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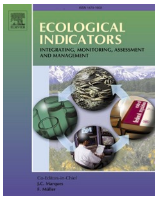

Original Articles

Synergistic effects in mine offsite landscapes: Predicted ecosystem shifts could exacerbate mining effects on bryophyte community structure

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ABSTRACT

Global change is shifting ecosystem type relative abundance in boreal forests, while the green energy transition results in increased mining activities around the globe. The interaction and consequent effects of these two trends on biodiversity have not been examined in depth. Bryophytes species can be used as indicators to measure these effects because they play key ecological roles in boreal forests. We identified and evaluated the interaction between ecosystem type (i.e., coniferous, deciduous, mixed forest and open canopy) and mining on microhabitat scale bryophyte diversity and composition in 1-km landscapes surrounding six mine sites at different stages of the mining lifecycle in the Canadian boreal forest. Irrespective of microhabitat type, the combined effects of ecosystem type and mining stage were interactive on bryophytes. Bryophyte richness and community composition were negatively affected by offsite effects of mines in only deciduous and mixed forests. The interacted effects on bryophyte richness mainly occurred on the ground r microhabitats. We also found that deciduous, mixed forests (coniferous forest as a reference) and mines had a negative impact on the abundance of feather mosses and sphagna. Furthermore, indicator species were identified for areas affected by mines (*Pohlia nutans* and *Dicranum polysetum*) and for control areas (*Sphagnum angustifolium* and *Plagiomnium cuspidatum*). Our results suggest the predicted ecosystem shifts with global changes, from coniferous to deciduous forests, could potentially increase the effects of mining on forest ecosystem resistance through the changes in bryophyte community structure. Adding microhabitats (i.e., adding coarse woody debris) near mine sites is a potential strategy to maintain species richness. Collectively, these findings advance our understanding of how mining affects biodiversity and highlight the importance of considering mine offsite landscapes in future environmental evaluations of development projects in the context of global changes.

1. Introduction

Global changes are modifying the distribution of ecosystem types across the globe. Changes include shifts from boreal coniferous to deciduous forest and from northern peatlands to forests (Hirota et al., 2011; van der Velde et al., 2021). How the effects of these global changes will interact with accelerated ongoing human activities is an important area of study. A synergistic effect appears when the combined effects of two disturbances is greater than their sum (Coors and De Meester, 2008; Raiter et al., 2014). An example is the interactions between global changes and forest fires (Hessburg et al., 2021), logging (Anderson et al., 2017; Cusack et al., 2016), and agricultural activity (Anderson et al., 2017; Cusack et al., 2016; Danneyrolles et al., 2019), which all present synergistic results in effects on biodiversity and the provision of ecosystem services. However, the effects of mining and their potential interactions with global changes have received little attention despite the fact that mines are a significant source of disturbances in forest ecosystems globally (Martins and Lima, 2020; Maynard et al., 2014). Numerous mines and mineral deposits are located in the boreal forest (Fig. 1) and more mining projects will be established in this area in coming decades as the energetic transition increases the world's demand for minerals such as rare earths for clean technologies and uranium for power generation (Sonter et al., 2020; Watari et al., 2021; Yin et al., 2021). This will lead to more intact boreal landscapes being exposed to mining disturbances while they are also facing the consequences of global changes.

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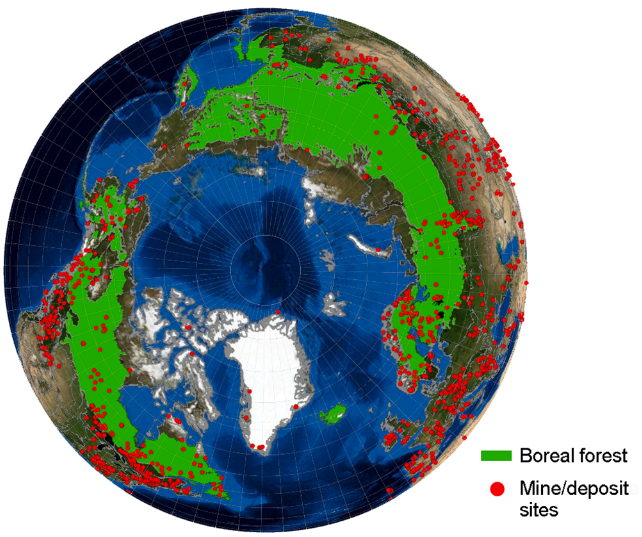


Fig. 1. The distribution of mines and deposits of major mineral commodities in global boreal forests (March 9th, 2022). Datasets for mine sites was retrieved from Mineral resources online spatial data, United States Geological Survey (Labay et al., 2017).

Coniferous, deciduous and mixed forests as well as open canopy (primarily peatlands) are four main ecosystem types in boreal landscapes. Predicted shifts from coniferous needle-leaved to deciduous broad-leaved tree dominance and from peatlands to forests are two scenarios under global change (Boisvert-Marsh and de Blois, 2021; Mack et al., 2021). The shifts could affect the response of forest biodiversity and function to mining disturbances through changes in plant community structure, given the plant communities of different ecosystems generally differ in tolerance and resilience capacities under stressors (Barbier et al., 2008; Jean et al., 2017). For example, low light intensity below coniferous trees appears to support high cover of bryophyte (Király and Ódor, 2010), while bryophyte cover in deciduous and mixed forest is constrained by the fall of broadleaf litter (Bartels et al., 2018). Furthermore, coniferous canopies buffer environmental variations (e.g., temperature, moisture, irradiance and wind in the understory) in the understory to a greater degree than deciduous forests, as persistent foliage and dense branching patterns; (Barbé et al., 2020; de Jalón et al., 2019). Boreal forests, including coniferous forest and peatlands, store large amounts of carbon (Bradshaw and Warkentin, 2015), while predicted ecosystem shifts and increasing mining activities (Fig. 1) could interact and affect ecological services via plant diversity and composition, including the bryophyte layer.

Bryophytes are widely distributed globally and particularly contribute ecological services in boreal ecosystems such as carbon and nitrogen cycling, water balance and forest succession (Arróniz-Crespo et al., 2014; Nilsson and Wardle, 2005, Rousk et al., 2013, Xia et al., 2020). Particularly, two most abundant groups, feather mosses and Sphagna, shape ecological function and resilience. Feather mosses can account for as much as 30 % of net primary productivity and contribute over 50 % of total nitrogen sources in boreal coniferous forests (Wardle et al., 2012, Jean et al., 2021). *Sphagnum* is the ecosystem engineer of peatlands (Rydin and Jeglum, 2013), which store around 25 % of global soil carbon and represent important resources to mitigate climate changes (Turetsky et al., 2015). Despite the critical roles bryophytes play in the ecosphere, they lack true roots, vascular systems and thick cuticles and are therefore highly sensitive to the surrounding environment. These characteristics result in bryophytes being widely used as indicators of natural and human disturbances including climate changes and heavy metal deposition (Balabanova et al., 2017; Mahapatra et al., 2019; Printarakul and Meeinkuirt, 2022).

The type and abundance of microhabitats have been shown to be more important than mesohabitats for bryophyte diversity (Cole et al., 2008; Király and Ódor, 2010). Microhabitats for bryophytes are generally defined as the smallest subunit of forest habitat including pieces of deadwood and rocks (Barbé et al., 2020). Microhabitats can protect bryophytes from the effects of global changes and anthropogenic disturbances (Paquette et al., 2016; Scheffers et al., 2014). Usually, microhabitats provide a relatively stable substrate in terms of temperature and moisture to effectively buffer extreme climate events and environmental variations, for example bryophyte composition was more dependent on the characteristics of coarse woody debris than environmental features in boreal coniferous stands (Barbé et al., 2020).

The negative effects of mining on biodiversity and ecological services have been well documented in directly disturbed areas (Maus et al., 2020; Odell et al., 2018; Sonter et al., 2018), but offsite effects that occur in relatively intact landscapes surrounding mine sites (mine offsite landscapes) have received little attention (Raiter et al 2014). The main mechanisms of offsite effects associated with mines are dust, salt, excess nutrients, or other contaminants that move from mines to surrounding ecosystems via air, water or human activities (e.g., vehicle movement, Raiter et al., 2014). An increase in the number of mining projects will lead to the exposure of more landscapes to offsite effects. Furthermore, the disturbance of biodiversity and ecological services associated with mining is also dependent on the mining lifecyle as operating mine sites with more activities (e.g., digging, blasting, transportation) usually have a larger influence on surrounding biodiversity than non-operating sites (Adesipo et al., 2020; Bartels et al., 2019).

The aim of this study is to evaluate whether the effects of mining and predicted ecosystem shifts could be synergistic in mine offsite landscapes, resulting in changes in the bryophyte community at the microhabitat scale. Bryophytes were sampled from various microhabitats (i.e. ground, trees, logs, snags, stumps and rocks) in the boreal forest of Québec (Canada) inside 1-km intact landscapes surrounding six mine sites (from operating and non-operating stages). The offsite landscapes were grouped into coniferous, deciduous, mixed forest and open canopy ecosystems. We hypothesized that mine sites at the operating stage have more offsite effects on bryophyte community structure (diversity and composition) than those at the non-operating stage (**H1**) and that ecosystem type affects the presence and magnitude of the offsite effects of mines (**H2**). The interactions between offsite effects of mines and ecosystem type on bryophytes are affected by microhabitats (**H3**). We expect a reduced abundance of important functional groups (i.e., feather mosses and sphagna) as a consequence of offsite effects of mines and the predicted shifts in ecosystem type (**H4**). How bryophyte structure is altered in boreal offsite mine landscapes and potential factors under global changes have not been addressed in previous studies; therefore our study provides a first look at these industrial impacts.

2. Materials and methods

2.1. Study area

The study was conducted in six gold mine sites in the regions of Abitibi-Témiscamingue and Nord-du-Québec in the province of Québec, Canada (Fig. 2): Akasaba (48°3'12″N; 77°32'8″W, Agnico Eagle Mines ltd), Canadian Malartic (48°7'21″N; 78°5'23″W, Canadian Malartic Partnership.), Casa Berardi (49°33'43″N; 79°14'8″W, Hecla Québec Inc.), Joutel (49°29'28″N; 78°21'8″W, Agnico Eagle Mines ltd), Lapa (48°13'45″; 78°17'1″, Agnico Eagle Mines ltd), LaRonde (48°15'14″N; 78°25'59″W, Agnico Eagle Mines ltd). The gold mines were selected in the region as high-intensity gold mining and the pollution associated with gold processing is a primary focus of government and the public. Furthermore, the by-products of gold mining are toxic, including chromium, lead and arsenic. They differ in size, mining method, life stage and bioclimate domain. Lapa is a small underground mine, while Canadian Malartic is one of the largest open pit mines in North America. Three of them (Casa Berardi, LaRonde and Canadian Malartic) are

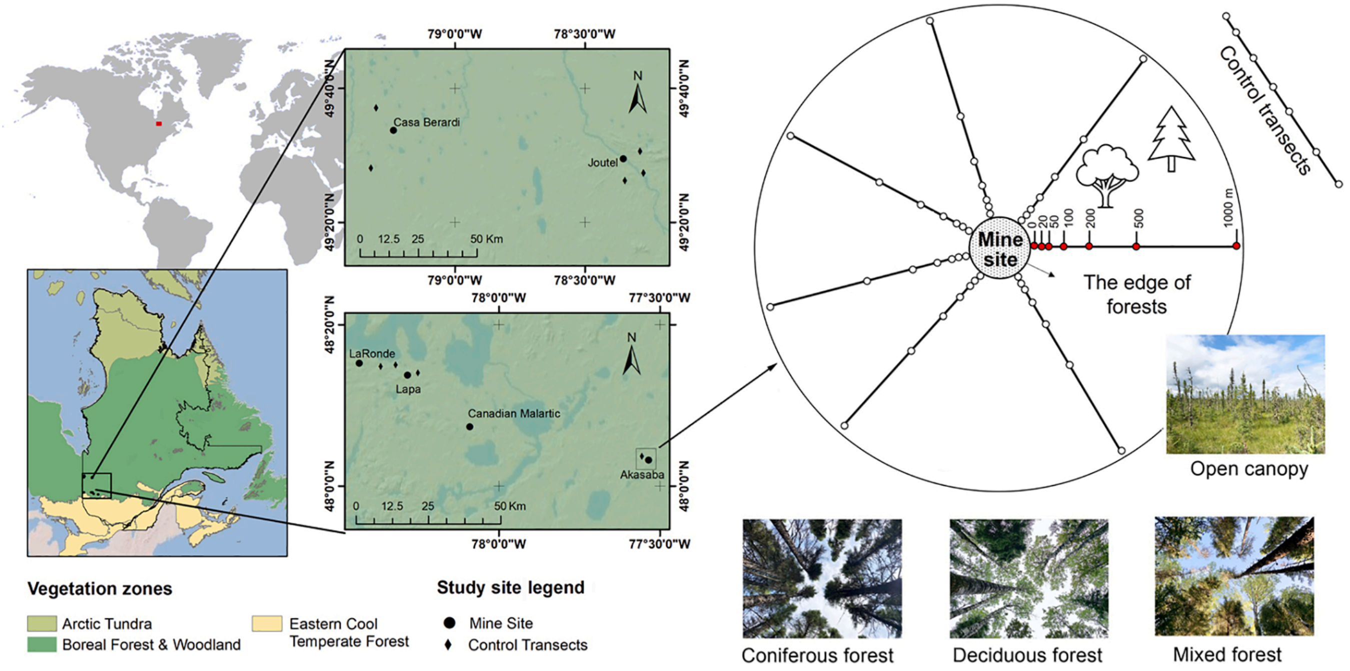


Fig. 2. Study area. Left, map of Canada and Quebec showing the main vegetation zones. Center, map of study region indicating the position of sampling sites at six gold mine sites and 9 control transects (August 9th, 2021).

operating and the other three (Akasaba, Joutel and Lapa) are non-operating. More information about the six mine sites can be found in the platform of Mining Data Online (https://miningdataonline.com/). Furthermore, Casa Berardi and Joutel are located in the *Picea mariana*-moss bioclimatic domain, while the other four mine sites are all located in the *Abies balsamea – Betula papyrifera* bioclimatic domain. This region is characterized by a cold and humid continental climate with the mean temperature in January between − 17 °C to − 20 °C and between 16 °C and 17 °C in July. Mean annual precipitation ranges from 850 mm to over 900 mm (Bergeron et al., 2004). More detailed information about the six mines is available in Table S1.

2.2. Fieldwork design and sampling

2.2.1. Fieldwork design

In each mine site, 6–8 transects (the number of transects was selected based on the size of each mine area, see Fig. S1) were established perpendicular to each mine periphery through different ecosystem types (See Table S2) in 2017–2019. Nine control transects (over three 3 km from the mine sites) were established in undisturbed natural sites, avoiding down wind from the mines, five in the *Picea mariana* – moss bioclimatic domain and four in the *Abies balsamea* – *Betula papyrifera* bioclimatic domain. As the environmental effects of mines (deposition of dust or heavy metals) are usually felt farther than 1 km from mines (Gillings et al., 2022; Mattielli et al., 2009), the 1 km long transects were deigned to be within the potentially influenced areas. In order to avoid other non-mining disturbances (like highways and towns), transects were not established in all cardinal directions at each mine. This is particularly true for two sites, Canadian Malartic and Lapa, as north of Canadian Malartic mine is the town of Malartic and south of the Lapa mine is a main highway, natural gas pipeline and hydro-corridor (See Fig. S1).

Seven vegetation plots (3 m in radius) were established along each transect at distances from the edge of the area directly disturbed by mining activities at 0, 0.02, 0.05, 0.1,0.2, 0.5, 1 km. Three 1-m^2 quadrats per plot were randomly established to determine the cover of each macroscopic terricolous bryophyte species and different substrates (leaf litter, woody debris, organic matter, water, rock, lichen). The forest stand of each plot was categorized into one of four types based on tree species (diameter at breast height (DBH) ≥ 10 cm) composition in a prism plot with a 2 M basal area factor centered on each vegetation plots: coniferous forest (>70 % of coniferous trees, N = 173), deciduous forest (>70 % deciduous trees, N = 47), mixed (coniferous tree stems between 69 % and 31 %, n = 37), and open ecosystems (DBH of all trees below 10 cm, primarily peatlands in our study area, N = 107). In total, 371 plots were established, but 364 plots were analyzed because two control plots were destroyed by logging and some missing data.

2.2.2. Bryophyte sampling

The bryophyte community was sampled using a modified floristic habitat sampling technique (Newmaster et al., 2005) in the summer of 2019 and 2020. All bryophytes on each microhabitat (ground, trees, logs, snags, stumps and rocks, classification criteria in Table S3) within each vegetation plot were sampled and stored in individual paper bags with plot and microhabitat information. Samples were identified to the species level based on the “Flore des bryophytes du Québec-Labrador” (Faubert, 2012) at the bryophyte lab of Université du Québec en Abitibi-Témiscamingue. Species Latin names in our database were checked using The Plant List database in the R package Taxonstand version 2.4 (Cayuela et al., 2012). In total, 186 bryophyte species (132 moss species and 54 liverwort species) belonging to 89 genera were identified (species list see Table S4) and the feather moss *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Sphagnum angustifolium* (Warnst.) C.E.O. Jensen were dominant species with 8.96 % and 7.09 % ground cover, respectively.

2.2.3. Environmental variable sampling

Canopy openness and organic soil depth were measured three times in each plot, and shrub diameter at breast height (DBH, measured 1.3 m from ground level) was measured in the same plot as the tree basal area. Conifer proportion (%) was calculated by the percentage number of individuals of coniferous trees in the prism plot. The live crown ratio of each shrub (vegetation plot) and trees (prism plot) were measured and recorded (Table S5). Furthermore, environmental variables were compared among mine sites in Table S6.

2.3. Statistical analysis

2.3.1. Effect of ecosystem type and mining stage on bryophyte community structure

The sum of species occurring in all microhabitats per plot was used as the species richness of the bryophyte community at each plot. This study uses the species richness for diversity indices as its high sensitivity to environmental changes (Wilsey and Stirling, 2007; Andersen et al., 2020). Bryophyte species were classified by taxonomy (moss and liverwort), so in each plot ($N = 364$), we obtained the species richness and composition for three groups: total bryophytes, mosses and liverworts.

Species richness. Generalized linear mixed models (GLMMs, "glmmTMB" function from *glmmTMB* package, Brooks et al., 2017) were used to determine if mining stage, ecosystem type and their interaction influenced total bryophyte, moss and liverwort richness. The richness, referring to the species richness per plot, is the total number of bryophytes/moss/liverwort species identified in each plot. Considering the nested structure of the sampling design, "plot" was nested in "site" as random effects, as microhabitat was the smallest sampling unit. All models were first performed with Poisson error distribution and a log-link function, but when overdispersion was detected, a negative binomial distribution was used in final models. One model (moss richness) showed convergence errors and was corrected by optimization of the model via the Broyden–Fletcher–Goldfarb–Shanno (BFGS) algorithm (Dai, 2002) in the function of the "glmmTMBControl" from the *glmmTMB* package. Significance of the predictors (mining stage, ecosystem type and their interaction) was tested by type II Wald chi-square (χ^2) tests with the "Anova" function in *car* package (Fox et al., 2012). A Tukey post hoc test ("emmeans" function in the *emmeans* package, Lenth and Lenth, 2018) was performed to assess interaction terms (the differences between mining stage in each ecosystem type).

2.3.2. Community composition

Permutational multivariate analysis of variance with 999 permutations (PERMANOVA, "adonis" function from the *vegan* package, Oksanen et al., 2010) were run to assess the interacting effects of ecosystem type and mining stage on bryophyte community composition. in the PERMANOVA analysis, non-significant interaction terms were removed in final analysis. Results were visualized using principal coordinates analysis (PCoA, "PCOA" function in the *vegan* package) with Bray–Curtis dissimilarity matrices. The "envfit" function in *vegan* was then used to fit vectors of environmental parameters (microhabitat number, stand structure and soil properties) onto the ordinations with p-values (>0.05) derived from 999 permutations. When significant interactions between mining stage and ecosystem type were detected, the interaction effects on bryophyte composition shifts were qualified by calculating the Euclidean distances between centroids of PCoA cluster for each mining stage (distances between centroids of operating mines and controls, non-operating mines and controls as well as operating and non-operating mines, respectively) within each ecosystem type following a changed method by Martineau et al. (2020). The calculated distances were used to determine whether the combined effects of predicted ecosystem shifts and mining stage were synergistic or not (coniferous forest as references, details in Fig. S2). In addition, to identify species that characterized the communities of each mining stage, point biserial-correlation coefficient (phi) was calculated for indicator species analysis ("multipatt" function in the *indicspecies* package, De Caceres et al., 2016). The value of "stat" (the point-biserial-serial-correlation-coefficient) was used to measure the strength of the co-occurrence pattern observed between a bryophyte species and each ecological state of mining stage.

Moreover, generalized linear mixed models were also used to test the differences in 17 environmental variables between mining stages in each ecosystem type and the results are present in Table S6.

2.3.3. Role of microhabitats in mediating the effects of ecosystem type and mining stage on bryophyte structure

Bryophyte richness for each microhabitat in each plot was calculated as the sum of all species detected on each microhabitat of a given type in the plot. Composition on each microhabitat type (trees, logs, snags, stumps and rocks) per plot were determined using relative species frequency, where $F_m = n_m/N_t * 100$, F_m is the relative frequency of species m on each microhabitat type; n_m is the number of occurrences of species m in each microhabitat per plot; N_t is the total number of all microhabitat types per plot (ground counted as one individual microhabitat). Considering it is impossible to count the number of ground microhabitat elements, the bryophyte composition on the ground was determined using species raw cover measured in the 1 m^2 quadrats.

The analysis process for richness and composition per microhabitat was similar to the description in 2.3.1. However, there are some differences in models for richness associated with the characteristics of each dataset. Considering the lack of certain microhabitats in some plots, zero-inflated (ZI) models ("zi=~." used in "glmmTMB" function) were used in all models for bryophyte richness on each microhabitat. The model for bryophyte richness on rocks was analyzed with Poisson error distribution instead of negative binomial distribution because overdispersion was not detected. Furthermore, non-significant interaction terms (ecosystem type * mining stage) were removed from the final models (richness on trees, logs, stumps, snags and rocks).

2.3.4. Does a shift in forest composition and mining disturbance affect the ecological roles of bryophytes through abundance of important functional groups?

Structural equation modeling (SEM, "sem" function in *lavaan* package, Rosseel, 2012) was used to obtain a mechanistic understanding of how differences in ecosystem type, mining stage and microhabitats mediated changes the abundance of feather mosses and *Sphagnum* (% ground cover). A good model fit was evaluated using: 1) a Root Mean Square Error of Approximation (RMSEA) equal to or higher than 0.07 (Steiger, 2007) and 95 % confidence interval (CI) = 0.054–0.086; 2) Comparative Fit Index (CFI) equal to or higher than 0.96; and 3) Tucker-Lewis Index (TLI) equal to or lower than 0.96 (Hu and Bentler, 1999).

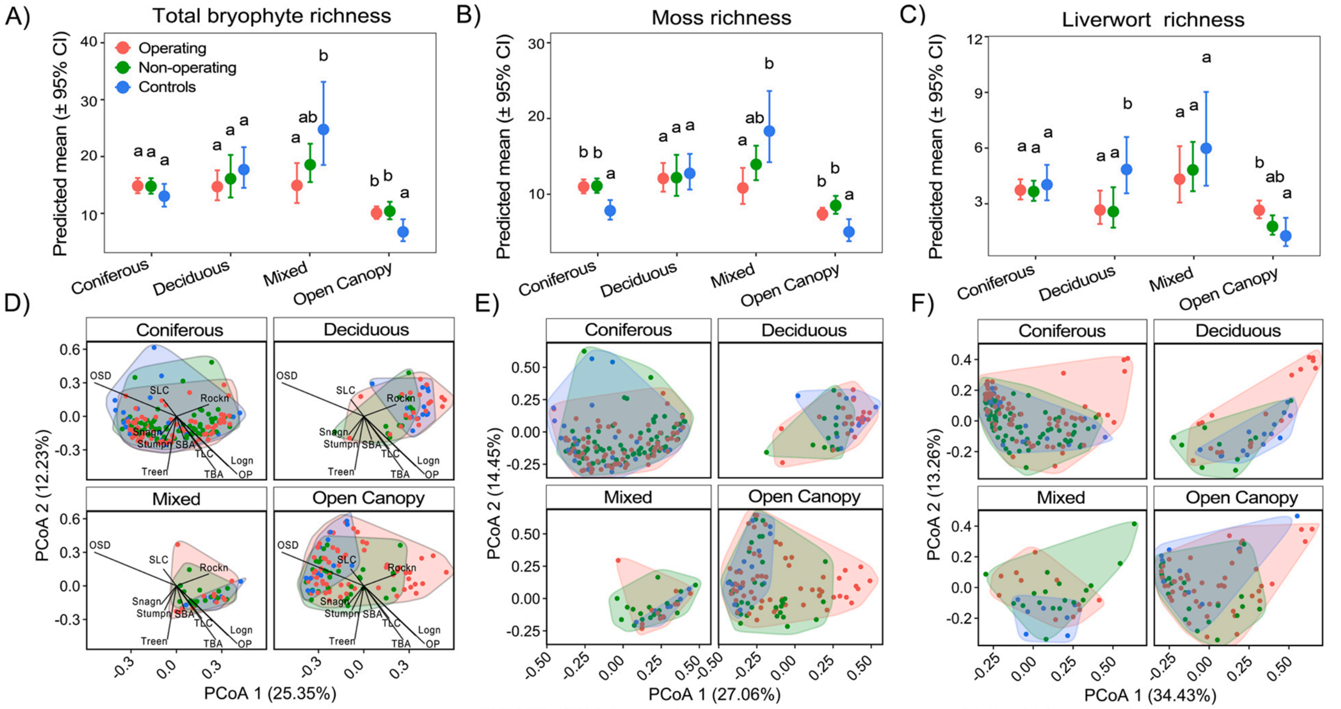
All analyses were performed with the statistical platform R 4.0.5 (2021–03-31) with R Studio software. Results were visualized with the *ggplot2* package (Wickham, 2011).

3. Results

3.1. Synergistic effects of ecosystem type and mining stage on bryophyte richness and composition

Bryophyte richness in mine offsite landscapes was affected by the interaction between ecosystem type and mining stage (the results of GLMMs for total bryophyte, moss and liverwort richness, ANOVA type II sums, $P < 0.05$, Table S8). Generally, mines present a positive effect on bryophyte richness in coniferous forests and open canopies, but a negative influence in deciduous and mixed forests (the results of Tukey HSD pairwise comparisons, Fig. 3 A-C). Specifically, moss richness was higher near both operating and non-operating sites than in controls in coniferous forest and open canopy, while it was significantly lower near operating sites than controls in mixed forest (Fig. 3 B). Furthermore, more liverwort species were found near operating sites than controls in open canopy, but less liverwort species were observed near both operating and non-operating sites in deciduous forests (Fig. 3 A).

Similarly, bryophyte community composition near mine sites was also affected by the interaction between ecosystem type and mining stage (PERMANOVA results in Fig. 3 D-F and Table S9). Overall, ecosystem type (PERMANOVA, 8.97 % $< R^2 <$ 13.42 %, Table S9) explained more differences in richness of total bryophytes, moss and liverwort species than mining stage (PERMANOVA, 1.42 % $< R^2 <$ 1.58 %, Table S9) and the interaction ecosystem type - mining stage



PERMANOVA (total bryophytes):

P Ecosystem types = 0.001 *P* Mining stages = 0.001

P Ecosystem types : Mining stages = 0.001

PERMANOVA (mosses):

P Ecosystem types = 0.001 *P* Mining stages = 0.001

P Ecosystem types : Mining stages = 0.001

PERMANOVA (liverworts):

P Ecosystem types = 0.001 *P* Mining stages = 0.002

P Ecosystem types : Mining stages = 0.023

Fig. 3. Comparison of bryophyte community structure between mining stages for each ecosystem type. A) Total bryophyte richness; B) Moss richness; C) Liverwort richness; D) Total bryophyte composition; E) Moss composition; F) Liverwort composition. Significant effects based on the results of generalized linear mixed model. Different letters denote significant differences ($\alpha \leq 0.05$) between mining stages (plots near operating mines, N = 167; plots near non-operating sites, N = 136; plots in controls, N = 61) within each ecosystem type (plots in coniferous forest, N = 173); plots in deciduous forest, N = 47; plots in mixed forest, n = 37; plots in open canopy, N = 107) from generalized linear mixed models with Tukey HSD pairwise comparisons (A, B, C). Principal co-ordinate analysis is used to visualise composition structure and present the results of PERMANOVA based on Bray–Curtis dissimilarity in D, E, F.

interaction (PERMANOVA, 2.43 % < R^2 < 3.1 %, Table S9). Specifically, there were greater differences in bryophyte composition among mining stages in deciduous and mixed forests, and open canopy (pairwise PERMANOVA results for total bryophytes, mosses and liverworts, 3 % < R^2 < 11 %, Table S9) than in coniferous forest (pairwise PERMANOVA, R^2 < 3, Table S10). Furthermore, liverwort composition shifts present more synergistic effects (Table S11). The Euclidean distances between centroids of mining stages of liverworts in deciduous and mixed forests were almost greater than those in coniferous forest, while the synergistic effects were only detected in deciduous forests for mosses (Table S11). Also, the results were supported in PCoA of liverworts where some plots near operating mines are in the top right corner far from the plots near non-operating sites in mixed and deciduous forests (Fig. 3F), while in moss composition, differences between operating and non-operating sites were visible only in open canopy (Fig. 3E).

Forest structure, the number of individual microhabitat types, and organic soil depth were all correlated with total bryophyte species composition (Fig. 3D). Canopy openness (OP, R^2 = 0.45, p = 0.001, Table S11), organic soil depth (OSD, R^2 = 0.40, p = 0.001, Table S11) and number of logs (logn, R^2 = 0.33, p = 0.001, Table S11) appeared to be significant environmental gradients structuring the community. OSD was more related with bryophyte composition in open canopy, while OP, TBA and logn was associated with the composition in coniferous and mixed forests (Fig. 3D).

Six indicator species were identified near operating mine sites (Table 1; 5 moss species and 1 liverwort species), 2 indicator species (both moss species) were identified for non-operating sites and 12 indicator species (8 moss species and 4 liverwort species) for controls. Almost all indicators for mining sites (operating and non-operating) were moss species and *Pohlia nutans* (Hedw.) Lindb. (stat = 0.207, p = 0.002, Table 1) and *Dicranum polysetum* Sw. (stat = 0.175, p = 0.009, Table 1) were the best indicators for operating and non-operating sites, respectively, while *Sphagnum angustifolium* (Warnst.) C.E.O. (stat = 0.235, p = 0.001, Table 1) was the best indicator for control sites.

3.2. *Role of microhabitats in mediating bryophyte response to ecosystem type and mining*

No statistically significant interactions were found for bryophyte richness on all microhabitats except ground (results of GLMMs, ANOVA type II sums, Table S13). Ecosystem type influenced bryophyte richness in most microhabitats (except stumps) with generally, more species in deciduous and mixed forest than that in coniferous and open canopy (the results of Tukey HSD pairwise comparisons, Fig. 4 A-F). In contrast to richness, bryophyte composition was affected by the interaction between mining stage and ecosystem type on all microhabitats except rocks (PERMANOVA results in Fig. 3 G-L and Table S14). Generally, the Euclidean distances between centroids of mining stage were greater in deciduous, mixed forest and open canopy ecosystems than those in coniferous forest for all microhabitat although some opposite patterns were detected (e.g., Euclidean distances between centroids of operating and non-operating stages in mixed forest were lower than that in coniferous forest for total bryophytes on ground, trees and logs, Table S11). The interaction explained a greater proportion of differences in bryophytes species composition on snags (PERMANOVA, R^2 = 7.8 %, Table S14) than on other microhabitats (PERMANOVA, R^2 < 4.0 %, Table S14). Bryophyte composition in coniferous forest was only different between mining stages on the ground, while in deciduous forest and open canopy, differences between mining stages were found on the ground, trees, logs and stumps (pairwise PERMANOVA,

Table 1
List of indicator species for each mining stage with their point biserial correlation coefficient and p value (only significant species shown, $P < 0.05$).

Species	Abbreviation	Type	stat	*P* value
Operating (6)				
Calliergonella lindbergii (Mitten) Hedenas	Cal.lind	Moss	0.144	0.03*
Hygroamblystegium varium (Hedwig) Mönkemeyer	Hyg.vari	Moss	0.144	0.018*
Hypnum cupressiforme Hedw.	Hyp.cupr	Moss	0.17	0.01**
Mylia anomala (Hook.) J.J. Engel & Braggins	Myl.anom	Liverwort	0.185	0.002**
Plagiothecium laetum Schimp.	Pla.laet	Moss	0.154	0.01**
Pohlia nutans (Hedw.) Lindb.	Poh.nuta	Moss	0.207	0.002**
Non-operating (2)				
Brachythecium erythrorrhizon Schimp.	Bra.eryt	Moss	0.165	0.006**
Dicranum polysetum Sw.	Dic.poly	Moss	0.175	0.009*
Controls (12)				
Barbilophozia attenuata (Nees) Loeske	Bar.atte	Liverwort	0.17	0.006**
Barbilophozia barbata (Schreb.) Loeske	Bar.barb	Liverwort	0.14	0.017*
Brachythecium reflexum (Starke) Schimp.	Bra.refl	Moss	0.138	0.036*
Breidleria pratensis (Koch ex Spruce) Loeske	Bre.prat	Moss	0.125	0.03*
Mnium spinulosum Bruch & Schimp.	Min.spin	Moss	0.163	0.01**
Mylia taylorii (Hook.) Gray	Myl.tayl	Liverwort	0.147	0.01**
Plagiomnium cuspidatum (Hedw.) T.J. Kop.	Pla.cusp	Moss	0.231	0.002**
Scapania mucronata H. Buch	Sca.mucr	Liverwort	0.141	0.024*
Sphagnum angustifolium (Warnst.) C.E.O. Jensen	Sph.angu	Moss	0.235	0.001***
Sphagnum capillifolium (Ehrh.) Hedw.	Sph.capi	Moss	0.151	0.024*
Sphagnum magellanicum Brid.	Sph.mage	Moss	0.185	0.005**
Sphagnum quinquefarium (Lindb.) Warnst.	Sph.squa	Moss	0.142	0.014*

Table S15). Bryophyte composition in mixed forest was only affected by mining stages on stumps (pairwise PERMANOVA, Table S15).

3.3. *Effects of ecosystem type, mining stage on the abundance of major bryophyte functional groups*

The SEM explained 21.3 % and 22 % of the variation in the ground cover of feather mosses and sphagna, respectively (Fig. 5). Deciduous (β (standardized coefficient) = -0.212) and mixed (β = -0.113) forests were negatively correlated with feathermoss ground cover, with coniferous forest as reference (Fig. 5A). Operating mine sites (β = -0.183) also had a negative effect on surrounding feathermoss cover (Fig. 5A), while the numbers of trees (β = 0.234), snags (β = 0.185) and stumps (β = 0.126) were positively correlated with feathermoss cover but the number of logs (β = -0.148) was negatively correlated with feather moss cover (Fig. 5A).

Similarly, compared to coniferous forest, *Sphagnum* cover was reduced in deciduous (β = -0.125, Fig. 5B) and mixed (β = -0.068, Fig. 5B) forests. However, it was increased in open canopy (β = 0.288, Fig. 5B). Both operating and non-operating sites had negative effects on *Sphagnum* cover in the surrounding landscape (Fig. 5B). Only log number (β = −0.19, Fig. 5B) was associated with the ground cover of *Sphagnum* among microhabitat types. Open canopy and operating sites were the most parsimonious explanatory variables for *Sphagnum* cover near mine sites. Therefore, ecosystem type and microhabitats were more important than mining stages in determining feather moss cover near mine sites, while mining stages were the most important variable influencing *Sphagnum* cover in the study.

4. Discussion

4.1. *Mine offsite effects and their synergistic interaction with ecosystem type on bryophytes*

Offsite effects of mine sites on bryophytes were confirmed based on the differences in richness and composition of bryophyte communities in 1 km radius landscapes near mine sites (operating or non-operating) compared to controls. The results extend offsite effects of mines from vascular plants (Boisvert et al., 2021; Chen et al., 2017; Dyer et al., 2001) to cryptogamic community structure. At the same time, operating mines had more effects on bryophyte structure (richness and composition) than non-operating ones (e.g., total bryophyte richness was affected by operating mines in mixed forest but not by non-operating sites in Fig. 3A). Compared with non-operating sites, more mining associated activities (e.g., blasting, digging, and transporting) occur in operating sites, which lead to more disturbances (e.g., atmospheric particulate matters and heavy metals) in offsite landscapes (Betancourt et al., 2005; Corriveau et al., 2011; Wang and Mulligan, 2006) and consequently bryophytes were more affected, confirming H1.

The presence and magnitude of the offsite effects is largely dependent on ecosystem type based on the significant interaction effects, which confirms H2. Offsite effects of mines reduced bryophyte richness in deciduous and mixed forest sites, however, the opposite pattern was observed in coniferous forest and open canopy sites. Combined with the microhabitat results (Fig. 4), we found that the increase in species richness mainly occurred on the ground in coniferous forest and in open canopy ecosystems. On the one hand, changes in species interactions may contribute to the positive impact of mine offsite effects. Reduced ground cover of "large" dominating moss species (i.e., feather mosses and sphagna Fig. 5) caused by the offsite effects in coniferous and open canopy ecosystems might lead to less competition in disturbed habitats and provide opportunities for smaller bryophytes, such as *Pohlia nutans*, *Plagiothecium laetum* Schimp., *Hypnum cupressiforme* Hedw. and *Hygroamblystegium varium* (Hedw.) Mönk. to establish (Table 1). This finding is consistent with an earlier result where disturbed areas with less competitive species supported more bryophyte species (Zielińska et al., 2016). However, this mechanism did not apply to mixed and deciduous forests, possibly because larger bryophytes are not a limiting factor for other bryophyte species in these environments (Jean et al., 2020; Oechel and Van Cleve, 1986). The high ground cover of broadleaf litter (up to over 70 % near operating and non-operating sites, see Table S7) could mainly contribute to reduced bryophyte richness (Márialigeti et al., 2009; Saetre et al., 1997) near mined sites in deciduous and mixed forests. Low decomposition rates due to low activity of microorganisms in polluted soil near mine sites could lead to an increase in the ground cover and thickness of deciduous litter (Freedman and Hutchinson, 1980; Horodecki and Jagodziński, 2017; Strojan, 1978). On the other hand, the differences in resistance of each ecosystem type can be also attributed to the canopy structure and environmental characteristics. Conifers have higher canopy cover, leaf area index, and a more persistent foliage than deciduous trees, which may intercept more dust, heavy metals, and other pollutant emissions generated by mining (Augusto et al., 2002; Barbier et al., 2008; Nguyen et al., 2015). Furthermore, deciduous trees can translocate high amounts of heavy metals into the foliage which can then result in more heavy metal accumulation in topsoil than under coniferous trees (Van Nevel et al., 2011).

Bryophytes indicator species were identified for offsite landscapes at different mining stages. *Calliergonella lindbergii* (Mitt.) Hedenäs, *Hygroamblystegium varium*, *Hypnum cupressiforme*, *Mylia anomala* (Hook.) Gray, *Plagiothecium laetum* and *Pohlia nutans* were indicators of operating mines, and they are tolerant or pioneer species (Barrett and Watmough, 2015; Petschinger et al., 2021; Rydgren et al., 2004; Salemaa et al., 2001). In particular, *P. nutans* had the highest indicator value in

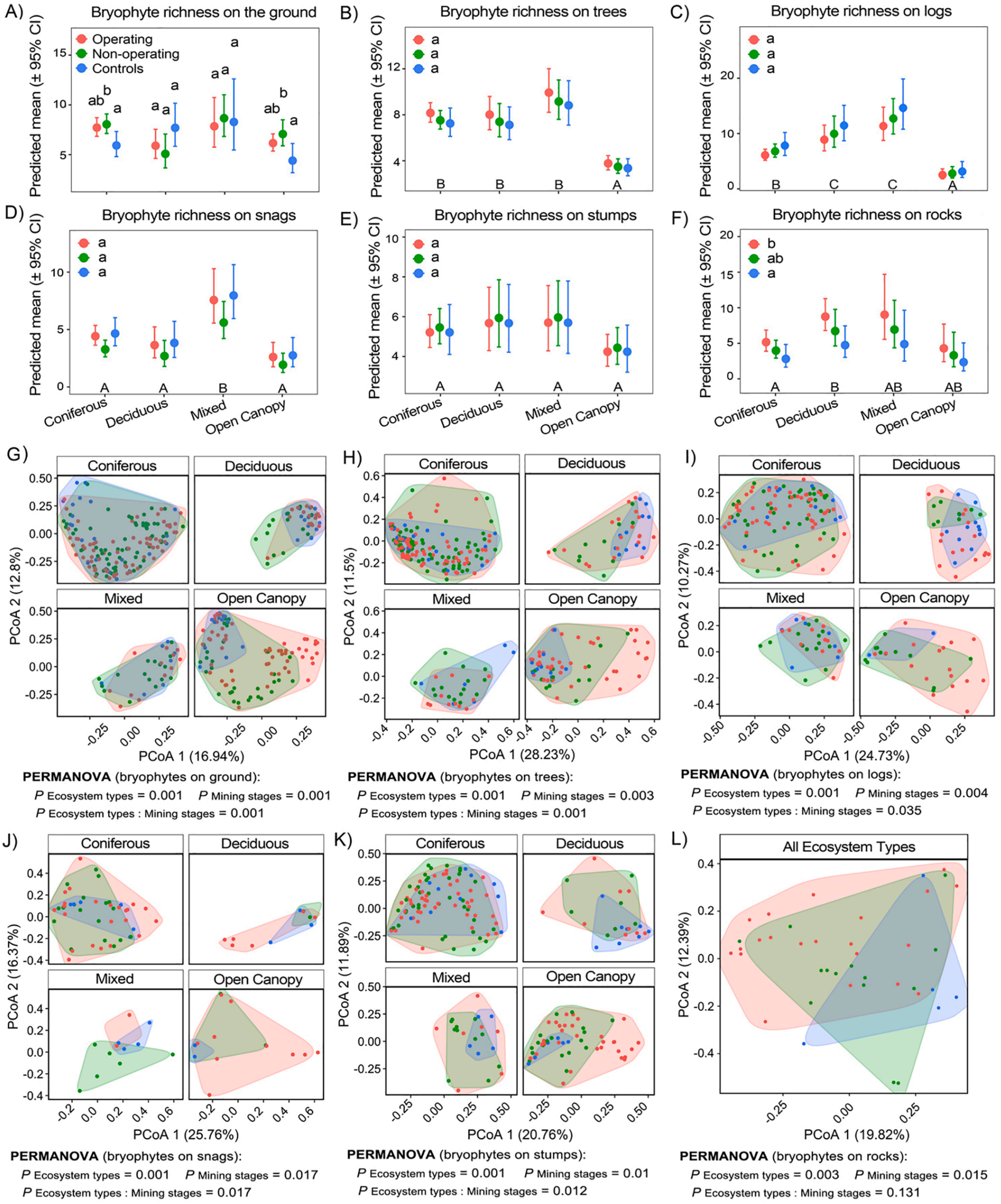


Fig. 4. Comparison of the richness and composition of bryophytes on each microhabitat between mining stages for each ecosystem type. A) Total bryophyte richness on ground; B) Total bryophyte richness on trees; C) Total bryophyte richness on logs; D) Total bryophyte richness on snags; E) Total bryophyte richness on stumps; F) Total bryophyte richness on rocks; G) Total bryophyte composition on ground; H) Total bryophyte composition on trees; I) Total bryophyte composition on logs; J) Total bryophyte composition on snags; K) Total bryophyte composition on stumps; L) Total bryophyte composition on rocks. Principal co-ordinates analysis and present the results of PERMANOVA using the Bray–Curtis distance in G, H, I, J, K, L.

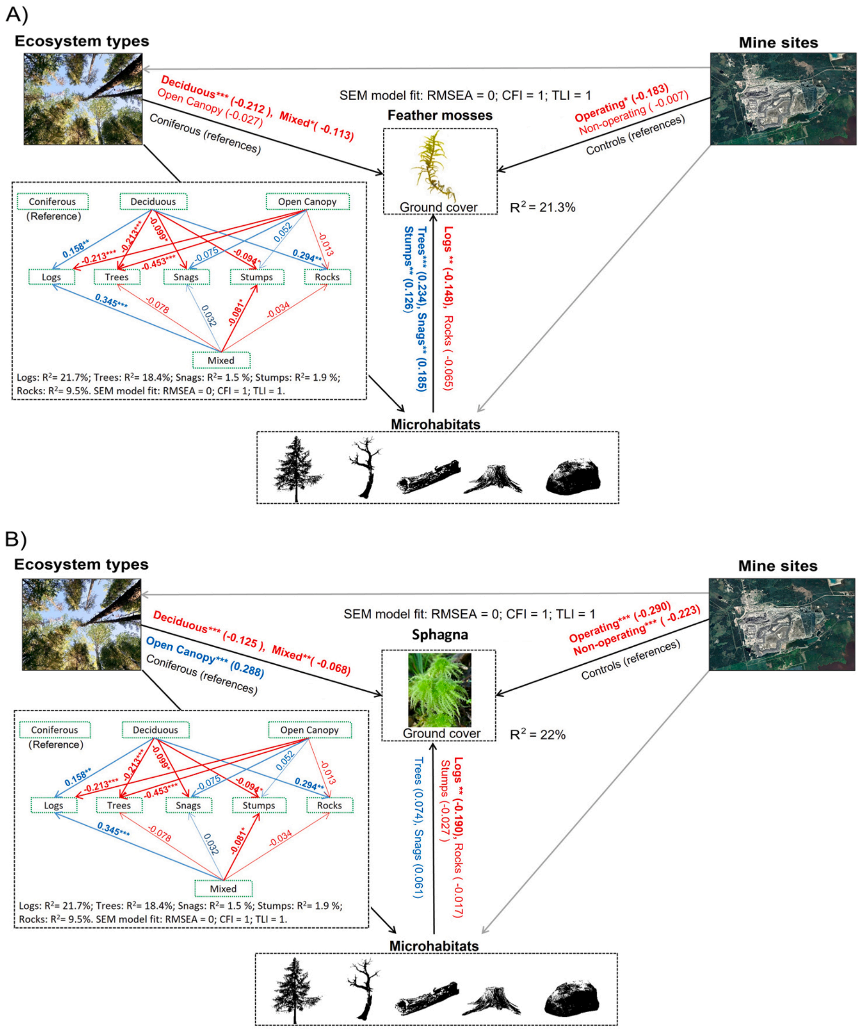


Fig. 5. Structural equation models (SEM) of ecosystem type, mining stage and microhabitats as predictors of the ground cover of important functional bryophyte groups (i.e., feather mosses and sphagna). A) Feather moss ground cover; B) *Sphagnum* ground cover. Red text represents negative effects, blue text represents positive effects and significant parameters ($\le$0.05) are indicated in bold. The associations between ecosystem type and the number of individual microhabitats were evaluated in a separate structural equation model because of poor fit when all elements were included in one model. Overall fit of piecewise SEM was evaluated using RMSEA (root mean square error of approximation), CFI (comparative fit index) and TLI (Tucker-Lewis index). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

operating sites and has been reported as one of most tolerant moss species growing in the immediate vicinity of mines and associated disturbed areas (Gignac and Beckett, 1986; Helmisaari et al., 1995; Salemaa et al., 2001). More species (13 species) occurred more abundantly in undisturbed landscapes (controls), suggesting that they have low tolerance to mining disturbances and high indicator values for intact landscapes. Four *Sphagnum* species including *Sphagnum angustifolium*, which had the highest indicator value, suggests that the *Sphagnum* group could be particularly sensitive to offsite effects, which is consistent with previous results that *Sphagnum* was a key indicator of mining effects on vegetation (Mullan-Boudreau et al., 2017; Spratt and Wieder, 1988). Interestingly, only two indicator species were detected for non-operating sites, which suggests that bryophyte species composition near non-operating sites was generally similar with that either near operating mines or in controls and few specific species were associated with this condition where neither tolerant nor sensitive groups were particularly supported.

Therefore, ecosystem type and mining stage are two drivers for offsite effects of mines on bryophyte richness and composition. The combined effects of predicted ecosystem shift from coniferous to deciduous forest dominance and mining on bryophytes could be synergistic in the offsite boreal landscapes. Meanwhile, indicators for the offsite effects have potential value for future ecological assessment in mining projects.

4.2. Microhabitats mitigated the synergistic effects of ecosystem type and mining on bryophyte structures

Whether microhabitats can mitigate effects from predicted global change on bryophytes was still unclear, but our results did confirm their potential buffer role in the scenario of predicted ecosystem shifts and increases of mining projects (H3). Some types of microhabitats mitigated the offsite effects of mines and their synergistic effects with predicted ecosystem shifts, which indicates that they could play the role of mining-refugia in offsite landscapes. The possible explanation is that microhabitats, and especially coarse woody debris (logs, snags and stumps), are specialised substrates which retain moisture, offering a more stable microclimate environment than soil (Haughian and Frego, 2017; Jönsson and Jonsson, 2007). Furthermore, offsite effects of mines on bryophyte richness were only found on the ground and rocks (Fig. 4 A, F). These results indicate that bryophytes growing in microhabitats located near or on the forest ground are more vulnerable to offsite effects of mines than those colonizing vertical microhabitats (i.e., trees, stumps, snags). Microhabitats in the forest ground layer could accumulate higher amounts of dust deposition than standing microhabitats considering that dust deposited on tree and shrub leaf surfaces will finally deposit on the forest ground through the action of wind, rainwater and defoliation (Sase et al., 2012). Meanwhile, loss of canopy cover by the edge affects mainly communities on the ground, where the level of incident light, soil moisture and nutrient availability can be changed by canopy openness, while non-ground microhabitats having vertical dimensions might lead to less exposure probabilities to the changes in environmental variables (e.g., lightness, treefalls and soil moisture).

In contrast to richness, microhabitats generally did not mitigate the interaction and synergistic effects on bryophyte composition, indicating that community composition is generally much more vulnerable to environmental changes than species richness, a response that has been found after other disturbances (Oldén et al., 2014). Species richness is an emergent property of ecosystems and it is relatively constant after disturbances if local compensatory colonisations occurred (Legendre et al., 2005; Parody et al., 2001). Nevertheless, our results firstly confirmed the buffer roles of microhabitats for bryophytes in mine offsite landscapes, although the interaction and synergistic effects could still be detectable in community composition.

4.3. *The offsite effects of mine sites on important functional bryophyte groups*

Predicted shifts in ecosystem composition and mining could both limit the abundance of feather mosses and sphagna in mine offsite landscapes, which supports H4. Less feather moss and *sphagnum* abundances in deciduous and mixed forests than coniferous forest and open canopy ecosystems can be attributed to their strong environmental preferences. Feather mosses occur in closed-canopy, well-drained coniferous forests and sphagna occur in the more open-canopy, poorly-drained coniferous forests and peatlands (Bisbee et al., 2001; Peckham et al., 2009). Furthermore, compared with feather moss abundance, sphagna was more effected by offsite effects of mines. It indicates that *Sphagnum* abundance should be highly sensitive to mining activities, which might be attributed to the fact that *Sphagnum* growth is more susceptible to water and peat depth than feather mosses (Bergeron et al., 2009; Bisbee et al., 2001) since the landscapes near mine sites are characterized by low water table and depletion of organic soil content (Glina et al., 2019). Feather mosses occurred in a wider range of microhabitats than sphagna. The dominating habitat of sphagna is the ground while feather mosses can colonize various microhabitats (e.g. logs and rocks) which can serve as shelter from environmental changes (e.g. water content and temperature) by providing microclimatic buffering for species growing on them (Dražina et al., 2016; Haughian, 2018). The results reveal predicted ecosystem shifts and increasing mining activities might affect ecological services of boreal forests through reducing abundances of important functional groups.

Although the offsite effects of mines on bryophyte diversity, community structure and composition and drivers (ecosystem types, mining stages and microhabitats) were confirmed, further research is required to identify the source of the stress and that other studies (e.g., measuring heavy metal concentrations in the soil, installing dust samplers to see the amounts of dust and level of contamination of the dust coming from the mines) will be needed in order to do that.

5. Conclusion

Our study provides the evidence that mine offsite landscapes could be a growing threat to boreal biodiversity of sensitive groups such as bryophytes as offsite effects extended mining effects beyond the areas originally degraded. Overall, our results revealed that ecosystem type and mining stage are the predictor of bryophyte community structure in mine offsite landscapes and their combined effects are generally interacted, although microhabitats have the potential to mitigate the interaction effects in maintaining bryophyte richness. Bryophyte communities in coniferous forest seemed more resistant to the offsite effects than other ecosystem types. Reduced abundance of important functional groups in offsite landscapes could be a challenge for ecological services in boreal forests, especially in coniferous forest and open canopy ecosystems. With global changes, the predicted shifts in ecosystem type might exacerbate the effects of mining on biodiversity and ecological services in mine offsite landscapes. Cumulative areas exposed to mine offsite effects could be large at global scales, and therefore mine offsite landscapes should be considered in future impact evaluations and landscape management. A certain level of coarse woody debris storage near mine sites could be an effective conservation strategy. Our findings further encourage future studies to evaluate how these changes in bryophyte structure affect ecological services (e.g., carbon and nitrogen cycle) of the boreal forest and the microhabitat refugia under the global change.

CRediT authorship contribution statement

Xiangbo Yin: Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Christine Martineau:** Methodology, Formal analysis, Supervision, Writing – review & editing. **Nicole J. Fenton:** Methodology, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors 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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109555.

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