryophyte guild (mosses, liverworts, and sphagna). Sphagna was classified as a distinct guild due to its specialized morphological and physiological traits that enable water retention, thus facilitating peat accumulation (van de Koot et al., 2021). Additionally, its diversity is influenced by environmental factors that differ from those affecting other moss species in the boreal forest (Cerrejón et al., 2020). To calculate species diversity, we used the Hill numbers (Jost, 2006). Hill numbers include the q0 (species richness), which do not consider species abundances and highlight the rare species value, q1 (Shannon exponential), which weighs species in proportion to their frequency (typical or common species), and q2 (Inverse of Simpson) that considers the frequency of abundant species without rare species (dominant species) (Chao et al. 2014). To evaluate the sample coverage and calculate the Hill numbers, we used the *entropart* package (Marcon and Hérault, 2015) in the program R version 4.1.2 (R Core Team, 2021). We performed a correlation analysis between the richness (q0), common (q1) and dominant species (q2) of the entire bryophyte community and the guilds using the Hmisc package (Harrell, 2022). We found that, except for the common liverworts, the richness of each guild was correlated with the number of common and dominant species (r >=0.7, p < 0.001, Table A1, Appendix A). Therefore, we used the richness of mosses, liverworts and Sphagna and the number of common liverworts for further analyses.

2.4. Spatial data and landscape metrics

To define our study landscapes, we used a forest map from the Gouvernement du Québec (2020), where we created a 10 km radius buffer around each old forest target patch (Fig. 1). The radius scale was established considering the bryophyte dispersal capacity (Patiño and Vanderpoorten, 2018) and the potential influence of the size of managed areas in the regional boreal forests (Gouvernement du Québec, 2022). We then classified all the forest patches in our landscapes (buffer areas) based on two criteria, the first on the forest age and the second based on the forest type (Fig. 1b, c). The forest patch age classification in the landscape included: young forest (< 40 years old), medium aged forest (>40 to <80 years old), old forest (>80 years old). For the forest type classification, we considered the cover of coniferous, mixed, and deciduous forests, already categorized in the forest map based on the dominant tree species in forest stands with a minimum of 0.5 ha (Gouvernement du Québec, 2020). To establish the buffer area and to complete the landscape classification we employed the software ArcMap 10.8 (ESRI, 2010).

We used the Patch Analyst extension (Rempel et al. 2012) in ArcMap 10.8 (ESRI, 2010) to estimate the number of patches (n) and the area in hectares by class (C-ha) in the landscapes. Then, we calculated the percent landscape area covered by each class, by dividing the area of each class by the landscape area (C-ha/L-ha) (landscape composition metric). Subsequently, we calculated patch density by dividing the number of patches in each class by landscape area (n/L-ha) (landscape configuration metric). Consequently, we had 12 landscape metrics from six forest cover classes (three age classes and three forest type classes) by two landscape variables ("percentage of area" and "patch density").

2.5. Statistical analyses

We included the target patch size variable in our statistical models because it can also influence bryophyte diversity (Alvarenga et al. 2007). Thus, to assess the relationships between landscape metrics and target patch size, and bryophyte taxonomic diversity and composition (for both observed and expected data) we used generalized additive models (GAMs) using the gam function from the mgcv R package. The GAM models considered landscapes metrics based on the age and forest type separately (four GAMs sets). Subsequently, we assessed concurvity, a nonlinear measure like collinearity in linear regression (Gu et al. 2010), among landscape metrics using the mgcv package. After excluding correlated landscape metrics, we improved our model fit by applying a log transformation to the bryophyte diversity values. Model fit was also improved based on Akaike's Information Criterion by testing multiple models with all variables and removing step by step non-significant ones. Details of GAM and concurvity analysis are provided in Methods A1, and Tables A2-A3, Appendix A. Consequently, the model for landscape age classification included the percent cover of the old, medium, and young forest area and the density of young forest patches as explanatory variables. In the case of forest type classification, the most parsimonious models included the percent of coniferous, mixed, and deciduous forest patches, conifer patch density, and the target patch size.

Finally, we ran a principal coordinates analysis (PCoA) using Sørensen dissimilarity coefficient matrix (Legendre and Legendre, 2012) to evaluate if bryophyte community composition in our old forest target patches changed with LCC considering the landscape metrics based on age and forest type. We created our matrix using the R package *ade4* (Dray and Dufour, 2007) and ran the PCoA with the package *vegan* (Oksanen et al. 2022). We also checked the correlation between the main axes of the landscape metrics with no concurvity and diversity values of the whole bryophyte community, as well as by guild, using the R function *envfit* (Oksanen et al. 2022) with 999 permutations.

3. Results

In this study, we analyzed 30 897 bryophyte records that represent 185 species (100 mosses, 68 liverworts, and 17 sphagna; Table A4, Appendix A) in 92 old forest patches. Mosses, for both observed and expected data, had the highest mean values for richness, common and dominant species per old forest patch followed by liverworts and then sphagna (Fig. A1, Appendix A).

We found different results for observed and expected data (diversity values extrapolated based on the observed data) when examining the LCC effects on bryophyte diversity. Specifically, some significant landscape metrics (p < 0.05) in observed data were not in expected data, while those with p < 0.01 and < 0.001 in observed data were still significant in expected data. Therefore, we present here the results with the expected data as they are more conservative. Observed data results are presented in Appendix A (Table A5).

Bryophyte guild diversity in target patches responded differently to landscape attributes based on patch age and forest type. Examining landscape age, moss richness (q0) was negatively influenced by the percent cover of young and medium aged forest in the landscape (Table 1, Fig. 2). Similarly, a decrease in the total richness (q0) and common liverworts (q1) was found when the percent cover of young forest exceeds 40% in the landscape. The significance of those declines were assessed through GAMs with the same variables structure described in methods section but focusing on the range of young forest cover percentages (35–60%) where the species decline was observed (Fig. 2). Also, liverwort q0 and q1 responded to changes in the density of young forest patches in the landscape. In the case of sphagna richness (q0), no explanatory variables based on the landscape age were related to their diversity values.

Regarding the effect of forest types in the landscape, although an increase in the mixed forest percent cover had marginal effects on moss richness, the target patch size explained most of the variation. (Fig. 3). Liverwort diversity (q0 and q1) was significatively affected by the percent of mixed forest and by coniferous patch density. A remarkable effect for liverworts was an increase in their common species number when the mixed forest percentage increased in the landscape. The increase in species number driven by mixed forest abundance was not observed for the liverwort total richness (q0). The model also suggests that the increasing density of conifer patches decreases the number of common liverworts. For sphagna, only the density of conifer forest patches was significant negative.

Landscape variables explaining bryophyte diversity also influenced community composition. The percent cover of medium age forest in the landscape is the most significant contributing variable to bryophyte community composition in general ($r^2 = 0.10$, p < 0.01), followed by the coniferous patch density ($r^2=0.18$, p < 0.01) (Fig. 4A). This pattern is the same when the community of bryophytes is analyzed by guild (Fig. 4, Table 2). The liverwort community composition, unlike mosses

Table 1

Generalized additive models assessing the landscape composition and configuration effects based on the a) age and b) forest type using expected bryophyte diversity (*q*0=richness, *q*1=number of common species). Edf = estimated degrees of freedom for each model parameter. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.

a) Age landscape classification									
Response variables	Explanatory variable	edf	p-value						
Mosses q0	Percentage of young forest area	1	0.04 *						
•	Percentage of medium age forest area	4.28	<0.00 **						
	Percentage old forest area	1	0.06 (.)						
	Density of young forest patches	1	0.36						
Liverworts q0	Percentage of young forest area	5.05	0.01 **						
	Percentage of young forest area	3.37	0.03*						
	(threshold)								
	Percentage of medium age forest area	2.93	0.31						
	Percentage old forest area	1	0.08						
	Density of young forest patches	2.65	0.05 *						
Liverworts q1	Percentage of young forest area	5.86	0.01 **						
	Percentage of young forest area (threshold)	3.28	0.03*						
	Percentage of medium age forest area	1	0.64						
	Percentage old forest area	2.75	0.17						
	Density of young forest patches	3.86	<0.00 ***						
Sphagna q0	Percentage of young forest area	1	0.68						
	Percentage of medium age forest area	3.924	0.13						
	Percentage old forest area	1	0.47						
	Density of young forest patches	1	0.87						
b) Forest type lands	scape classification	10	,						
Response	Explanatory variable	edf	p-value						
variables	Demonstration of the life of the second	0.(1	0.05()						
Mosses qu	Percentage of confirms area	2.61	0.05 (.)						
	Density of confirer forest patches	2.79	0.18						
	Percentage of desiduous forest area	1	0.06 (.)						
	Terest netch size	1 07	0.43						
Liverworts a0	Percentage of conjfers area	1.97	0.00						
Liver worts qu	Density of conifer forest natches	1.05	0.09 (.) <0.00 **						
	Density of conner forest parenes	1	0.28						
	Percentage of deciduous forest area	3.06	0.07()						
	Target patch size	1	0.07()						
Liverworts a1	Percentage of conifers area	1.94	0.07(.)						
Livermonto q1	Density of conjfer forest patches	2.07	< 0.00						
	F		***						
	Percentage of mixed forest area	1	0.02 *						
	Percentage of deciduous forest area	1.94	0.05 (.)						
Sphagna q0	Target patch size	1.15	0.52						
	Percentage of conifers area	1.83	0.09 (.)						
	Density of conifer forest patches	1	<0.00 **						
	Percentage of mixed forest area	1	0.28						
	Percentage of deciduous forest area	3.06	0.07(.)						
	rarget patch size	1	0.07 (.)						

and sphagna, was more influenced by the amount of young forest in the surrounding landscape than the medium age forest percent cover. Community composition changes were consistent with the results of liverwort diversity (q0 and q1) in the GAMs. For example, we observed that changes in liverwort community composition were associated with an increase in species richness as the percent cover of young forest and conifer patch density decreased in the landscape (Fig. 4D). Thus, we observed that the changes in community composition are related to a gradient in bryophyte species richness influenced by LCC (Fig. 4).

4. Discussion

We found that boreal landscape composition and configuration (LCC), specifically variation in age and forest stand type, has a significant impact on bryophyte diversity at the patch scale. Also, we found that the response to LCC varies among bryophyte guilds. Surprisingly, we found that young forests can have negative effects on the old forest bryophyte diversity even when it was not a dominant cover in the landscape.

4.1. Landscape context explains bryophyte diversity at the local scale

Studies in Europe suggest that bryophyte richness at the local scale is influenced by changes in habitat amount in the landscape (in radii ranging from 500 m to 5 km) (Löbel et al., 2006; Paltto et al., 2006; Randlane et al., 2017). In this study, we found similar effects over a greater distance in less intensively managed landscapes. Furthermore, our results reveal the relative landscape impact by looking not only habitat amount, but also its heterogeneity (age and forest-type covers), and its spatial arrangement.

Bryophyte diversity was reduced on old forest patches surrounded by a large area of young forest. Unexpectedly, this decrease in diversity differs between guilds. Moss richness decreases linearly with increasing percentage of young forest in the landscape. In contrast, liverwort diversity (q0 and q1) seems to be much more resilient to this change as their numbers do not decline until young forest exceeds 40% of the landscape area. These patterns are consistent with the extinction thresholds theory refering to a critical value of some attribute, such as the amount of habitat in the landscape, below which species cannot persist (Lande, 1987; Fahrig, 2003; Ovaskainen and Hanski, 2003). In particular, we observed that the decline in moss richness corresponds to a deterministic model (Levins, 1969, 1970), where the species will become extinct when the amount of young forest reaches a high percentage in the landscape. In contrast, liverworts show a threshold corresponding to a stochastic model (Ovaskainen and Hanski, 2003) in which the maximum amount of young forest that allows the species to persist is observed. Thus, our study shows that species loss thresholds can differ between mosses and liverworts and depending on the diversity scale (q0 vs. q1).

We detected species loss thresholds as young forest increases in the landscape, but not as old forest decreases as originally proposed by the extinction threshold hypothesis. Specifically, the variation of between 20% and 80% of old forest in the landscape did not affect the diversity of any of the bryophyte guilds (Table 1). This is interesting because old forests are reservoirs of specialist bryophyte species compared to areas of young forests or disturbed areas (Barbé et al. 2017). Also, old forest are considered to contribute to the regional background level of spore bank (Hylander, 2009) which could maintain species richness at the landscape scale. Thus, we expected that the increase in old forest area in the landscape would correspond to an increase in target patch richness. Our results suggest that although the proportion of the young forest is lower (5-40%) compared to the old forest (20-80%) in the landscape, the former can have a greater effect on the local bryophyte diversity. Young forests may act as a source of generalist species propagules for target old forest patches through a mass effect (Shmida and Whittaker, 1981). In turn, although old forests have a larger area in our landscapes, their characteristic species may not have the same dispersal efficiency. Alternatively, 20% of the landscape in old forest may not be low enough to see an effect in species richness over the short period of forest management (50 years).

With respect to the young forest effect, Barbé et al. (2017) found that patches of residual old forest left over from wildfires have higher richness than continuous old forest. However, because young forests harbor different species than those found in old forests, their dispersal into old forest patches affects the species composition of the latter. Furthermore, the authors also found that the community composition of the remnant patches was characterized by specialist species loss and the inclusion of disturbance-adapted species. Consequently, it is important to consider that although young forest can act as a source of propagules for old forest patches, the excessive increase in the area of the former can cause the loss of specialist species in the old forest patches due to source-sink dynamics (Holt, 1985; Pulliam, 1988). If the old forest patches are



Fig. 2. Effect of the composition and configuration of the landscape classified according to the age of its patches for mosses (*q0*), liverworts (*q0* and *q1*), and sphagna (*q0*) using expected data. The dotted lines in the liverwort models represent the threshold percentage of young forest cover, evaluated separately, at which the species decline occurred. Asterisks on chart tops indicates the significance level of the variable: *** = p < 0.0001, ** = p < 0.001, * = p < 0.05.

immersed in landscapes dominated by young forests, the former will not have an incoming flow of propagules of their characteristic species to allow them to maintain their richness and community structure. Other studies have also found that the surrounding matrix influences the loss of local vascular plants species (e.g.,Metzger, 2000; Williams et al. 2006). Thus, our study contributes to demonstrate the influence of non-dominante land cover on the local diversity of non-vascular plants.

Our results support the idea that habitat loss is the main driver of species loss (Fahrig, 2003, 2017). We also note that fragmentation, measured here as patch density, affects bryophyte diversity and

Forest type landscape classification - Expected data



Fig. 3. Effect of the composition and configuration of the landscape classified according to the forest type of its patches for mosses (*q0*), liverworts (*q0* and *q1*), and sphagna (*q0*) based on expected data. Asterisk on chart tops indicates the significance level of the variable: *** = p < 0.0001, ** = p < 0.001, * = p < 0.001.

community structure. In addition to the amount of young forest in the landscape, we observed that the density of its patches affects liverwort diversity (q0 and q1). Furthermore, we found that the number of species fluctuates depending on the distance between the patches of young forest. Specifically, we found that liverwort diversity decreases when young forest patches become closer together but increases when the young forest patches start to form defined group patches in the

landscape. This represents a process of species loss and gain (Socolar et al. 2016), affecting the structure of the liverwort community. These findings support the beta diversity dominance hypothesis, which posits that local-scale species loss can be offset by an increase in beta diversity in the landscape. This, in turn, helps to maintain original values of gamma diversity in the landscape (Tscharntke et al. 2012; Socolar et al. 2016; Arroyo-Rodríguez et al. 2019). According to Arroyo-Rodríguez



Fig. 4. Principal coordinate analysis (PCoA) of 90 old forest target patches based on their a) all bryophyte guilds, b) mosses, c) liverworts, and d) sphagna community composition with Sørensen dissimilarity index. Eigenvalues are represented in parenthesis. Non-colinearity age and forest type landscape metrics were added by correlation to the axes using *envifit* function. The landscape metrics lines' length indicates the correlation's strength to the axes. The circle size at the top indicates the number of species in the patches. Species are represented by acronyms (for full name see Table A4). Liverworts are represented in bold in the A) figure section.

et al. (2019), these effects are typical of landscapes with low or moderate disturbances. Although the effects result in local species loss, their impact on beta diversity promotes the maintenance of landscape diversity.

Changes in the liverwort community can also be attributed to forest composition. An increase in mixed forest percentage results in an increase in common liverwort species (q1). This change may be the result of increased dispersal pressure in target old forests by common

generalist species associated with mixed forests (Hernandez-Rodriguez et al. submitted). Factors such as natural and anthropogenic disturbances decrease the presence of conifers and promote the emergence of deciduous species (Marchais et al. 2020), potentially resulting in altered composition of boreal bryophyte species over time. Our study is limited to landscapes with approximately 20% mixed forest coverage. Further research on landscapes dominated by this forest type can offer a more comprehensive understanding of its role as a source of species for other

Table 2

Landscape metrics related to the bryophyte community composition considering all the species and guilds presented in the PCoA by *envfit*. Significance is marked in bold with asterics. $r^2 =$ variation explained by the model of multiple regression; Pr(>r) = significance of the multiple regression calculated by permutation test.

	All bryophytes		Mosses		Liverworts		Sphagna	
Age landscape metrics	r ²	Pr(>r)	r ²	Pr(>r)	r ²	Pr(>r)	r ²	Pr(>r)
Old forest (%)	0.03	0.27	0.02	0.35	0.05	0.1	0.05	0.1
Medium age forest (%)	0.10	0.01**	0.11	0.01**	0.06	0.07	0.09	0.03*
Young forest (%)	0.08	0.04*	0.06	0.04*	0.07	0.03*	0.03	0.29
Young forest density	0.04	0.17	0.05	0.11	0.03	0.21	0.04	0.18
Forest type landscape metrics								
Conifers (%)	0.05	0.12	0.05	0.134	0.02	0.45	0.05	0.13
Conifers density	0.18	<0.00***	0.08	0.02*	0.16	<0.00**	0.23	<0.00***
Mixed forest (%)	0.09	0.02*	0.06	0.07	0.04	0.18	0.07	0.06
Deciduous (%)	0.07	0.05	0.05	0.08	0.05	0.09	0.08	0.03*
Target patch size	0.05	0.13	0.07	0.05*	0.03	0.31	0.05	0.13

vegetation types.

Landscape classification based on forest types also enables detection of the impact of other LCC attributes. We found that larger target patches (>5000 ha) tend to have fewer moss species than smaller patches. This may be due to the dispersal of species from the matrix of young forest or mixed forest, which increases their distribution and probability of colonizing old forest small patches (Nordén and Larsson, 2000). In contrast, larger patches that maintain structural connectivity (connectedness, Baudry and Merriam, 1988) may possess characteristic old forest species due to more extensive homogeneous conditions (Löbel et al. 2017). These results are related to the decrease in the diversity of liverworts (q0 and q1) and sphagna (q0) when the density of coniferous patches increases. This may be because an increase in coniferous patch density could maintain the structural connectivity of the old forest through patch connectivity, thus allowing for species persistence (Baudry and Merriam, 1988; Tischendorf and Fahrig, 2000a, 2000b). Therefore, when conifer density is lower, species from other forest types, such as mixed forests, can colonize the target patches.

4.2. Species driven by landscape composition and configuration

Some examples of species influenced by the LCC, particularly with increasing percent cover of young forests, include Atrichum altecristatum (Renauld & Cardot) B.B. Smyth & L.C.D., Ditrichum pusillum (Hedw.) Hampe Smyth and Pellia epiphylla (L.) Corda (Atr alt, Dit pus, Pel epi respectively, Fig. 4). The marked presence of these species in old forest target patches when young forest increase in the landscape is most likely because their distribution was favored by the disturbances (Schuster, 1992; FNAEC, 2007) that produced the young forests, promoting their presence in nearby old forests. Another species that may be favored by increasing its characteristic habitat is Hypnum fauriei Cardot (Hyp fau). According to the FNAEC (2007), H. fauriei is commonly found in mixed forests. Therefore, the expansion of mixed forest might have led to an increase in its occurrence within the old forests patches. Finally, species such as Dicranum flagellare Hedw. and Radula complanate (L.) Dumort., (Dic fla and Rad com, Fig. 4) were associated with patch density, suggesting that they could be favored by coniferous forest connectivity. Substrate requirements, such as decaying wood and humidity conditions (Damsholt, 2002), typical of old coniferous forests, along with dispersal limitations imposed by large propagules and spores (> 25 µm) (Söderström and During, 2005), suggest that these species exhibit a preference for landscapes with nearby patches of old forest, which could facilitate their dispersal.

4.3. Considerations for forest management and future studies

Although our study demonstrates the impact of LCC on bryophyte diversity in old forest patches, we did not rule out the influence of local factors on their diversity. Martin et al. (2018) found that old forests can be differentiated based on their structural diversity defined by the

influence of environmental and temporal factors (such as slope, time since the last fire, and depth of the organic horizon) on variables such as tree density and the basal area of the site. The effect of temporal factors is reinforced by works such as that of Fenton and Bergeron (2013), which also demonstrate that the severity of fires, as founder effects of the habitat, influences the current composition of bryophytes in old forests.

Our study emphasizes the landscape context significance in explaining local diversity, especially considering the attributes of its forest cover based on age and forest type. Furthermore, our results are useful for ecosystem-based forest management. We suggest not exceeding 40% of young forest in the landscape and avoiding the aggregation of these patches to mitigate the effects on the turnover of old forest species, especially when the matrix (young forest) has a stronger influence than the old forest. The findings of this work are consistent with the proposal of Arroyo-Rodríguez et al., (2020) to maintain a quality forest cover equal to or greater than 40% of the landscape. However, to deepen our understanding of landscape effects, we suggest that the response of bryophyte functional and phylogenetic diversity to landscape effects should be assessed to identify impacts on ecological and evolutionary processes driven by changes in the boreal landscape.

5. Conclusions

We show that richness and community structure of bryophytes are affected by LCC. In particular, these effects are different for each guild but stronger for liverworts. We also demonstrate the importance of considering the age and forest type of vegetation in the landscape to understand the drivers of bryophyte biodiversity at the local scale. Finally, we provide information about species loss thresholds (not exceeding 40% of young forest in landscapes) of bryophyte communities and propose avoiding young forest aggregation as a landscape planning strategy. Thus, these findings can serve as thresholds for forest harvesting, which is a critical need to maintain the biodiversity of one of the regulatory biomes of the global climate.

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CRediT authorship contribution statement

Enrique Hernández-Rodríguez: Writing – review & editing, Writing – original draft, Visualization, Validation, Software,

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Methodology, Investigation, Formal analysis, Data curation. Juan C. Villarreal: Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. Nicole J. Fenton: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors have no competing interests to declare.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121978.

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