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Université du Québec en Abitibi-Témiscamingue

COMPRENDRE LES EFFETS DES PERTURBATIONS MULTIPLES SUR LES
COMMUNAUTÉS VÉGÉTALES DU SOUS-BOIS DANS LA FORÊT BORÉALE

Mémoire
présenté
comme exigence partielle
de la maîtrise en écologie et aménagement des écosystèmes forestiers

Par
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UNDERSTANDING THE EFFECTS OF MULTIPLE DISTURBANCES ON
UNDERSTOREY PLANT COMMUNITIES IN THE BOREAL FOREST

Thesis
submitted
in partial fulfillment of the requirements
for the master's degree in ecology and management of forest ecosystems

By
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FOREWORD

This Master's thesis is divided into three parts. The first chapter provides a general introduction to the study and includes a literature review. The second chapter consists of a scientific article to be submitted for publication. Similarly, the third chapter presents a synthesis of findings, highlights implications for forest management, and suggests avenues for future research. Specifically, Chapter II presents the core components of the research: the introduction, study area, methodology, results, discussion, and conclusion. This chapter is structured in the form of an article entitled "Understanding how multiple natural and anthropogenic disturbances shape the understory plant communities in the boreal forest", authored by Ghimire, S., Valeria, O., and Fenton, N.J. Finally, Chapter III elaborates a general discussion on future research directions and forest management implications based on the findings outlined in Chapter II.

RÉSUMÉ

Les bryophytes et les plantes vasculaires sont des éléments essentiels de la biodiversité de la forêt boréale, qui est façonnée par les perturbations. Une poignée d'études a été menée dans ce contexte pour évaluer le changement de succession dû à des perturbations individuelles telles que l'exploitation forestière et minière sur les bryophytes et les plantes vasculaires. Cependant, peu d'études ont été consacrées à l'identification de la manière dont les perturbations multiples, y compris leur interaction, modulent la structure des plantes vasculaires et des bryophytes qui constituent les éléments vitaux de la végétation du sous-étage. Cette étude examine comment la richesse et la composition des hépatiques, des mousses et des plantes vasculaires changent en réponse à de multiples perturbations directes et indirectes dans les régions écologiques de l'Abitibi-Bas-Terres et du lac Matagami au Québec. L'échantillonnage stratifié a été utilisé pour répartir les parcelles dans la zone centrale et la zone environnante de six types de perturbations : feux de forêt, défoliation par la tordeuse des bourgeons de l'épinette et la livrée des forêts, récolte, exploitation minière, construction de routes et lignes de transport d'énergie. Au total, 556 parcelles pour les bryophytes et 401 parcelles pour les plantes vasculaires provenant d'ensembles de données préexistants, ainsi que des données de terrain supplémentaires provenant de 25 parcelles, ont été utilisées. Les bryophytes ont été échantillonnés dans chaque parcelle de 5 m × 10 m à l'aide de la méthode d'échantillonnage de l'habitat floristique modifiée. Les plantes vasculaires ont été recensées dans trois quadrats de 1 m × 1 m situés au hasard, sur la base d'estimations du pourcentage de couverture. Un modèle linéaire généralisé avec régression quasi-Poisson a été appliqué pour évaluer les effets sur la richesse des espèces. Dans toutes les perturbations directes, à l'exception du feu, un nombre croissant de perturbations multiples a entraîné une diminution de la richesse en hépatiques, une stabilité de la richesse en mousses et une augmentation de la richesse en plantes vasculaires. Dans les parcelles touchées par le feu, des perturbations supplémentaires ont favorisé une plus grande richesse dans tous les groupes de plantes. Sous l'effet de perturbations indirectes, la richesse des hépatiques et des plantes vasculaires a diminué, tandis que la richesse des mousses n'a pas montré de tendance cohérente. Nous avons également observé un changement clair dans la composition des espèces avec l'augmentation des perturbations. Les perturbations directes ont été associées à une transition vers des communautés de sous-bois dominées par les feuillus, tandis que les perturbations indirectes ont favorisé les assemblages associés aux conifères. Le déclin de la richesse des hépatiques souligne leur dépendance à l'égard de microhabitats et de substrats stables et humides tels que le bois mort, les chicots et les souches. La stabilité de la richesse en mousses est probablement due au renouvellement des espèces qui maintient la diversité globale. L'augmentation de la richesse en plantes vasculaires peut refléter l'établissement d'espèces pionnières adaptées aux perturbations et aux environnements à feuilles caduques. Ainsi, parmi les plantes du sous-étage, les hépatiques présentent une sensibilité accrue à un nombre croissant de perturbations, avec des effets plus prononcés observés sur les sites directement touchés par rapport à ceux qui le sont indirectement. Cette recherche met en évidence les effets cumulatifs et additifs des

perturbations, ce qui devrait aider les développeurs et les gestionnaires à prévoir l'impact des perturbations en cours au niveau du paysage. L'intégration des effets directs et indirects des perturbations dans la planification au niveau du paysage est plus efficace pour la conservation des communautés de sous-bois dans des régimes de perturbation changeants.

Mots-clés : perturbations multiples, hépatiques, mousses, plantes vasculaires, richesse, composition, perturbations directes et indirectes.

ABSTRACT

Bryophytes and vascular plants are essential components of biodiversity in the boreal forest, which is shaped by disturbance. Several studies have been conducted in this context to evaluate successional change due to individual disturbances such as fire, forest harvest, and mines on bryophytes and vascular plants. However, there are limited studies focused on identifying how multiple disturbances, including their interactions, modulate the structure of vascular plants and bryophytes that are vital components of the understorey vegetation. This study evaluates how the richness and composition of liverworts, mosses, and vascular plants change in response to multiple direct and indirect disturbances across Quebec's Abitibi-Lowlands and Lake Matagami ecological regions. Plots were classified after sampling based on their proximity to disturbances, distinguishing core (direct) and surrounding (indirect) zones for six disturbance types: forest fire, forest harvest, spruce budworm and forest tent caterpillar defoliation, mines, forest roads, and transmission lines. The total number of plots was 556 for bryophytes and 401 for vascular plants from pre-existing datasets, along with an additional 25 plots inventoried for this study in 2024. Bryophytes were sampled in each 5 m × 10 m rectangular plot using the floristic habitat sampling method. Vascular plants were surveyed in three randomly located 1 m x 1 m quadrats within the rectangular plot based on percent cover estimates. A generalized linear model with quasi-Poisson regression was applied to assess the effects of multiple disturbances on species richness. In all direct disturbances except fire, an increasing number of disturbances led to a decline in liverwort richness, no change in moss richness, and an increase in vascular plant richness. In plots affected by fire, additional disturbances supported higher richness for all plant groups. Under indirect disturbances, liverwort and vascular plant richness declined, while moss richness remained relatively stable. We also observed a clear shift in species composition with increasing disturbance. Direct disturbances were associated with a transition toward deciduous-dominated understorey communities, whereas indirect disturbances favoured conifer-associated assemblages. The decline in liverwort richness with increasing number of disturbances underscores their dependence on stable moist microhabitats dominated by substrates like deadwood, snags, and stumps. The stable moss richness, despite increasing disturbance number, is likely due to species turnover maintaining overall diversity. The increase in vascular plant richness with increasing number of disturbances may reflect the establishment of pioneer species adapted to deciduous and disturbed environments. Hence, among the understorey plants, liverworts exhibit heightened sensitivity to an increasing number of disturbances, with more pronounced effects observed at directly impacted sites compared to those affected indirectly. This research successfully highlights the cumulative and additive effects of disturbances, which are expected to help developers and managers predict the impact of ongoing disturbances at a landscape level. Incorporating both the direct and indirect effects of disturbances into landscape-level planning is more effective for conserving understorey communities under changing disturbance regimes.

Keywords: multiple disturbances, liverworts, mosses, vascular plants, richness, composition, direct and indirect disturbances.

TABLE OF CONTENTS

ACKNOWLEDGMENTS	V
FOREWORD	VII
RÉSUMÉ	IX
ABSTRACT	XI
TABLE OF CONTENTS	XIII
LIST OF FIGURES	XV
LIST OF TABLES	XIX
GENERAL INTRODUCTION	1
1. MANUSCRIPT	9
1.1 Introduction	10
1.2 Methodology.....	13
1.2.1 Study area	13
1.2.2 Data compilation.....	15
1.2.3 Sampling design	16
1.2.4 Statistical analysis	17
1.3 Results	20
1.3.1 Species richness and direct disturbances	20
1.3.2 Species richness and indirect disturbances	25
1.3.3 Bryophyte composition and direct disturbances.....	30
1.3.4 Vascular plant composition and direct disturbances	33
1.3.5 Bryophyte composition and indirect disturbances	36
1.3.6 Vascular plant composition and indirect disturbances.....	39
1.4 Discussion.....	42
1.4.1 Ecosystem types as drivers of microclimatic and structural variations	43
1.4.2 Severity of direct and indirect disturbances.....	46
1.4.3 Time since disturbance.....	48
1.4.4 Limitations and perspectives.....	48
1.5 Conclusion	49
GENERAL CONCLUSION.....	51

ANNEX A - EXPLANATION OF SAMPLING DESIGN VARIATION AMONG DIFFERENT PROJECTS.....	53
ANNEX B - SPECIES RICHNESS ACROSS ECOSYSTEM TYPES FOR DIRECT DISTURBANCES.....	55
ANNEX C - PLOT DISTRIBUTION ACROSS DIRECT DISTURBANCE AND ECOSYSTEM TYPES.....	57
ANNEX D - ADDITIVE EFFECTS OF DIRECT DISTURBANCES ACROSS ECOSYSTEM TYPES.....	59
ANNEX E - PLOT DISTRIBUTION BY NUMBER OF DIRECT DISTURBANCES AND ECOSYSTEM TYPES.....	61
ANNEX F - SPECIES RICHNESS ACROSS ECOSYSTEM TYPES FOR INDIRECT DISTURBANCES.....	63
ANNEX G - PLOT DISTRIBUTION ACROSS INDIRECT DISTURBANCE AND ECOSYSTEM TYPES.....	65
ANNEX H - ADDITIVE EFFECTS OF INDIRECT DISTURBANCES ACROSS ECOSYSTEM TYPES.....	67
ANNEX I - PLOT DISTRIBUTION BY NUMBER OF INDIRECT DISTURBANCES AND ECOSYSTEM TYPES.....	69
ANNEX J - LIST OF BRYOPHYTES.....	71
ANNEX K - LIST OF VASCULAR PLANTS.....	76
LIST OF REFERENCES.....	83

LIST OF FIGURES

- Figure 1 Map of the study area showing the location of sampling plots grouped by databases within two ecological regions in Abitibi-Temiscamingue. The top left and bottom left squares show the boundary of Canada and Quebec, with vegetation zones, respectively..... 14
- Figure 2 Predicted patterns of species richness for liverworts, mosses, and vascular plants in response to an increase in the number of direct disturbances experienced at a site. The x-axis represents the cumulative number of direct disturbances experienced at a site, while the y-axis shows the predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. Shaded areas around the lines indicate 95% confidence intervals. 21
- Figure 3 The richness of liverworts, mosses, and vascular plants in sites affected by various direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar) in the absence of other disturbances. The x-axis represents each type of direct disturbance, while the y-axis displays the predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. The bars with an asterisk (*) mark denote a statistically significant difference in the richness of the respective plant category compared to the undisturbed plots. The dataset contains no vascular plant plots impacted by fire disturbance. 22
- Figure 4 Predicted species richness of liverworts, mosses, and vascular plants in response to increasing disturbance numbers, shown separately for plots where different direct disturbance types: fire, forest harvest, spruce budworm, and forest tent caterpillar outbreak were the primary disturbance type. The x-axis represents the number of disturbances, while the y-axis represents the predicted species richness. Brown, blue, and green lines correspond to the richness of liverworts, mosses, and vascular plants, respectively. 24
- Figure 5 Predicted patterns of species richness of liverworts, mosses, and vascular plants according to an increase in the number of indirect disturbances. The x-axis represents the cumulative number of indirect disturbances, while the y-axis shows the

predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. Shaded areas around the lines indicate 95% confidence intervals.....	25
Figure 6 The predicted richness of liverworts, mosses, and vascular plants across different indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, transmission lines, mines, and forest roads). The x-axis represents the individual indirect disturbances, while the y-axis displays the predicted species richness. The brown, blue, and green bars correspond to the richness of liverworts, mosses, and vascular plants, respectively. The asterisk mark (*) denotes a statistically significant difference in the richness of liverworts, mosses, and/or vascular plants compared to the undisturbed sites.	27
Figure 7 Predicted species richness of liverworts, mosses, and vascular plants in response to increasing disturbance numbers across indirect disturbance types: fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, and transmission lines. The x-axis represents the number of indirect disturbances, while the y-axis represents the predicted species richness. The brown, blue, and green lines correspond to the richness of liverworts, mosses, and vascular plants, respectively.	30
Figure 8 Principal coordinates analysis (PCoA) for the bryophyte composition across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and direct disturbances were added by correlation to the axes. In the species codes, the initial letters indicate bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data from 289 plots, where a total of 290 species were recorded; however, only 115 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J.....	31
Figure 9 Principal coordinates analysis (PCoA) for the bryophyte composition across different ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and the number of direct disturbances were added by correlation to the axes. In the species codes, the initial letters indicate bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data	

from 449 plots, where a total of 290 species were recorded; however, only 113 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J. 32

Figure 10 Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous and deciduous) using the Bray-Curtis dissimilarity index. Species names and direct disturbances were added by correlation to the axes. The mixed ecosystem type is not indicated in the PCoA plot, as no vascular plant plots were representative of this ecosystem type. This plot comprises data from 166 plots, where a total of 266 species were recorded; however, only 52 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K. 34

Figure 11 Principal coordinates analysis (PCoA) for the vascular plant composition under ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and the number of direct disturbances were added by correlation to the axes. This plot comprises data from 322 plots, where a total of 266 species were recorded; however, only 71 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K. 35

Figure 12 Principal coordinates analysis (PCoA) for the composition of bryophytes across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and indirect disturbances were added by correlation to the axes. Species codes begin with letters that denote bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data from 290 plots, where a total of 290 species were recorded; however, only 121 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J. 37

Figure 13 Principal coordinates analysis (PCoA) for the bryophyte composition under ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and disturbance number were added by correlation to the axes. Species codes begin with letters that denote bryophyte guilds: m for

mosses, s for sphagnum, and h for liverworts. This plot comprises data from 420 plots, where a total of 290 species were recorded; however, only 136 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J..... 39

Figure 14 Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and indirect disturbances were added by correlation to the axes. This plot comprises data from 148 plots, where a total of 266 species were recorded; however, only 45 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K. 40

Figure 15 Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and disturbance number were added by correlation to the axes. This plot comprises data from 218 plots, where a total of 266 species were recorded; however, only 56 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K. 42

LIST OF TABLES

Table 1 Generalized Linear Model (GLM) results showing the effects of the number of direct disturbances on the richness of liverworts, mosses, and vascular plants. The table provides the estimates, standard errors (SE), t-values, and p-values for each variable. The intercept represents the average predicted richness of liverworts in undisturbed sites. Significant effects ($p < 0.05$) are indicated with an asterisk (*)....	21
Table 2 Generalized Linear Model (GLM) results for species richness of liverworts, mosses, and vascular plants concerning the individual direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar). The table provides the estimates, standard errors (SE), t-values, and p-values for each predictor, with significant effects ($p < 0.05$) marked by an asterisk (*). The intercept indicates the average predicted liverwort richness under undisturbed conditions.	23
Table 3 Generalized Linear Model (GLM) results illustrating how species richness of liverworts, mosses, and vascular plants responds to the number of indirect disturbances. Estimates, standard errors (SE), t-values, and p-values are provided for each variable. The intercept represents the estimated average liverwort richness in undisturbed sites. Significant effects ($p < 0.05$) are indicated with an asterisk (*)....	26
Table 4 Generalized linear model (GLM) results for the effects of indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, transmission lines) on liverworts, mosses, and vascular plants. The table includes the estimates, standard errors (SE), t-values, and p-values for each predictor, with significant effects ($p < 0.05$) marked by an asterisk (*). The intercept captures the average predicted liverwort richness under undisturbed conditions.	28
Table 5 Effects of direct disturbances, number of disturbances, and ecosystem types on the bryophytes community using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.....	33
Table 6 Effects of direct disturbances, number of disturbances, and ecosystem types on vascular plants using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.....	36

Table 7 Effects of indirect disturbances, number of disturbances, and ecosystem types on bryophytes using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level. 38

Table 8 Effects of indirect disturbances, number of disturbances, and ecosystem types on vascular plants using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level. 41

GENERAL INTRODUCTION

Ecosystem types and understorey plant communities in the boreal forest.

Boreal forests consist mainly of coniferous, deciduous, and mixed ecosystems, and the differences between these forest types influence the understorey vegetation. Coniferous stands, with their evergreen foliage and dense branching, limit light penetration and create stable microclimatic conditions such as cooler temperatures, consistent moisture, and reduced wind exposure, which favour shade-tolerant bryophytes but suppress vascular plant diversity due to low light and poor nutrient availability (Hart & Chen, 2006; Bartels et al., 2018; García De Jalón et al., 2019; Barbé et al., 2020). In contrast, deciduous and mixed ecosystems allow more sunlight to reach the ground and enrich the soil with deciduous leaf litter, supporting higher vascular plant richness while reducing bryophyte cover through increased litter accumulation (Bartels & Chen, 2013; Su et al., 2019). These structural and environmental differences across ecosystem types strongly influence the composition, diversity, and ecological dynamics of understorey plant communities.

The understorey vegetation consists primarily of vascular (herbs, shrubs, ferns, and tree seedlings) and non-vascular (mosses, liverworts, and lichens) plants, which form a significant component of boreal forest diversity. Within these communities, species differ in their ecological characteristics, which broadly categorize them as either generalists or specialists. Generalist species have good dispersal capacity and display broad environmental tolerances (Poisot et al., 2011; Johansson et al., 2012). In boreal forests, the majority of moss and vascular plant species are primarily composed of species that are well-adapted to withstand harsh climatic conditions and frequent natural and/or anthropogenic disturbances (Johansson et al., 2012; Noualhaguet et al., 2023); therefore, they are distinguished as generalists. Whereas specialist species, such as liverworts, exhibit a narrow ecological niche, possess limited dispersal capacities, and typically inhabit selective microhabitats, like deadwood, stumps, and snags (Poisot et al., 2011; Nurmi & Parvinen, 2011). For instance, some liverworts such as *Cephalozia lunulifolia* (Dumort.) and *Tritomaria exsectiformis* (Breidl. Schiffn) are associated with coniferous deadwood, whereas species like

Chiloscyphus pallescens (Ehrh. Ex Hoffm.) tend to dominate on the decayed deciduous wood (Caners et al., 2013). Thus, understanding the distinct ecological roles and habitat preferences of generalist and specialist understorey species is essential for assessing how boreal forest biodiversity responds to environmental changes and disturbance regimes.

Vascular plants. The boreal region in Canada is characterized by its diverse array of overstorey and understorey plant communities within coniferous to deciduous ecosystems. The boreal forest is mainly inhabited by coniferous trees, which include white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.] B.S.P.), larch or tamarack (*Larix laricina* [Du Roi] k. Koch), Jack pine (*Pinus banksiana* L.), and balsam fir (*Abies balsamea* [L.] Mill.) (Brandt et al., 2013). These coniferous trees have evolved a set of adaptations that have made them well-suited to the challenging environmental conditions characterized by cold temperatures, heavy snowfall, and the occurrence of wildfires (Brandt et al., 2013). However, the composition and dynamics of these coniferous tree species change due to natural and human-induced disturbances. These disruptions can result in the mortality of forest vegetation and canopy gaps within the forest (De Grandpré et al., 2011). Canopy opening allows more sunlight to reach the forest floor, which in turn creates favourable growth conditions for fast-growing, shade-intolerant deciduous trees such as trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.) (Brandt et al., 2013). Therefore, resource heterogeneity (light, soil nutrients, and moisture) created by canopy gaps enables the coexistence of both early and late successional stage tree species, which helps maintain understory plant diversity (Hart & Chen, 2006; De Grandpré et al., 2011).

In addition to overstorey changes, disturbances significantly influence the composition and structure of vascular plants in the understorey. The resources available after stand-replacing fire promote the growth of shade-intolerant and nutrient-demanding vascular plants such as fireweed (*Epilobium angustifolium* L.), raspberry (*Rubus idaeus* L.), bracken fern (*Pteridium aquilinum* [L.] Kuhn), and blueberry (*Vaccinium myrtilloides* Michx.) (Hart & Chen, 2006). In some scenarios, increased dominance by

invasive herbaceous plant species after disturbances causes resource competition and affects the abundance and diversity of native vascular plants (McDonald et al., 2008; Su et al., 2019). Thus, the disturbances play a crucial role in shifting the overall species composition and population dynamics within boreal forests.

Bryophytes and their role in the ecosystem. Bryophytes are non-vascular plants recognized by the absence of roots and vascular tissues. They absorb water and nutrients directly through single-layer cells present on their leaves (León-Vargas et al., 2006). Bryophytes are categorized into three groups based on their unique morphological and physiological characteristics: Marchantiophyta (liverworts), Bryophyta (mosses), and Anthocerotophyta (hornworts). Bryophytes are poikilohydric, which means that they can rapidly gain and lose water, and have no internal control over water loss like vascular plants (Proctor et al., 2007). Therefore, changes in microhabitat factors such as light, humidity, and wind patterns due to canopy removal have effects on bryophyte diversity (Zhang et al., 2023). Moreover, habitat transformation caused by disturbances alters woody substrates and the chemical and physical properties of soil, which indirectly affects bryophyte species composition (Fenton et al., 2003; Riffo-Donoso, 2021). Consequently, these changes result in disturbed habitats being dominated by generalist species, while specialist species are more frequent in undisturbed habitats (Riffo-Donoso, 2021). Thus, these different habitats and physiological requirements make them sensitive to natural and human-induced disturbances.

Among bryophytes, liverworts are specialist species with specific ecological requirements (Caners et al., 2013; Johansson et al., 2012; Noualhaguet et al., 2023). These species are highly dependent on high moisture conditions and typically thrive in the cool and more humid coniferous forest floor (Caners et al., 2013; Hernández-Rodríguez et al., 2019). Therefore, changes in soil moisture, alterations in suitable substrates, and shifts in temperature and humidity patterns due to disturbances make these species particularly vulnerable (Fenton et al., 2003; Noualhaguet et al., 2023). In contrast, mosses are ubiquitous and less sensitive to disturbances in comparison to liverworts (Riffo-Donoso, 2021). Most moss species exhibit a remarkable ability to

tolerate desiccation and thrive in less shady habitats (Turetsky et al., 2012). This resilience makes them less susceptible to increased light exposure following a disturbance (Fenton et al., 2003). Thus, mosses and liverworts have differential responses to disturbance.

Bryophytes are key constituents of ecosystems and help to promote important ecological processes such as carbon and nitrogen cycling, water balance, as well as soil temperature and moisture regulation, which regulate the stability of the boreal ecosystem (Turetsky et al., 2010; Turetsky et al., 2012). Their ability to form a symbiotic association with cyanobacteria is advantageous for increasing the availability of nitrogen to plants through nitrogen fixation (Rousk et al., 2013). Furthermore, the thick carpet of mosses over the ground surface present in some ecosystems acts as an insulation layer, which helps to reduce soil temperature fluctuation and stabilizes it to control nutrient loss (Gornall et al., 2007). The dense layer of mosses on the forest floor sometimes exceeds the biomass production of overstorey plants (Turetsky, 2003). For example, mosses contribute between 20% and 48% to the above-ground primary productivity in forests and wetlands, respectively (Turetsky et al., 2010). Accordingly, bryophytes provide habitat, food, and nesting material for micro and macroinvertebrates. They create a favourable substratum, seedbed and aid in the establishment of plant seedlings, and offer habitats for cyanobacteria (Rousk et al., 2013). Similarly, some birds like hummingbirds (*Sephanoides sephanoides*) use mosses (*Ancistrodes genuflexa*) to build their nests (Riffo-Donoso, 2021). Thus, the ecological functions of bryophytes are far-reaching, as they provide habitat and regulate the diversity of plants and other associated organisms.

Driving factors of bryophytes and vascular plants composition and diversity.

Understorey diversity and composition are shaped by a combination of biotic and abiotic factors across different scales and environmental conditions. These factors include light availability, relative humidity, stand age, forest composition, substrate characteristics, soil moisture, soil nutrients, and micro-habitat availability (Fenton & Bergeron, 2008; Sun et al., 2013; Paquette et al., 2016). The availability of light for

understorey plants depends on the amount of canopy density (Rola et al., 2021). The change in overstorey composition, size, and arrangement of leaves can influence the amount of light reaching the forest floor, and this modification affects the composition and diversity of understorey plants (Barbier et al., 2008; Bartels & Chen, 2010).

The composition and diversity of understorey plants are influenced by resources like soil nutrients and moisture in their habitats. The overstorey composition influences soil moisture levels by intercepting rainfall and extracting water uptake from deep soil layers (Hart & Chen, 2006; Bartels & Chen, 2010). The coniferous root system helps to regulate water uptake from deeper soil layers, and this higher soil moisture level creates a moist environment that favours bryophyte growth (Barbier et al., 2008; Bartels et al., 2018; Su et al., 2019). The availability of soil nutrients also depends on the overstorey composition. For example, an increase in the abundance of deciduous overstories increases soil nutrients due to their nutrient-rich litterfall, which decomposes easily and enhances the diversity of shade-intolerant vascular plants (Bartels & Chen, 2013; Su et al., 2019). In contrast, the fallen leaves from deciduous trees act as physical barriers that limit the access of non-vascular plants to essential resources (Schmalholz & Granath, 2014). For example, obstruction of moisture affects the water dynamics within the soil and imposes additional challenges for non-vascular plants to establish and thrive in the competitive environment. Also, the dense layer of leaves on the forest floor intercepts sunlight that restrict the light accessibility to the non-vascular plants on the ground (Barbier et al., 2008; Su et al., 2019). When the decomposition process starts, it contributes to the formation of a nutrient-rich organic layer that alters the chemical composition of the soil and nutrient availability for plants (Hart & Chen, 2006). This association of physical, chemical, and hydrological factors collectively controls the access of understorey plants to essential resources like light, nutrients, and water. Hence, overstorey components and environmental factors influence the diversity and composition of vascular and non-vascular plants.

Time since disturbance is one of the important factors that influences the composition and diversity of both vascular plants and bryophytes after any type of disturbance. Immediately after disturbances, the increased availability of light, soil nutrients, and

growth space creates favourable conditions for the rapid establishment of shade-intolerant vascular plants, which results in high species richness and cover during the early successional stages (Hart & Chen, 2006; Kumar et al., 2018). In contrast, bryophyte abundance remains low at this stage due to intense resource competition and the dominance of vascular plants (Su et al., 2019). With the increase in time since disturbance, the canopy becomes more closed, which reduces light availability, and soil nutrient immobilization intensifies, leading to declines in the abundance and diversity of shade-intolerant vascular plants (Zhang et al., 2017). During this phase, bryophytes, with greater tolerance for low-light and low-nutrient conditions, expand in cover and diversity, supported by the accumulation of coarse woody debris and litter layers that provide suitable microhabitats (Chen & Popadiouk, 2002). After a long time since disturbance, the stands become mature, where gap dynamics enhance structural heterogeneity and diverse substrate conditions allow both vascular plants and bryophytes to coexist, which results in a resurgence of understorey species diversity (Kumar et al., 2017; Kumar et al., 2018). Therefore, successional shifts along with a span of time after disturbance generate distinct changes in the relative dominance of vascular plants and bryophytes, driven by resource conditions that evolve with stand development over time.

Multiple disturbances and their interaction. The occurrence of multiple disturbances, natural and/or anthropogenic, can have complex consequences in an ecosystem. These disturbances can occur at once or in a sequence, which ultimately alters the environmental and ecological integrity (Venier et al., 2021). Following the disturbance, there often occurs a shift in the forest's structure, productivity, and susceptibility of the ecosystem to upcoming disturbances (Bigler et al., 2005). For instance, the cumulative effects of insect outbreaks, forest fires, and drought disturbances have been shown to reduce the available timber volume in Canada's forests (Boucher et al., 2018). Understanding these cumulative effects requires consideration of not only disturbance frequency and intensity but also the mode and type of impact, as the ecological consequences differ depending on whether a disturbance is direct or indirect. Direct disturbance involves both habitat modification

and the in-situ physical disruption or removal of plant communities through mechanical or physical forces, such as canopy removal combined with the crushing of forest floor substrates and biota by forest harvest machinery, slash deposition, or soil scarification (Fenton et al., 2003). In contrast, indirect disturbance alters habitat without immediate physical damage but through a series of indirect effects developed on the periphery of the directly affected zone. For example, conditions such as microclimate, temperature, or humidity changes in the periphery of the canopy removal zone, and the species along the edges respond to such altered environmental conditions over time, which affects diversity and composition (Fenton et al., 2003). Interactions between disturbances can either be linked or compounded. In linked disturbance, the legacies of previous disturbances affect the spatial and temporal extent of subsequent disturbances (Buma, 2015). When disturbances like drought and fire are linked, dry conditions enhance fuel flammability, making forests more susceptible to catching fire. The resulting post-fire conditions affect the soil due to a reduction in water availability, making it tough for plants to grow (Foster et al., 2022). Furthermore, disturbances such as forest harvest, fire and insect outbreaks occurring within the same stand but at different time intervals can reduce seed sources, disrupt seed dispersal, and alter post-disturbance regeneration patterns. These sequential disturbances often force plant communities to deviate from predicted successional trajectories brought about by the alterations in species recruitment patterns and resource availability (Payette & Delwaide, 2003).

Multiple disturbances can interact in ways that alter and/or exceed the ecosystem's resilience, affecting its ability to recover from pre-disturbance conditions (Buma, 2015; Cannon et al., 2017). The effect produced by the interactions can be additive, synergistic, or antagonistic (Côté et al., 2016). Additive effects exhibit a linear behaviour, where the combined impact on the environmental response is equivalent to the combined effects of individual stressors (Venier et al., 2021). Synergistic effects occur when the combined impact of different stressors or factors is greater than the sum of their effect, and the direction of impact is always non-linear and detrimental to the ecosystem (Hewitt et al., 2016). On the other hand, when different factors act in

opposite directions, leading to a reduction in the overall environmental impact, it is an antagonistic effect (Venier et al., 2021). As an ecosystem can have the consequences of disturbances in different forms, it is essential to understand the impact of multiple disturbances and their interaction on the environmental and ecological processes (Venier et al., 2021).

1. MANUSCRIPT

Understanding how multiple natural and anthropogenic disturbances shape the understorey plant communities in the boreal forest.

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Abstract

Bryophytes and vascular plants are key components of boreal forest biodiversity, contributing to essential ecosystem functions such as nutrient cycling, moisture regulation, carbon sequestration, and soil stability. However, these understory communities are increasingly threatened by multiple disturbances. This study investigates the cumulative effects of multiple disturbances on liverworts, mosses, and vascular plants in Quebec. A total of 556 plots for bryophytes and 401 plots for vascular plants were compiled from pre-existing datasets. Twenty-five additional plots were established using a stratified sampling technique, and six disturbances were classified as either direct (areas directly affected by disturbance) or indirect (surrounding the directly disturbed areas): fire, forest harvest, insect outbreaks (spruce budworm and forest tent caterpillar), forest roads, mines, and transmission lines. Bryophytes were sampled from each microhabitat in each 5 m × 10 m plot, while vascular plants were surveyed using percent cover estimates. A generalized linear model with quasi-Poisson regression was used to assess the effects of cumulative disturbance number and the three plant types on species richness. The results showed that liverwort richness decreased with an increasing number of direct disturbances, whereas vascular plant richness exhibited a positive response to the number of direct disturbances. However, in indirect disturbances, liverwort and vascular plant richness declined as the disturbance number increased, while no consistent pattern was observed for moss richness. Additionally, as disturbance numbers increased, direct disturbances promoted deciduous-dominated understorey communities, and a distinct shift in species composition occurred. Therefore, we recommend considering the cumulative and additive effects of disturbances rather than evaluating them in isolation to support sustainable forest management.

Keywords: multiple disturbances, liverworts, mosses, vascular plants, richness, composition, direct and indirect disturbances.

1.1 Introduction

The boreal ecosystem is one of the largest terrestrial circumpolar biomes and supports a specific biological diversity (Burton et al., 2003). Understorey plant communities, such as vascular plants and bryophytes, are a key component of boreal ecosystem biodiversity and its dynamics (Roberts, 2004; Nilsson & Wardle, 2005). The majority of understorey species in the boreal ecosystem are categorized as generalist species. Generally, these species possess broad ecological tolerances, have large distribution ranges, and effective dispersal abilities that allow them to persist in frequently disturbed environments (Barbé et al., 2020). In the boreal ecosystem, most of the mosses and vascular plants fall under this category. However, it is important to note that while most of these taxa exhibit generalist traits, other species with specialist traits also persist within boreal ecosystems. This group of species have narrow ecological requirements, limited dispersal capacity, and is often found restricted to very specific microhabitats as deadwood, stumps, and snags (Johansson et al., 2012; Noualhaguet et al., 2023). In the boreal ecosystem, liverworts in the understorey component are identified as specialist species.

Within the Canadian boreal ecosystem, three primary forest ecosystem types are dominant: coniferous, deciduous, and mixed. Variation in environmental conditions across these ecosystems drives differences in the diversity and composition of understorey plant communities (Qian et al., 2003; Kembel & Dale, 2006; Barbier et al., 2008). Coniferous canopies, characterized by persistent foliage and dense branching structures, buffer understorey environmental conditions, such as temperature, moisture, irradiance, and wind, more effectively than deciduous canopies (García De Jalón et al., 2019; Barbé et al., 2020). As a result, coniferous ecosystems typically support bryophyte-dominated understorey communities adapted to shaded and stable environments, while vascular plant diversity tends to be lower due to limited light availability and nutrient-poor soils (Bartels et al., 2018). In contrast, deciduous and mixed ecosystems allow greater light penetration and deposit nutrient-rich deciduous litter, which promotes higher vascular plant species richness and diversity but constrains bryophyte cover through litter accumulation (Bartels & Chen, 2013; Bartels et al., 2018; Su et al., 2019). Therefore, factors that drive changes in ecosystem types

are likely to produce corresponding shifts in understorey communities and canopy structure.

Disturbances are key agents of change in boreal ecosystems, and the responses of plant communities vary depending on the type, intensity, and frequency of disturbance. Understorey plant communities are essential components of boreal ecosystems due to their contributions to nutrient cycling, soil stability, hydrological regulation, and carbon sequestration (Fenton & Bergeron, 2006; Caners et al., 2013); however, these communities are particularly sensitive to environmental changes triggered by disturbances, as their diversity and composition are closely tied to microclimatic conditions, substrate availability, and overstorey structure (Paquette et al., 2016; Bartels et al., 2018). Disturbances that damage the forest canopy significantly increase light penetration to the forest floor, altering the thermal and moisture regimes of the understorey environment (Caners et al., 2013; Harper et al., 2015). Increased light availability typically benefits light-demanding, fast-growing vascular plant species while simultaneously exposing moisture-sensitive bryophytes, particularly liverworts, to desiccation stress (Fenton & Bergeron, 2006). In addition to altered microclimatic conditions, disturbances influence the availability and quality of substrates essential for understorey plant establishment. Bryophytes, especially liverworts, rely on specific substrates such as decayed wood, stumps, and coarse woody debris, which are often diminished or degraded following forest harvest, fire, or intensive land-use practices (Fenton et al., 2003; Peckham et al., 2009).

In boreal forests, time since disturbance is a key driver of understorey plant community richness and composition, as resource availability and habitat conditions shift throughout different stages of stand development. Vascular plant richness typically peaks in early post-disturbance stages due to high light availability and nutrient-rich conditions, then declines with time as canopy closure reduces these resources (Hart & Chen, 2006; Reich et al., 2012; Zhang et al., 2017). In contrast, bryophyte richness, particularly of liverworts, tends to increase in older stands, where coarse woody debris accumulation, substrate decay, and micro-topographic heterogeneity create suitable habitats for these moisture-dependent and substrate-specific species (Chen &

Popadiouk, 2002; Bartels & Chen, 2010). Thus, the dynamic interplay of disturbance history and stand development shapes distinct patterns of vascular plant and bryophyte diversity in the boreal ecosystem.

While the ecological responses of understorey species to individual disturbances such as fire or forest harvest have been relatively well documented (Hart & Chen, 2006; Su et al., 2019), our understanding of the cumulative effects of multiple disturbances on understorey diversity and composition remains limited. In boreal ecosystems, where both natural and anthropogenic disturbances frequently occur, the occurrence of multiple disturbances, whether simultaneously or sequentially, can have complex consequences for ecosystem structure and function (Venier et al., 2021). These cumulative effects arise when the impacts of multiple disturbances accumulate over time, irrespective of their type, potentially resulting in more profound and lasting alterations to ecosystem structure and function. Additionally, additive effects represent the specific contributions of individual disturbance types, considered separately but combined, which can further intensify the overall impact on the ecosystem (Venier et al., 2021). Beyond additive effects, interactions between disturbances can also be synergistic or antagonistic. A synergistic interaction occurs when the effects of one disturbance increase the probability, intensity, or severity of a subsequent disturbance and amplify its ecological impact (Simard et al., 2011; Buma, 2015). In contrast, an antagonistic interaction occurs when the effects of one disturbance reduce the impact of a subsequent disturbance, either by lowering its probability or by diminishing its ecological consequences (Cannon et al., 2017; Venier et al., 2021). Understanding how these disturbances, individually and in combination, affect the richness and composition of vascular plants and bryophytes is essential for predicting the future trajectories of these ecosystems, particularly in the context of ongoing environmental change.

In this study, we aim to evaluate the richness and composition of understory plant communities (liverworts, mosses, and vascular plants) and their response to multiple direct and indirect disturbances. Direct disturbance involves both habitat modification and the in-situ physical disruption or removal of plant communities through mechanical

or physical forces, such as canopy removal combined with the crushing of forest floor substrates and biota by forest harvest machinery, slash deposition, or soil scarification (Fenton et al., 2003). In contrast, indirect disturbance alters habitat without immediate physical damage but through a series of indirect effects developed on the periphery of the directly affected zone. For example, conditions such as microclimate, temperature, or humidity changes in the periphery of the canopy removal zone, and the species along the edges respond to such altered environmental conditions over time, which affects diversity and composition (Fenton et al., 2003).

Our first hypothesis, in the context of direct disturbance, was that specialist species (liverworts) experience more synergistic declines in richness due to multiple direct disturbances than generalist species (some boreal mosses and vascular plants). Secondly, we hypothesized that the indirect effects of disturbance on the plant group (liverworts, mosses, and vascular plants) are less pronounced compared to the direct effect.

1.2 Methodology

1.2.1 Study area

The study area is situated within two ecological regions, the Abitibi Lowlands and the Lake Matagami plain in the western boreal forest of Quebec, Canada (Figure 1). This region is characterized by a cold and humid continental climate, with mean annual precipitation ranging from 850 mm to over 1300 mm (Bergeron et al., 2004). The vegetation is predominantly composed of coniferous forests, including black spruce (*Picea mariana* [Mill.] B.S.P.), balsam fir (*Abies balsamea* [L.] Mill.), and white spruce (*Picea glauca* [Moench] Voss). Furthermore, the area supports deciduous species such as paper birch (*Betula papyrifera* Marsh.) and pioneer species, including jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.), which often regenerate following wildfires (Dansereau & Bergeron, 1993). In addition to fire, the study area has been influenced by insect outbreaks, particularly spruce budworm (*Choristoneura fumiferana* Clemens) and forest tent caterpillar (*Malacosoma disstria* Hübner) (Moulinier et al., 2013; Navarro et al., 2018). Different forest management practices, like forest harvest, have been implemented in this region,

which supports a significant portion of the provincial wood production. Moreover, the region has undergone extensive land-use development, such as the mining industry, and the expansion of linear infrastructures (forest roads and transmission lines). Mining, in particular, has flourished significantly over the years, as parts of the region have been identified as an important source of minerals (Yin et al., 2022)

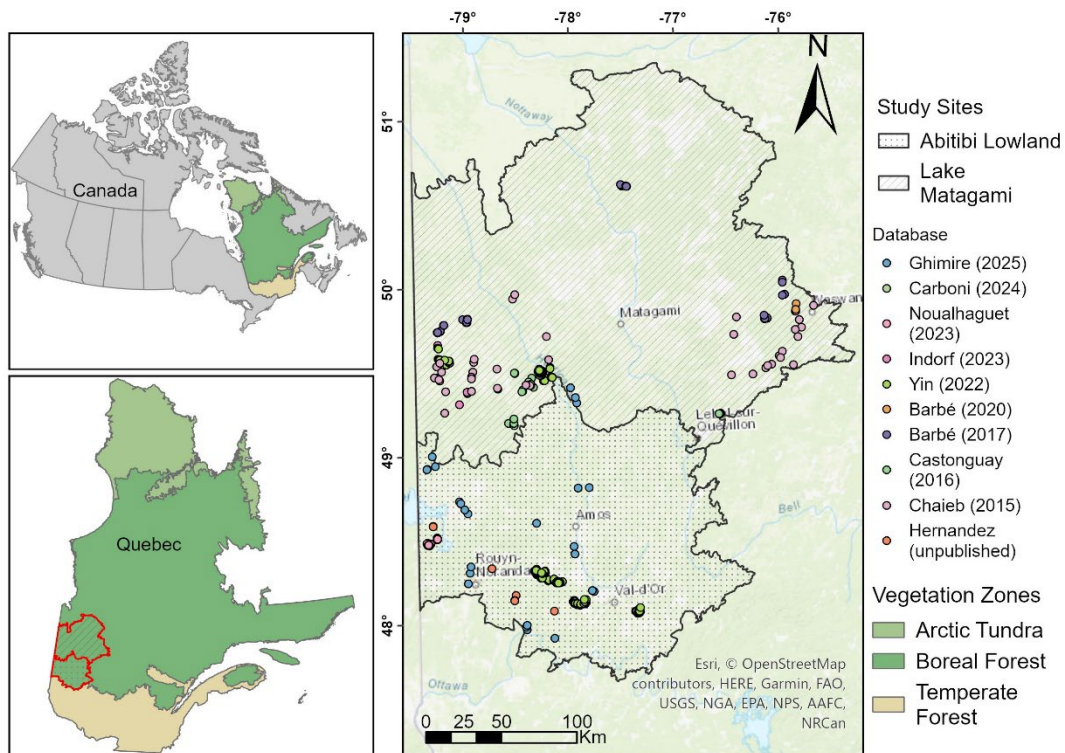


Figure 1
Map of the study area showing the location of sampling plots grouped by databases within two ecological regions in Abitibi-Temiscamingue. The top left and bottom left squares show the boundary of Canada and Quebec, with vegetation zones, respectively.

1.2.2 Data compilation

To assess the influence of past disturbances on the understorey vegetation in our study area, we utilized datasets from nine previous projects conducted between 2015 and 2023 in the study area (Chaieb et al., 2015; Castonguay, 2016; Barbé et al., 2017; Barbé et al., 2020; Yin et al., 2022; Noualhaguet et al., 2023; Indorf, 2023; Carboni, 2024; Hernandez, unpublished). Maps were generated to show the extent of fire, forest harvest, insect outbreaks (spruce budworm and forest tent caterpillar), mines, forest roads, and transmission lines using the *Forêt Ouverte* (www.foretouverte.gouv.qc.ca) mapping platform. Disturbances were classified into direct and indirect. Direct disturbance occurs in core areas that experience immediate physical alteration resulting from fire, forest harvest, and insect outbreaks (spruce budworm and forest tent caterpillar). In contrast, indirect disturbance occurs in the surrounding zones influenced by these core disturbances, where vegetation structure and composition may be affected through edge effects and altered microenvironmental conditions. In this study, multiple disturbances are defined as the addition of two or more disturbance types, either natural (fire, spruce budworm, and forest tent caterpillar outbreak) or anthropogenic (forest harvest, mines, forest road, and transmission lines), direct as well as indirect, occurring within the same site. For instance, a disturbance number of 0 indicates an undisturbed site, 1 indicates the presence of any single disturbance, 2 indicates the combination of two disturbances, and 3 represents sites affected by three distinct disturbances (Annex E and I).

While the onset of disturbances across sites was generally around the same period (approximately 50 years), plots with multiple disturbances may have experienced different disturbance types at slightly different times. We did not include time since disturbance as a variable for this study because the focus was on the number of disturbances, emphasizing their cumulative influence on understorey plant richness and composition rather than the exact timing or sequence of disturbances. With this consideration, sampling plots from the compiled datasets were classified based on their existing distance from a disturbed site. For this selection, disturbance-specific buffer distances were considered: 100 m for fire (1976–2022), forest harvest (1976–2021), forest roads, mines, and transmission lines, and 60 m for spruce budworm

(2015–2023) and forest tent caterpillar (1986–2017). The buffer distances were chosen in such a way that the edge effect of the associated disturbances can be identified within that distance range (Harper et al., 2005; Avon et al., 2010; Franklin & Harper, 2016; Deljouei et al., 2017). Ecosystem types (coniferous, deciduous, and mixed) were identified using data from the Ecoforestry Map of the 5th Forest Inventory of Quebec (MRNF, 2022). Ecosystems were defined as coniferous when coniferous tree cover exceeded 75%, deciduous when deciduous tree cover exceeded 75%, and mixed when coniferous tree cover ranged between 25% and 75%. Based on these criteria, we identified 556 plots for bryophytes and 401 plots for vascular plants (for a full breakdown, see Annex C and E). The maximum number of disturbances, either direct or indirect, observed in our sampling plot was three.

1.2.3 Sampling design

The pre-existing datasets were supplemented by additional fieldwork, which was conducted between June and August 2024, to ensure a homogenous distribution of sampling plots across the study area, representing each disturbance as equally as possible. A special focus was given to increasing the number of sampling plots for disturbance types that had been underrepresented in the compiled datasets. Thus, based on accessibility (within 500 m of a practicable road) and ecosystem types (coniferous, deciduous, and mixed), a total of twenty-five sampling plots were allocated within the study area using a stratified sampling approach. The additional plots were added for fire, forest harvest, spruce budworm, forest tent caterpillar, and transmission lines that had few or no replicates in the existing datasets. All plots from previous projects were considered independent sampling units in this study. In the field, first, a 5 m × 10 m rectangular plot was established. We then randomly placed three 1 m × 1 m quadrats within the rectangular plot. In each quadrat, we inventoried and recorded the presence of understorey plants (shrubs, tree seedlings, grasses, and ferns). We visually estimated vascular plant abundance as the percentage cover of each species. The taxonomic nomenclature of vascular plants was based on the VASCAN database (Brouillet et al., 2010). Similar methodological approaches were applied in most of the studies from which the datasets were compiled, except for a few studies. For instance, Yin (2022) used transects around each mine site, and

Noualhaguet (2023) applied a transect-based approach within permanent plots. A detailed explanation of between-studies variation can be found in Annex A.

We sampled bryophytes using a modified floristic habitat sampling technique (Newmaster et al., 2005) within each rectangular plot. All bryophytes were sampled from various microhabitat types: tree bases, roots, deadwood, stumps, snags, rocks, soil, and ground/litter. We then placed collected specimens in paper bags labelled with plot ID and microhabitat type information. Secondly, bryophyte samples were transported to the laboratory at the University of Quebec at Abitibi-Temiscamingue (UQAT), Rouyn-Noranda, where they were air-dried to prevent mould formation. Detailed species-level identification was then conducted using a dissecting and compound binocular microscope. We identified mosses and liverworts using the Moss Flora of the Maritime Provinces (Ireland, 1982), Maine Mosses (Allen, 2014), The Intricate Beauty of Sphagnum Mosses (Laine, 2009), and The Liverworts of the British Isles (Paton, 1999).

1.2.4 Statistical analysis

1.2.4.1 Species richness

To identify the effects of direct and indirect disturbances on species richness (the number of species), we fitted a generalized linear model (GLM). The response variable, species richness, was calculated separately for liverworts, mosses, and vascular plants. Bryophyte richness was quantified as the total number of unique species recorded across all sampled microhabitats within each plot, whereas vascular plant richness was assessed as the sum of distinct species identified within three quadrats per plot. The predictors included cumulative disturbance numbers and disturbance types (direct and indirect). The plant group (liverworts, mosses, and vascular plants) was included as a categorical factor to compare species richness between groups, while acknowledging that richness patterns are distinct for each plant group. Ecosystem type was included as a predictor in our richness models; however, similar patterns were observed across all ecosystem types (Annex D and Annex H). Therefore, we present the models without separating by ecosystem type.

Since species richness is count data, we assumed a Poisson distribution with a logarithmic link function. To assess overdispersion, we examined the Pearson's chi-square statistic ratio to the residual degrees of freedom. Upon detecting overdispersion (indicated by a ratio greater than 1, meaning that the variance of species richness was greater than expected under the Poisson assumption), we applied a quasi-Poisson model as an adjustment to standard errors in the data. We evaluated model assumptions using diagnostic plots. Predictors were considered statistically significant at a 95% confidence interval (p-value less than 0.05). We tested the significance of predictors (direct and indirect disturbances, plant type, and their interaction) using type II F-tests with the *anova* function in the *car* package (Fox et al., 2012). Furthermore, to compare the significant differences between undisturbed and disturbed sites, we conducted a Tukey post hoc test using the *emmeans* function in the *emmeans* package (Lenth and Lenth, 2018). For the single disturbance type analysis, each plot was affected by only one specified disturbance. This allowed us to compare how individual disturbances influenced understory plant richness, for example, examining plots affected solely by fire. For the sequential (additive) direct disturbance analysis, we considered plots that experienced a given disturbance type in combination with one or more additional disturbances, rather than repeated occurrences of the same disturbance, for instance, a plot affected by fire along with forest harvest and spruce budworm. Similarly, sequential indirect disturbances refer to areas where the buffer zones of two or more disturbance types overlap spatially, meaning that a single plot might be influenced by multiple offsite effects simultaneously.

1.2.4.2 Vegetation composition

We tested the interacting effects of ecosystem types and disturbances (direct and indirect) on plant composition using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, applying the *adonis* function from the *vegan* package (Oksanen et al., 2015). We conducted principal coordinates analysis (PCoA) using Bray–Curtis's dissimilarity to visualize compositional differences. Ordinations were performed separately for bryophytes and vascular plants, with disturbance type and disturbance number analyzed independently for both direct and indirect

disturbances, resulting in eight ordinations. For each ordination, the dataset was subset to include only plots corresponding to the disturbance category being evaluated; specifically, plots subjected to direct disturbances were analyzed separately from those affected by indirect disturbances. We used the PCoA function in the *vegan* package with the *lingoes* correction to correct negative eigenvalues (Lingoes, 1971).

To further interpret species associations within the ordination space, we applied the *envfit* function from the *vegan* package to fit species vectors to the PCoA ordinations, using 999 permutations, and only displayed significant species ($p \leq 0.05$). Additionally, we examined differences in vegetation composition across different ecosystem types using permutational multivariate analysis of variance (PERMANOVA) to better understand ecosystem variability on plant communities. All the statistical analyses were conducted in R-Studio version 4.2.2 (R Core Team, 2022).

1.3 Results

Our combined dataset, which integrates data from previous projects and recent fieldwork, recorded a total of 144 moss species, 21 *Sphagnum* species, 80 liverwort species, and 134 vascular plant species. In sites directly impacted by disturbances, we documented 130 moss species, 21 *Sphagnum* species, 72 liverwort species, and 115 vascular plant species. In contrast, sites subjected to indirect disturbances had the presence of 140 moss species, 21 *Sphagnum* species, 75 liverwort species, and 107 vascular plant species. In the undisturbed site, a total of 148 bryophyte species were documented, including 78 mosses, 17 *Sphagnum*, 53 liverworts, and 46 vascular plant species.

1.3.1 Species richness and direct disturbances

1.3.1.1 Direct disturbance number

Liverwort richness declined with increasing number of direct disturbances, vascular plant richness showed a positive response, and moss richness remained relatively stable (Figure 2). In undisturbed sites, the mean species richness for liverworts, mosses, and vascular plants was 7, 14, and 6 species, respectively (Table 1). Liverwort richness declined by 18% with each additional disturbance. In contrast, vascular plant richness increased by 51% per disturbance, while moss richness exhibited only a slight decline of 1%.

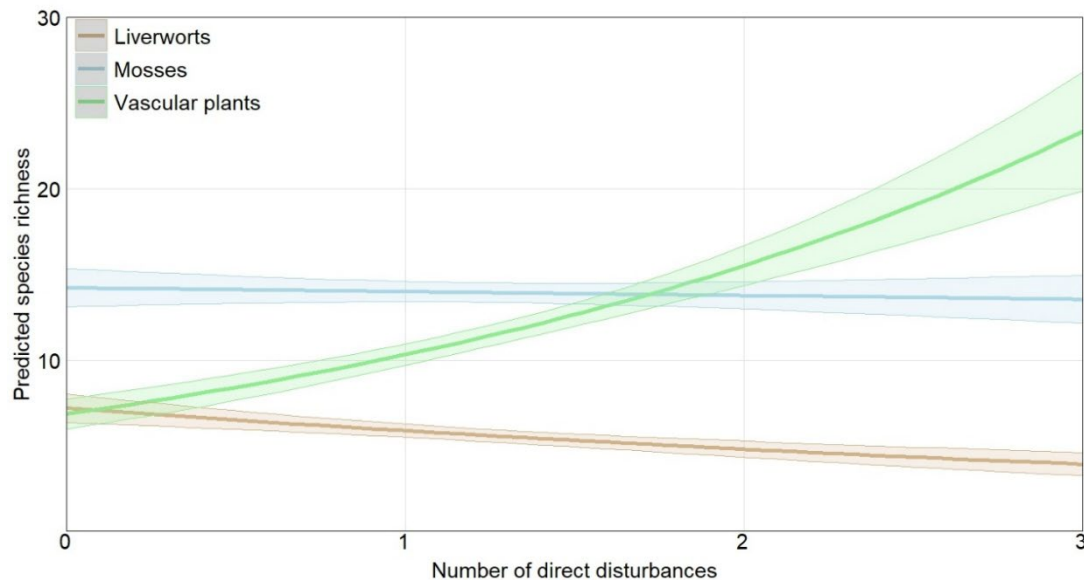


Figure 2

Predicted patterns of species richness for liverworts, mosses, and vascular plants in response to an increase in the number of direct disturbances experienced at a site. The x-axis represents the cumulative number of direct disturbances experienced at a site, while the y-axis shows the predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. Shaded areas around the lines indicate 95% confidence intervals.

Table 1

Generalized Linear Model (GLM) results showing the effects of the number of direct disturbances on the richness of liverworts, mosses, and vascular plants. The table provides the estimates, standard errors (SE), t-values, and p-values for each variable. The intercept represents the average predicted richness of liverworts in undisturbed sites. Significant effects ($p < 0.05$) are indicated with an asterisk (*).

Variables	Estimate	SE	t-value	p-value
Liverworts	1.97	0.06	33.39	<0.001*
Mosses	0.68	0.07	9.56	<0.001*
Vascular plants	-0.05	0.09	-0.55	0.582
Disturbance number	-0.20	0.04	-4.65	<0.001*
Disturbance number × mosses	0.19	0.05	3.62	<0.001*
Disturbance number × vascular plants	0.61	0.06	9.96	<0.001*

1.3.1.2 Effects of a single direct disturbance

When individual disturbance types were examined, all direct disturbances generally favoured mosses and vascular plants while negatively impacting liverworts, except in areas affected by fire (Figure 3). In sites with no other disturbances, fire exhibited a strong positive effect on liverwort richness, as it increased significantly by 77% compared to undisturbed sites (Table 2). Similarly, vascular plant richness more than doubled following forest harvest. The presence of spruce budworm increased moss and vascular plant richness by 8% and 42%, respectively. Similarly, forest tent caterpillar outbreaks had the most pronounced negative impact on bryophytes, with liverwort and moss richness declining by 32% and 4%, respectively. In contrast, vascular plant richness increased, tripled compared to undisturbed conditions.

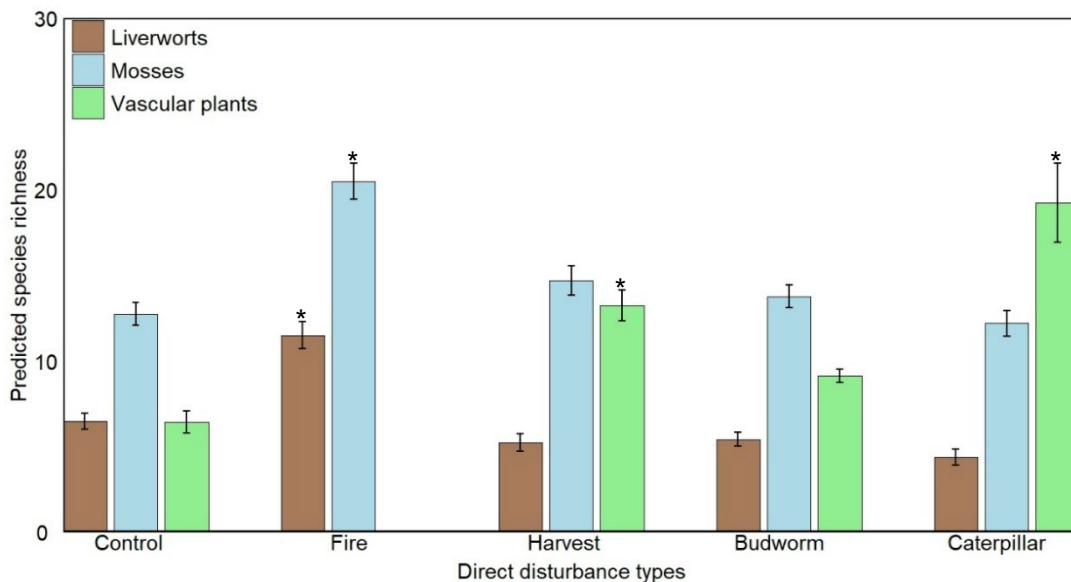


Figure 3

The richness of liverworts, mosses, and vascular plants in sites affected by various direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar) in the absence of other disturbances. The x-axis represents each type of direct disturbance, while the y-axis displays the predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. The bars with an asterisk (*) mark denote a statistically significant difference in the richness of the respective plant category compared to the undisturbed plots. The dataset contains no vascular plant plots impacted by fire disturbance.

Table 2
Generalized Linear Model (GLM) results for species richness of liverworts, mosses, and vascular plants concerning the individual direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar). The table provides the estimates, standard errors (SE), t-values, and p-values for each predictor, with significant effects ($p < 0.05$) marked by an asterisk (*). The intercept indicates the average predicted liverwort richness under undisturbed conditions.

Terms	Estimate	SE	t-value	p-value
Liverworts	1.87	0.07	25.43	<0.001*
Mosses	0.67	0.09	7.47	<0.001*
Vascular plants	-0.01	0.12	-0.06	0.950
Fire	0.57	0.10	5.72	<0.001*
Forest harvest	-0.21	0.12	-1.74	0.083
Spruce budworm	-0.18	0.11	-1.68	0.094
Forest tent caterpillar	-0.39	0.13	-3.08	<0.001*
Fire × mosses	-0.10	0.12	-0.78	0.433
Forest harvest × mosses	0.35	0.15	2.44	0.015*
Spruce budworm × mosses	0.26	0.13	2.01	0.045*
Forest tent caterpillar × mosses	0.35	0.15	2.31	0.021*
Forest harvest × vascular plants	0.93	0.17	5.46	<0.001*
Spruce budworm × vascular plants	0.53	0.15	3.48	<0.001*
Forest tent caterpillar × vascular plants	1.49	0.20	7.42	<0.001*

Note: No plots with vascular plants data experienced fire disturbance in the dataset; therefore, results for vascular plants under fire disturbance are not available. The model, therefore, treated the absence of vascular plants data under fire disturbance as a structural zero, excluding this combination from parameter estimation and producing estimates based solely on the available data for the remaining factors.

1.3.1.3 Additive effects of sequential direct disturbance

In all the disturbances except fire, with the occurrence of additional different types of disturbances, liverwort richness declined, moss richness remained stable, while vascular plant richness showed an increasing pattern (Figure 4). However, in fire-affected sites, when additional disturbances occurred, the richness of the liverworts, mosses, and vascular plants increased. In fire-disturbed sites, liverwort richness increased by 17% with each additional disturbance, though at a much lower rate than vascular plants. However, in response to forest harvest, liverwort richness declined with additional disturbances, for a total of 13% with each disturbance. Similarly,

liverwort richness decreased by 18% and 16% with each additional disturbance in spruce budworm and forest tent caterpillar disturbed sites, respectively.

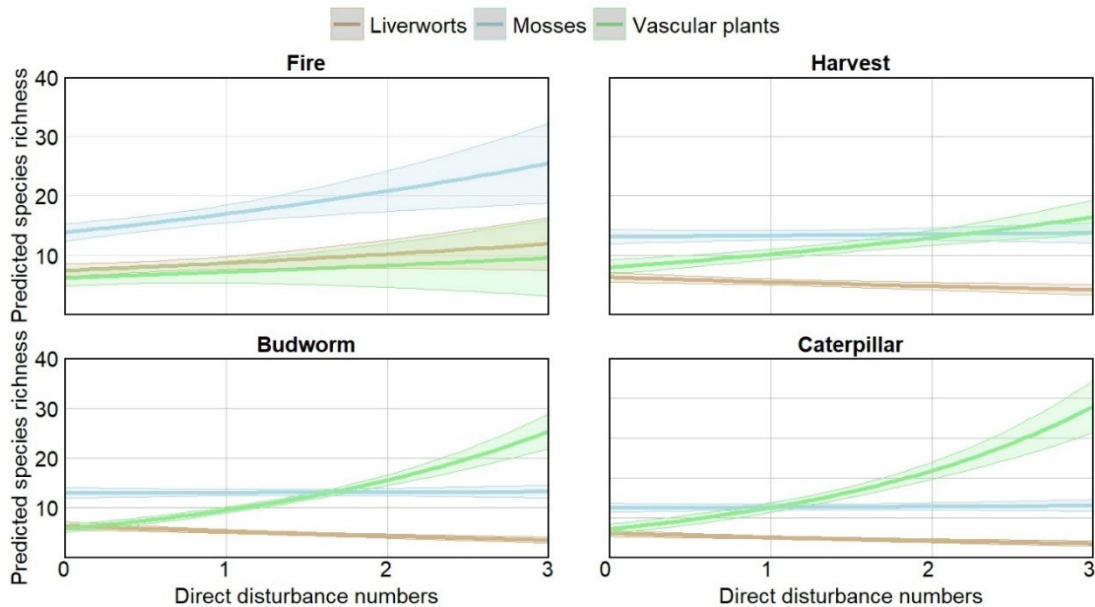


Figure 4
Predicted species richness of liverworts, mosses, and vascular plants in response to increasing disturbance numbers, shown separately for plots where different direct disturbance types: fire, forest harvest, spruce budworm, and forest tent caterpillar outbreak were the primary disturbance type. The x-axis represents the number of disturbances, while the y-axis represents the predicted species richness. Brown, blue, and green lines correspond to the richness of liverworts, mosses, and vascular plants, respectively.

Moss richness showed minimal response to specific disturbances, as with the overall results above, while vascular plant richness increased significantly, particularly under insect-driven disturbances. Moss richness increased by 23% per disturbance in fire-disturbed sites and by only 1% with each additional disturbance in response to forest harvest. Moss richness was unchanged in response to spruce budworm and forest tent caterpillar outbreaks. Vascular plant richness increased by 16% in fire-disturbed sites with each additional disturbance. In forest harvested sites, it rose by 27% per disturbance. Moreover, spruce budworm disturbances led to an increase of 63% in vascular plant richness with each additional disturbance. Forest tent caterpillar

outbreaks strongly increased vascular plant richness by 73% as the number of disturbances increased.

1.3.2 Species richness and indirect disturbances

1.3.2.1 Indirect disturbance number

The richness of liverworts and vascular plants decreased with more cumulative indirect disturbances, while no such pattern was found for mosses (Figure 5). However, the effects of indirect disturbance were statistically not significant. In undisturbed sites, the mean species richness was 6 for liverworts, 14 for mosses, and 9 for vascular plants (Table 3). The richness of liverworts declined by 8% with each additional indirect disturbance, while vascular plant richness decreased by 4% per indirect disturbance. In contrast, moss richness exhibited only a marginal decline of 1% per indirect disturbance.

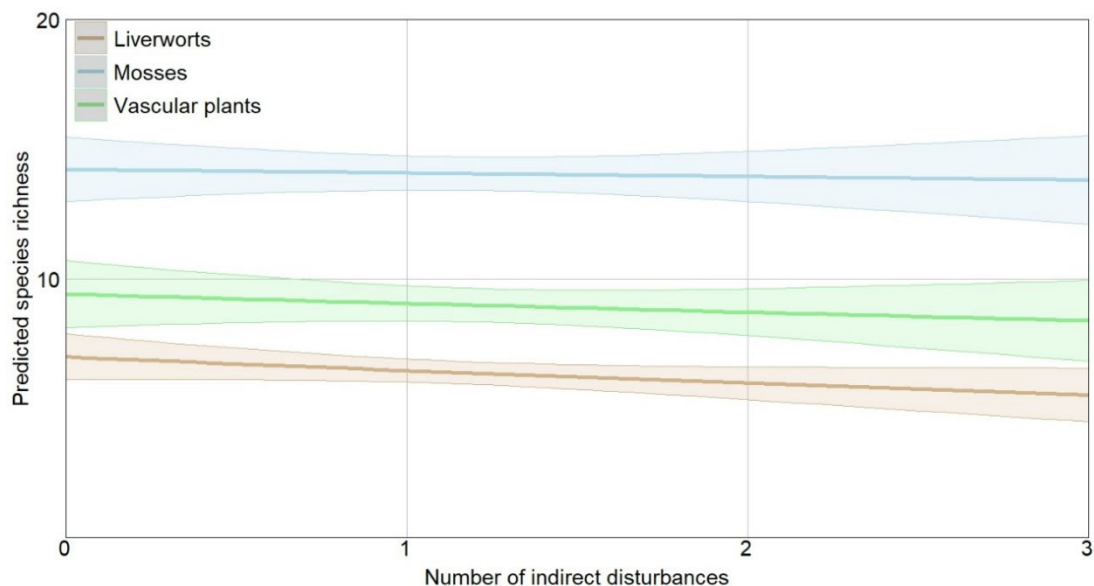


Figure 5
Predicted patterns of species richness of liverworts, mosses, and vascular plants according to an increase in the number of indirect disturbances. The x-axis represents the cumulative number of indirect disturbances, while the y-axis shows the predicted species richness. The brown, blue, and green lines represent the richness of liverworts, mosses, and vascular plants, respectively. Shaded areas around the lines indicate 95% confidence intervals.

Table 3
Generalized Linear Model (GLM) results illustrating how species richness of liverworts, mosses, and vascular plants responds to the number of indirect disturbances. Estimates, standard errors (SE), t-values, and p-values are provided for each variable. The intercept represents the estimated average liverwort richness in undisturbed sites. Significant effects ($p < 0.05$) are indicated with an asterisk (*).

Terms	Estimate	SE	t-value	p-value
Liverworts	1.94	0.06	30.13	<0.001*
Mosses	0.71	0.08	9.08	<0.001*
Vascular plants	0.30	0.10	3.12	<0.001*
Indirect disturbance number	-0.08	0.05	-1.64	0.100
Indirect disturbance number × mosses	0.07	0.06	1.20	0.232
Indirect disturbance number × vascular plants	0.04	0.07	0.59	0.557

1.3.2.2 Effects of a single indirect disturbance

Our results indicated that indirect disturbances generally led to an increase in the richness of mosses and vascular plants across all indirect disturbance types, except for mining sites, compared to undisturbed locations. Conversely, the richness of specialist species decreased except in sites associated with fire and forest harvest (Figure 6). In sites with no other indirect disturbances, fire indirect disturbance had a pronounced positive effect on liverwort richness, resulting in 92% more species compared to undisturbed sites (Table 4). Similarly, vascular plant richness in indirectly disturbed forest harvest sites increased by 93%. In contrast, the spruce budworm indirect disturbance led to a 48% decline in liverwort richness, while vascular plant richness increased by 22%.

The forest tent caterpillar's indirect disturbance exerted the strongest negative impact on liverwort richness, causing a 63% decline. However, moss richness increased by 15%, and vascular plant richness exhibited a 68% increase, nearly tripling relative to undisturbed conditions. Mining indirect disturbance was associated with a 35% decline in liverwort richness, while vascular plants showed the strongest response in the forest roads disturbance, increasing by 72%. Transmission line indirect disturbances also had notable effects, leading to a 28% increase in moss richness and a 70% increase in vascular plant richness.

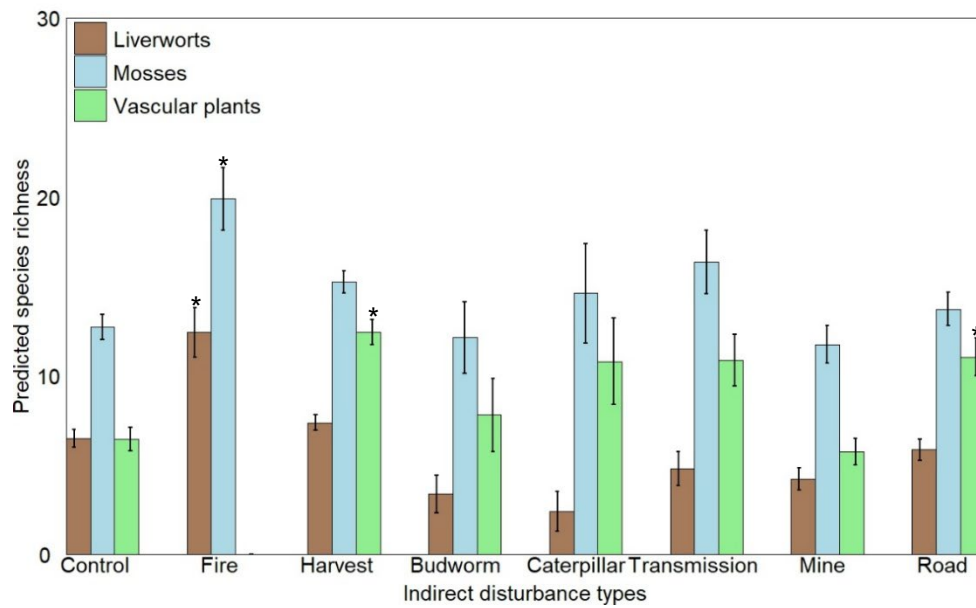


Figure 6

The predicted richness of liverworts, mosses, and vascular plants across different indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, transmission lines, mines, and forest roads). The x-axis represents the individual indirect disturbances, while the y-axis displays the predicted species richness. The brown, blue, and green bars correspond to the richness of liverworts, mosses, and vascular plants, respectively. The asterisk mark (*) denotes a statistically significant difference in the richness of liverworts, mosses, and/or vascular plants compared to the undisturbed sites.

Table 4

Generalized linear model (GLM) results for the effects of indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, transmission lines) on liverworts, mosses, and vascular plants. The table includes the estimates, standard errors (SE), t-values, and p-values for each predictor, with significant effects ($p < 0.05$) marked by an asterisk (*). The intercept captures the average predicted liverwort richness under undisturbed conditions.

Terms	Estimate	SE	t-value	p-value
Liverworts	1.87	0.08	24.45	<0.001*
Mosses	0.67	0.09	7.18	<0.001*
Vascular plants	-0.01	0.13	-0.06	0.952
Fire indirect	0.65	0.14	4.78	<0.001*
Forest harvest indirect	0.13	0.10	1.34	0.180
Spruce budworm indirect	-0.65	0.32	-2.02	0.043*
Forest tent caterpillar indirect	-0.99	0.48	-2.09	0.037*
Mines indirect	-0.43	0.17	-2.56	0.010*
Forest roads indirect	-0.10	0.13	-0.79	0.428
Transmission lines indirect	-0.30	0.21	-1.43	0.154
Fire indirect × mosses	-0.20	0.17	-1.19	0.235
Forest harvest indirect × mosses	0.05	0.12	0.45	0.655
Spruce budworm indirect × mosses	0.60	0.37	1.65	0.997
Forest tent caterpillar indirect × mosses	1.13	0.52	2.19	0.028*
Mines indirect × mosses	0.35	0.20	1.77	0.077
Forest roads indirect × mosses	0.18	0.15	1.14	0.254
Transmission lines indirect × mosses	0.55	0.25	2.26	0.024*
Forest harvest indirect × vascular plants	0.53	0.15	3.50	<0.001*
Spruce budworm indirect × vascular plants	0.85	0.43	1.98	0.048*
Forest tent caterpillar indirect × vascular plants	1.51	0.54	2.82	<0.001*
Mines indirect × vascular plants	0.32	0.24	1.35	0.177
Forest roads indirect × vascular plants	0.64	0.19	3.37	<0.001*
Transmission lines indirect × vascular plants	0.83	0.27	3.05	<0.001*

Note: Vascular plants data were not available for any plots affected by fire indirect disturbance; therefore, results for this category can not be found in the table.

1.3.2.3 Additive effects of sequential indirect disturbance

Liverwort species richness was highly affected by the presence of additional indirect disturbances (Figure 7). Under indirect disturbances, such as spruce budworm, forest tent caterpillar, mining, forest roads, and transmission lines, liverwort richness declined by 27%, 56%, 30%, 10%, and 21%, respectively, as the number of each indirect disturbance increased. However, under indirect fire disturbance, liverwort richness increased by 43% with the cumulative increase of each disturbance. In response to indirect forest harvest disturbance, liverwort richness showed a slight increase of 2% per indirect disturbance.

Mosses generally exhibited a stable or a bit of an increasing trend across most of the indirect disturbances. Under indirect effects of fire and forest harvest disturbances, moss richness showed an increase of 20% and 2%, respectively, in richness with each additional disturbance. However, the richness decreased by 3%, 1%, and 7% with each additional indirect disturbance in response to the indirect effects of spruce budworm, forest tent caterpillar, and mining sites, respectively. Interestingly, moss richness remained unchanged with the indirect effects of forest road disturbances. Indirect effects of transmission lines increased moss richness by 27% per indirect disturbance.

Generalist species, particularly vascular plants, tend to benefit from indirect disturbances. Vascular plant richness remained largely unaffected around forest harvested sites. Indirect effects of spruce budworm disturbance led to a 9% increase in vascular plant richness with each addition of indirect disturbance. After the forest tent caterpillar indirect disturbance, vascular plant richness increased by 27% with each cumulative disturbance. The indirect effect of mining disturbance caused vascular plant richness to remain relatively stable. The indirect effects of forest road disturbance led to an increase in vascular plant richness by 3% with the addition of each indirect disturbance. Around the indirect transmission line disturbance, vascular plant richness increased by 51% with each additional occurrence of indirect disturbance.

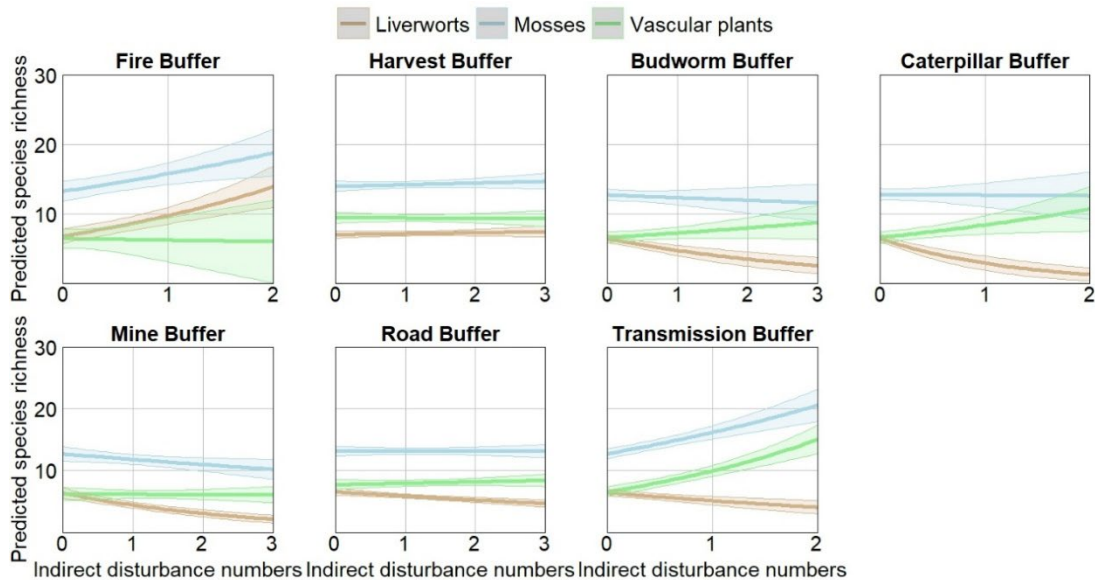


Figure 7
Predicted species richness of liverworts, mosses, and vascular plants in response to increasing disturbance numbers across indirect disturbance types: fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, and transmission lines. The x-axis represents the number of indirect disturbances, while the y-axis represents the predicted species richness. The brown, blue, and green lines correspond to the richness of liverworts, mosses, and vascular plants, respectively.

1.3.3 Bryophyte composition and direct disturbances

1.3.3.1 Direct disturbance types

Bryophyte composition demonstrated significant variation across disturbances (PERMANOVA; $p = 0.001$) and ecosystem types (PERMANOVA; $p = 0.001$), whereas the interaction between disturbances and ecosystem types was not significant (PERMANOVA; $p = 0.221$; Table 5). The PCoA of the bryophyte composition illustrated a gradient from coniferous to deciduous ecosystems along the first axis (9.09% of variance), with overlapping ellipses (Figure 8).

Fire was primarily associated with coniferous ecosystems, whereas forest harvest occurred across both coniferous and deciduous ecosystems. The coniferous ecosystem was dominated by peatland bryophyte species such as *Sphagnum capillifolium* (sSphcap), *Sphagnum fuscum* (sSphfus), *Sphagnum russowii* (sSphrus),

and *Sphagnum angustifolium* (sSphang), which clustered on the right side of the ordination. In contrast, the deciduous ecosystem plots were dominated by a different suite of species, such as *Brachythecium curtum* (mBracur), *Brachythecium starkii* (mBrasta), and *Brachythecium reflexum* (mBraref). The upper left portion of the ordination featured species such as *Sanionia uncinata* (mSanunc), *Dicranum scoparium* (mDicSCO), *Hypnum pallescens* (mHyppal), and *Chiloscyphus profundus* (hChipro). Spruce budworm and forest tent caterpillar disturbances predominantly affected coniferous and deciduous ecosystems, respectively; however, spruce budworm outbreaks extended into some deciduous ecosystems. *Dicranum flagellare* (mDicfla), *Dicranum fuscum* (mDicfus), *Dicranum montanum* (mDicmon), and *Amblystegium serpens* (mAmbser) were associated with the insect outbreak.

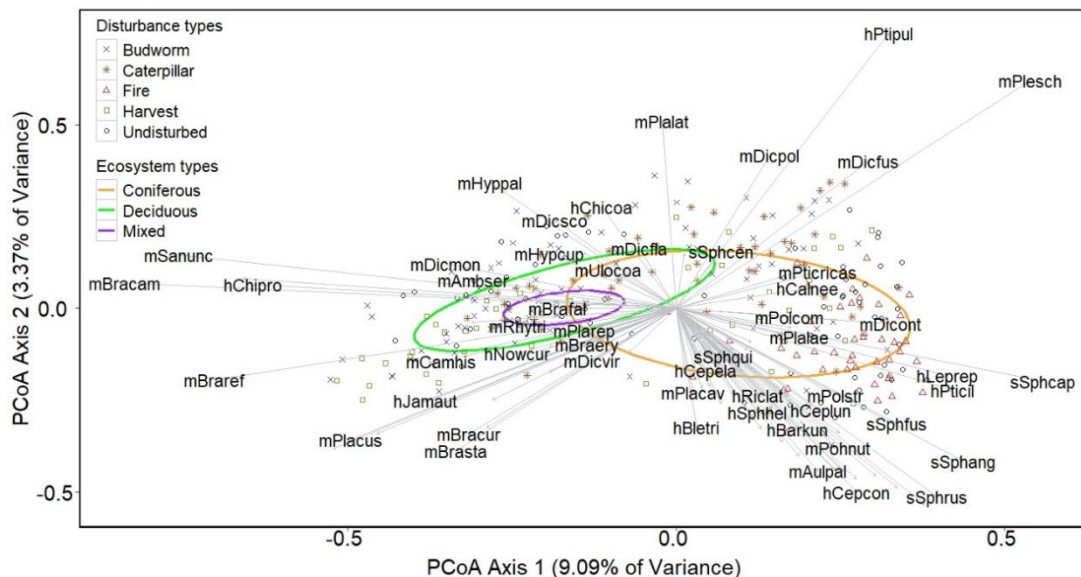


Figure 8
Principal coordinates analysis (PCoA) for the bryophyte composition across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and direct disturbances were added by correlation to the axes. In the species codes, the initial letters indicate bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data from 289 plots, where a total of 290 species were recorded; however, only 115 species are shown due to their significant

influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J.

1.3.3.2 Direct disturbance number

The bryophyte community composition varied significantly with disturbance number, ecosystem type, and their interaction (PERMANOVA; $p = 0.001$; Table 5). The principal coordinate analysis (PCoA) revealed distinct community shifts along the first axis (6.54% of variance), primarily driven by ecosystem type, while the second axis (2.71% of variance) captured variation related to disturbance number (Figure 9).

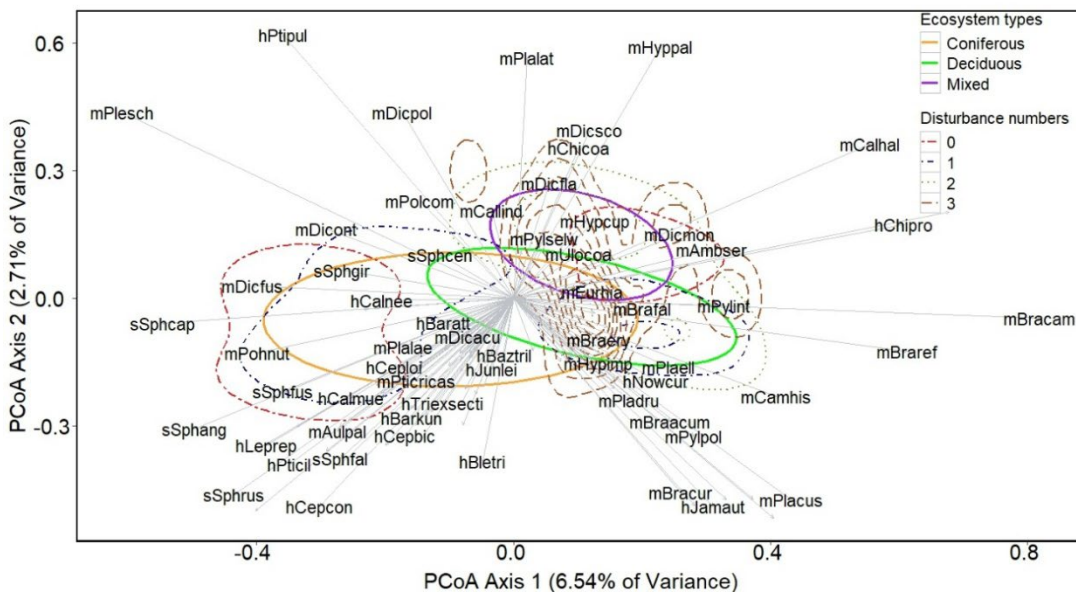


Figure 9
Principal coordinates analysis (PCoA) for the bryophyte composition across different ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and the number of direct disturbances were added by correlation to the axes. In the species codes, the initial letters indicate bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data from 449 plots, where a total of 290 species were recorded; however, only 113 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J.

Notably, species such as *Sphagnum fuscum* (sSphfus), *Sphagnum russowii* (sSphrus), *Sphagnum angustifolium* (sSphang), *Dicranum fuscescens* (mDicfus), *Lophozia ventricosa* (hLopven), and *Cephalozia connivens* (hCepcon) are positioned

toward the left side of the ordination and are associated with the lower number of disturbances and coniferous ecosystems. Whereas *Callicladium haldanianum* (mCalhal), *Chiloscyphus profundus* (mChipro), *Sanionia uncinata* (mSanunc), *Dicranum scoparium* (mDicsco), and *Hypnum pallescens* (mHyppal) are on the top-right side of the ordination and associated with higher numbers of disturbances. Species like *Brachythecium curtum* (mBracur), *Brachythecium acutum* (mBraact), *Campylophyllum hispidulum* (mCamhis), *Jamesoniella uncinata* (hJamunc), and *Plagiothecium cuspidatum* (mPlacus) are clustered toward the bottom-right corner. The overlapping ellipses for ecosystem types suggest that while coniferous, mixed, and deciduous ecosystems support distinct bryophyte assemblages, disturbance-driven shifts in species composition reduce these differences.

Table 5
Effects of direct disturbances, number of disturbances, and ecosystem types on the bryophytes community using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.

Direct disturbance	Variable	DF	SS	R ²	F statistics	p-value
Disturbance types	Ecosystem types	2	4.20	0.06	11.05	<0.001*
	Disturbances	4	10.05	0.15	13.22	<0.001*
	Ecosystem types × Disturbances	2	0.46	0.01	1.21	0.221
	Residuals	280	53.18	0.78	-	-
Disturbance number	Ecosystem types	2	6.34	0.06	15.25	<0.001*
	Disturbance number	1	1.85	0.02	8.89	<0.001*
	Ecosystem types × Disturbance number	2	1.80	0.02	4.33	<0.001*
	Residuals	443	92.14	0.90	-	-

1.3.4 Vascular plant composition and direct disturbances

1.3.4.1 Direct disturbance types

Vascular plant composition was affected by the interaction between direct disturbance type and ecosystem type (PERMANOVA). Overall, direct disturbance type (R²= 15%) explained more differences than ecosystem type (R²= 6%) and the disturbance type-ecosystem type interaction (R²= 3%, Table 6).

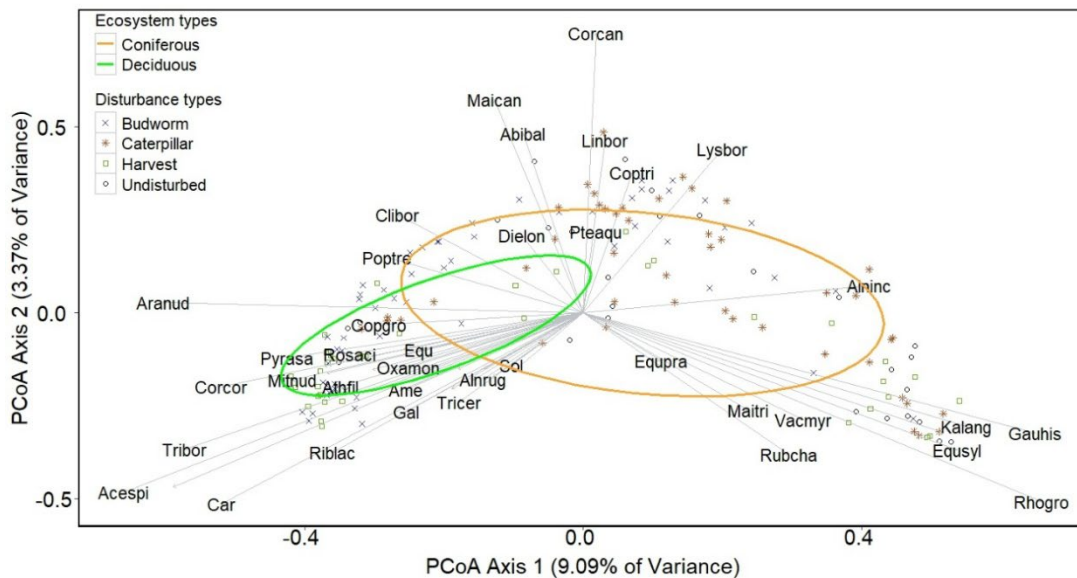


Figure 10
Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous and deciduous) using the Bray-Curtis dissimilarity index. Species names and direct disturbances were added by correlation to the axes. The mixed ecosystem type is not indicated in the PCoA plot, as no vascular plant plots were representative of this ecosystem type. This plot comprises data from 166 plots, where a total of 266 species were recorded; however, only 52 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K.

The PCoA illustrated a gradient from coniferous to deciduous ecosystems along the first axis (9.09% variation) (Figure 10). Coniferous ecosystem clusters toward the right side of the ordination, while deciduous ecosystems are more concentrated on the left. Species associations reflect these ecosystem patterns: deciduous ecosystems are associated with species such as *Corylus cornuta* (Corcor), *Trientalis borealis* (Tribor), *Aralia nudicaulis* (Aranud), *Ribes lacustre* (Riblac), and *Pyrola asarifolia* (Pyrasa). In contrast, coniferous ecosystems are more closely linked to species like *Gaultheria hispidula* (Gauhis), *Equisetum sylvaticum* (Equsyl), *Rubus chamaemorus* (Rubcha), *Vaccinium myrtilloides* (Vacmyr), *Rhododendron groenlandicum* (Rhogro), and *Kalmia angustifolia* (Kalang). Disturbance regimes further shape community composition: Forest tent caterpillar disturbance is primarily distributed in the upper part of the plot,

while forest harvested disturbance clusters toward the lower portion. Spruce budworm outbreak sites showed a scattered distribution and were associated with both coniferous and deciduous ecosystems. In contrast, the forest tent caterpillar showed a scattered distribution, but some signs of their association with coniferous ecosystems were also evident.

1.3.4.2 Disturbance number

Vascular plant composition varied in response to the combined effects of direct disturbance number and ecosystem type. Ecosystem type accounted for the largest proportion of compositional variation ($R^2 = 7\%$), followed by direct disturbance number ($R^2 = 2\%$), with a smaller yet significant interaction effect between disturbance number and ecosystem types ($R^2 = 1\%$, Table 6).

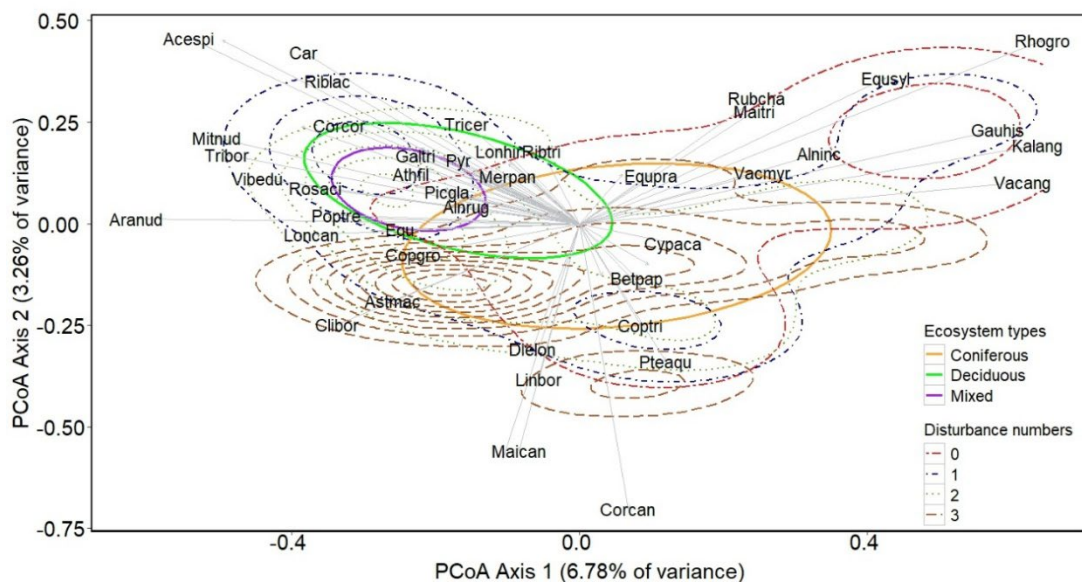


Figure 11
Principal coordinates analysis (PCoA) for the vascular plant composition under ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and the number of direct disturbances were added by correlation to the axes. This plot comprises data from 322 plots, where a total of 266 species were recorded; however, only 71 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K.

Species such as *Rhododendron groenlandicum* (Rhogro), *Equisetum sylvaticum* (Equsyl), *Gaultheria hispidula* (Gauhis), *Kalmia angustifolia* (Kalang), and *Vaccinium angustifolium* (Vaccang) were positioned in the top-right quadrant of the ordination space and were associated with sites that experienced no disturbance or only a single disturbance (Figure 11). In contrast, *Acer spicatum* (Acespi), *Ribes lacustre* (Riblac), *Trientalis borealis* (Tribor), *Mitella nuda* (Mitnud), and *Aralia nudicaulis* (Aranud) were associated with sites experiencing a relatively low number of disturbances, occupying the top-left quadrant. Meanwhile, species such as *Clintonia borealis* (Clinbor), *Linnaea borealis* (Linbor), *Cornus canadensis* (Corcan), and *Maianthemum canadense* (Maican) were associated with highly disturbed sites and were positioned in the lower portion of the ordination space.

Table 6

Effects of direct disturbances, number of disturbances, and ecosystem types on vascular plants using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.

Direct disturbance	Variable	DF	SS	R ²	F statistics	p-value
Disturbance types	Ecosystem types	2	3.16	0.06	5.91	<0.001*
	Disturbances	3	8.18	0.15	10.20	<0.001*
	Ecosystem types × Disturbances	2	1.42	0.03	2.65	0.003*
	Residuals	158	42.24	0.77	-	-
Disturbance number	Ecosystem types	2	6.61	0.06	11.19	<0.001*
	Disturbance number	1	2.41	0.02	8.17	<0.001*
	Ecosystem types × Disturbance number	2	1.22	0.01	2.06	0.004*
	Residuals	316	93.26	0.90	-	-

1.3.5 Bryophyte composition and indirect disturbances

1.3.5.1 Indirect disturbance types

Disturbance type, ecosystem type, and their interaction showed significant effects on bryophyte composition. The PERMANOVA model attributed approximately 5-8% of the total variation as explained by these factors (Table 7). Whereas PCoA indicated a

(mPlalat) occupying the upper portion of the plot where disturbances such as mining and forest harvest are more prevalent. In contrast, specialist species like *Lophozia ventricosa* (hLopven), *Cephalozia connivens* (hCepcon), *Geocalyx graveolens* (hGeogra), and *Blepharostoma trichophyllum* (hBletri) clustered in the lower section.

Table 7
Effects of indirect disturbances, number of disturbances, and ecosystem types on bryophytes using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.

Indirect disturbance	Variable	DF	SS	R ²	F statistics	p-value
Disturbance types	Ecosystem types	2	5.82	0.08	14.15	<0.001*
	Disturbances	7	4.80	0.07	3.33	<0.001*
	Ecosystem types × Disturbances	11	3.50	0.05	1.55	0.002*
	Residuals	269	55.28	0.80	-	-
Disturbance number	Ecosystem types	2	8.67	0.09	20.35	<0.001*
	Disturbance number	1	0.76	0.01	3.58	<0.001*
	Ecosystem types × Disturbance number	2	1.09	0.01	2.55	0.002*
	Residuals	414	88.22	0.89	-	-

1.3.5.2 Disturbance number

Bryophyte composition varied significantly in response to the number of disturbances ($R^2=1\%$), ecosystem types ($R^2=9\%$), and the interaction between disturbance number and ecosystem types ($R^2=1\%$) (Table 7). Species such as *Pleurozium schreberi* (mPlesch), *Ptilium pulcherrimum* (hPtipul), *Dicranum polysetum* (mDicpol), and *Plagiothecium laetum* (mPlalat) were associated with the top-left quadrant of the ordination space, indicating their preference for specific site conditions (Figure 13). In contrast, species such as *Lepidozia reptans* (hLeprep), *Lophozia ventricosa* (hLopven), *Cephalozia connivens* (hCepcon), and *Sphagnum russowii* (sSphrus) were positioned toward the bottom-left quadrant.

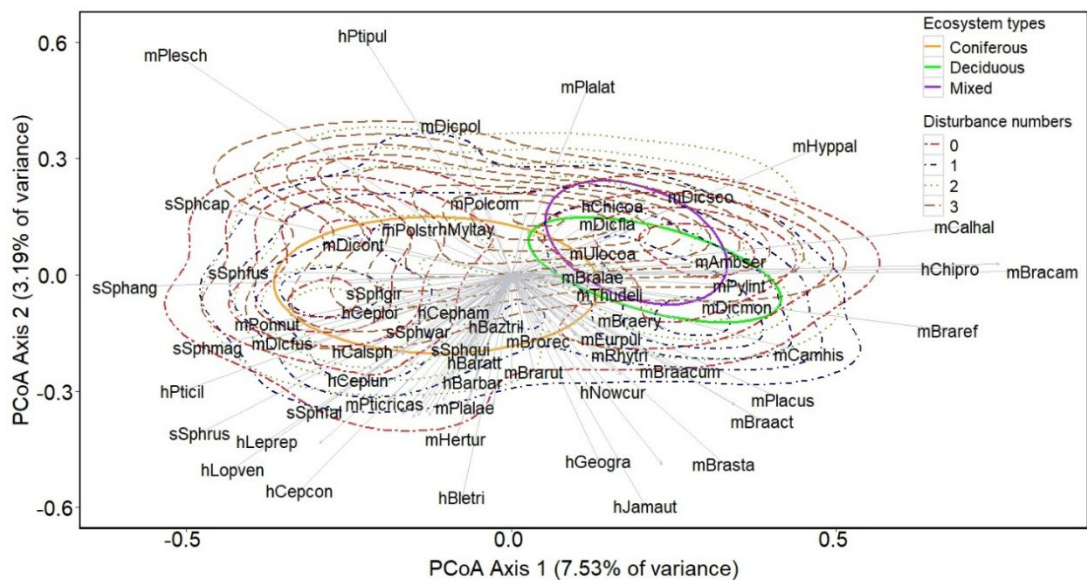


Figure 13
Principal coordinates analysis (PCoA) for the bryophyte composition under ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and disturbance number were added by correlation to the axes. Species codes begin with letters that denote bryophyte guilds: m for mosses, s for sphagnum, and h for liverworts. This plot comprises data from 420 plots, where a total of 290 species were recorded; however, only 136 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX J.

1.3.6 Vascular plant composition and indirect disturbances

1.3.6.1 Indirect disturbance types

The interaction between disturbance and ecosystem type was not significant (PERMANOVA, $R^2 = 0.006$, $p = 0.209$, Table 8). The PCoA ordination significantly separates understory vegetation across ecosystem types along the first axis (11.10% of variance), while the second axis (5.16% of variance) captures variation by disturbance types (Figure 14). The effect of the mine buffer is primarily distributed across the coniferous ecosystem, associated with species such as *Coptis trifolia* (Coptri), *Cornus canadensis* (Corcan), *Gaultheria hispidula* (Gauhis), and *Kalmia angustifolia* (Kalang). Forest harvest appears across all ecosystem types, while the

forest road buffer is more associated with deciduous ecosystems and the transmission buffer with coniferous ecosystems

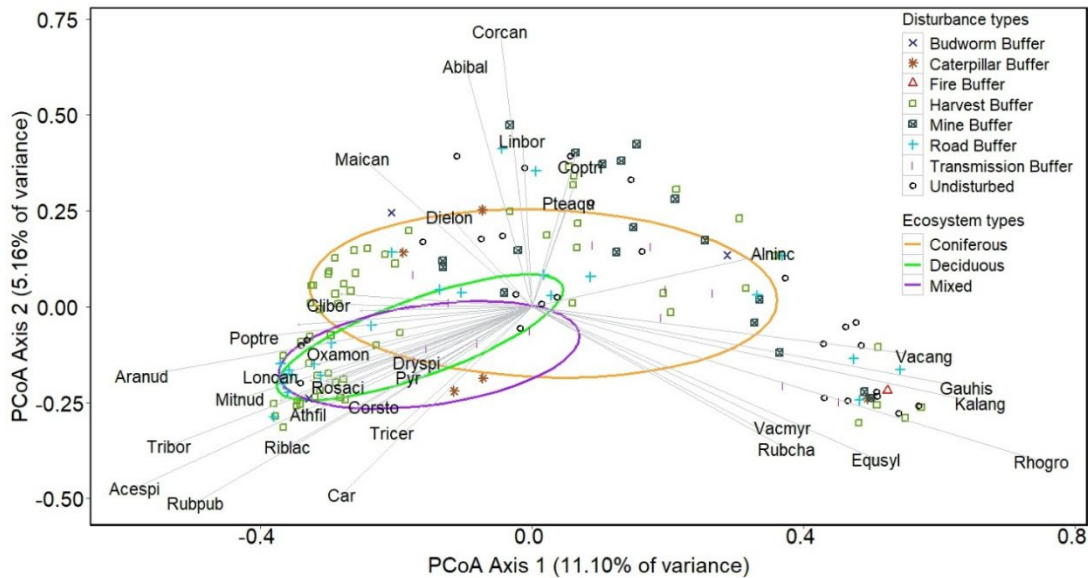


Figure 14
Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and indirect disturbances were added by correlation to the axes. This plot comprises data from 148 plots, where a total of 266 species were recorded; however, only 45 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K.

Table 8
Effects of indirect disturbances, number of disturbances, and ecosystem types on vascular plants using permutational multivariate analysis of variance (PERMANOVA) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom, SS = sum of squares, * = $\alpha \leq 0.05$ significance level.

Indirect disturbance	Variable	DF	SS	R ²	F statistics	p-value
Disturbance types	Ecosystem types	2	2.26	0.04	3.70	<0.001*
	Disturbance types	7	5.88	0.12	2.75	<0.001*
	Ecosystem types × Disturbance types	9	3.03	0.06	1.10	0.209
	Residuals	129	39.43	0.78	-	-
	Ecosystem types	2	2.84	0.04	4.28	<0.001*
Disturbance number	Disturbance number	1	0.48	0.01	1.45	0.134
	Ecosystem types × Disturbance number	2	0.72	0.01	1.09	0.343
	Residuals	212	70.16	0.95	-	-

1.3.6.2 Disturbance number

Vascular plant composition varied significantly across ecosystem types but showed no significant association with the number of disturbances or their interaction with ecosystem types. PERMANOVA results indicated that ecosystem types explained 4% of the variation in vascular plant composition (Table 8). Species like *Aralia nudicaulis* (Aranud), *Rubus pubescens* (Rubpub), *Acer spicatum* (Acespi), and *Trientalis borealis* (Tribor) are in the top-right corner of the ordination and are associated with deciduous and mixed ecosystem types (Figure 15). In contrast, species like *Kalmia angustifolia* (Kalang), *Vaccinium angustifolium* (Vacang), *Gaultheria hispidula* (Gauhis), *Rhododendron groenlandicum* (Rhogro), and *Equisetum sylvaticum* (Equisyl) have occupied the top-left part of the ordination, where all disturbance numbers are overlapping and seem not to have a close association with ecosystem type.

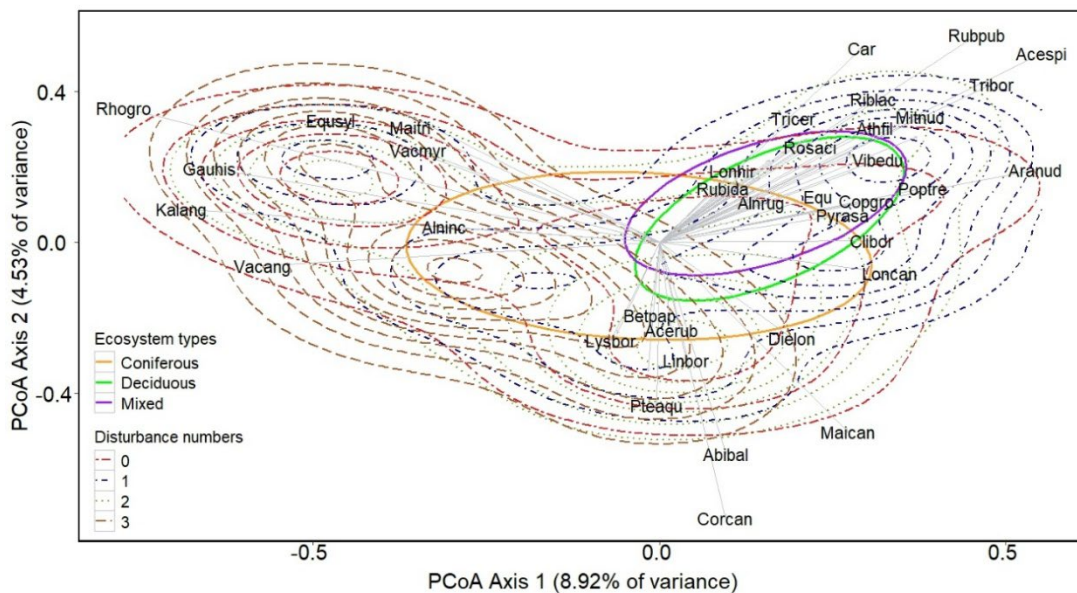


Figure 15
Principal coordinates analysis (PCoA) for the composition of vascular plants across ecosystem types (coniferous, deciduous, and mixed) using the Bray-Curtis dissimilarity index. Species names and disturbance number were added by correlation to the axes. This plot comprises data from 218 plots, where a total of 266 species were recorded; however, only 56 species are shown due to their significant influence on the axis and high relevance. The complete list of species codes and their corresponding names is provided in ANNEX K.

1.4 Discussion

Our study revealed a significant influence of multiple disturbances on the richness and composition of understory plant communities, with contrasting responses between specialist and generalist species in directly and indirectly disturbed sites. Liverwort richness decreased, boreal vascular plant richness increased, and moss richness remained relatively unchanged in response to the increasing number of direct disturbances. The richness of liverworts and vascular plants decreased with multiple indirect disturbances, while no consistent trend was found for moss richness. Despite these general patterns, the effects of an individual disturbance on vascular and non-vascular plants were modified by another disturbance occurring in the same location. This means that, depending on the type of disturbance, each additional disturbance could either decrease or increase species richness. The analysis accounts solely for

the number of disturbances, without considering the sequence or temporal order of their occurrence. For instance, when fire occurred with an additional disturbance (forest harvest, spruce budworm, or forest tent caterpillar outbreak) with spatial overlap (regardless of temporal sequence), the species richness of liverworts, mosses, and vascular plants was observed to increase.

These findings align with previously reported patterns in boreal ecosystems for individual disturbances; for example, after a canopy-opening disturbance, boreal vascular plant richness was found to increase, while bryophytes, particularly liverworts, declined due to microclimatic alterations (Fenton & Bergeron, 2006; Bartels & Chen, 2013). Such patterns of species richness are, thus, expected to be driven by disturbance-induced changes in ecosystems. These changes can eventually influence environmental factors such as light availability due to canopy opening, humidity regimes, substrate availability, and variation in overstorey composition. Although we did not directly measure variables like light, humidity, or substrate conditions, their ecological influences can be reasonably inferred from the forest structural characteristics, such as overstorey composition and disturbance type.

1.4.1 Ecosystem types as drivers of microclimatic and structural variations

Ecosystem type has a fundamental role in shaping understory diversity patterns following disturbance, as it directly influences microenvironmental drivers and resource availability. In our study, species composition progressively shifted toward deciduous dominance with an increasing number of direct disturbances. This trend reflects the rapid establishment of shade-intolerant deciduous species in open and early successional conditions with high resource availability (Bergeron & Fenton, 2012). The shift was especially pronounced in areas affected by salvage logging, where mechanical disturbance and overstorey mortality created canopy gaps and enhanced light transmission (Royo et al., 2016; Spence & MacLean, 2012). These conditions favoured fast-colonizing, light-demanding species and restructured the understory community composition.

Disturbance-driven changes to forest structure, particularly canopy openness, strongly regulate light and moisture availability, which in turn differentially affect liverworts, mosses, and vascular plants. Deciduous ecosystems often support higher vascular plant richness even after successive disturbances, largely due to improved light conditions, warmer soils, and nutrient availability from deciduous leaf litter (Barbier et al., 2008; Cavard et al., 2011; Anyomi et al., 2022). Increased light penetration, coupled with reduced competition, facilitates the establishment of early successional vascular plant species that rapidly colonize the available space (Bergeron & Fenton, 2012; Roberts, 2004; Hart & Chen, 2006). The structural heterogeneity created by canopy disturbances also enhances vascular plant diversity within forest ecosystems (Barbier et al., 2008). For instance, when spruce budworm rapidly defoliates coniferous trees, it increases canopy gaps and permits more sunlight to reach the understory communities and support the development of deciduous species (Noualhuget et al., 2023; Subedi et al., 2023). Similarly, generalist mosses such as *Ptilium crista-castrensis* and *Pleurozium schreberi*, which tolerate increased light and variable humidity, contribute to the maintenance of overall moss richness even though composition changes with a series of disturbances (Paquette et al., 2016). In contrast, liverworts and Sphagnum mosses such as *Sphagnum angustifolium*, *Sphagnum fallax*, *Sphagnum fuscum*, *Sphagnum magellanicum*, and *Sphagnum russowii* decline in response to canopy loss and light-driven drying of the understory (Proctor et al., 2007; Peckham et al., 2009; Bartels et al., 2018). Though such peatland sphagna are adapted to open conditions, physiological shock, like greater evaporative demand resulting from exposure to direct solar radiation and higher temperatures after canopy removal, could lead to their decline (Fenton & Bergeron, 2007; Leonard et al., 2017). Hence, moisture-sensitive bryophytes such as liverworts and a few sphagna might decline with canopy loss and drying, while boreal vascular plants and generalist mosses benefit from light enrichment and reduced competition.

While changes in forest structure and microclimate are key drivers of understory community shifts, the response of species is also moderated by the physiological and ecological traits. Boreal vascular plants and mosses often have broad substrate

preferences as well as higher tolerance to microclimatic variability that allow them to colonize disturbed areas (Mills & Macdonald, 2004). In addition, these species also tend to possess strong physiological adaptations, such as greater desiccation tolerance or structural traits that reduce water loss and enable them to persist under elevated vapour pressure deficits due to successive disturbances (Proctor et al., 2007). In contrast, many liverworts, despite being poikilohydric like mosses, are physiologically vulnerable to desiccation. Particularly, liverworts from moist and shaded habitats tend to be restricted to humid microenvironments beneath intact canopies due to their sensitivity to rapid or severe drying (Proctor et al., 2007; Caners et al., 2013). Post-disturbance environments thus favour generalist taxa with higher colonization capacity and broader ecological roles, whereas specialist species, by contrast, may decline.

Forest structural legacies can partially buffer microclimatic shifts. Sites with higher residual basal area, coarse woody debris, and partial canopy closure provide moisture-retaining microhabitats that benefit liverworts and sensitive mosses (Fenton et al., 2003; Arseneault et al., 2012; Noualhaguet et al., 2023). Coniferous canopies, with persistent foliage and dense branching structure, are an example of an effective buffering of environmental variation such as temperature, moisture, and wind in the understorey (García De Jalón et al., 2019; Barbé et al., 2020). These structures create refugia by maintaining localized shade and humidity, sustaining communities vulnerable to drying and thermal stress (Brais et al., 2013; Caners et al., 2013). However, successive disturbances progressively alter forest microhabitat conditions, particularly when compounded by fire or salvage logging, which remove both canopy and ground-layer structure (Fettig et al., 2022). Fire, particularly, creates a more heterogeneous environment—removing dense canopy cover, exposing mineral soil, and releasing nutrients (Greene et al., 2007). These changes enhance light penetration and create new microsites favourable for colonization by early successional bryophytes, which increase their richness. In contrast, other disturbances, such as insect outbreaks, primarily alter canopy structure while leaving much of the ground layer and organic horizon intact (Franklin et al., 2015). As a result,

microhabitat conditions remain relatively stable, limiting the establishment of new species and leading to a weaker response in species richness compared to fire. Hence, the way disturbances modify microhabitat conditions and resource availability is likely a key factor leading to the contrasting responses between disturbances.

1.4.2 Severity of direct and indirect disturbances

The effect of indirect disturbances on understorey community richness was less strong in comparison to direct disturbances. It is evident that an increasing number of direct disturbances lead to modification of the microhabitat, alter resource availability, and result in the loss of understorey species (Harper et al., 2015). For example, disturbances, such as mechanical forest harvest, reduce the quantity and quality of coarse woody debris, which in turn limits the availability of suitable substrates for colonization of liverworts (Fenton et al., 2003). Forest harvest machinery often shreds wood at decay stages that are considered to be optimal for liverworts establishment, and ploughs over the soil and disrupts its quality. Additional disturbances, such as insect outbreaks, can further modify microhabitat conditions through increased canopy openings and altered substrate suitability (Chen & Popadiouk, 2002). Moreover, when simultaneous multiple direct disturbances occur, for instance, lighter insect outbreaks followed by a quick succession of wildfire, it exacerbates these effects by accelerating surface drying, exposing mineral soils, and removing organic layers, which ultimately reduces the availability of substrates that are deemed essential for liverworts colonization and persistence (McCullough et al., 1998; James et al., 2011; Fettig et al., 2022). However, extensive defoliation, which lowers fuel availability, can reduce the severity of subsequent fire and its overall impact on species; thus, the magnitude of the preceding disturbance can produce different effects of the simultaneous disturbance. On the other hand, severe fires followed by forest harvest not only damage reproductive propagules but also disrupt the forest's capacity to buffer temperature and humidity, which creates more extreme microclimatic conditions that are unfavourable for understorey species (Rowe, 1983; De Frenne et al., 2021). However, in our study, wildfire alone appeared to favour mosses and liverworts because fire-tolerant or pioneer species are well adapted to tolerate high light, heat, and dry conditions (Bradbury, 2006). These species can rapidly colonize burned

substrates such as scorched soil and charred wood, taking advantage of reduced competition and newly available microsites following fire (Bradbury, 2006).

However, disturbance effects are less pronounced in indirectly affected areas due to the development of conditions that favour understorey communities. This reduced impact can be attributed to a buffering effect, whereby forest edges and nearby undisturbed areas retain cooler, moister microclimates due to residual canopy cover and structural complexity, which help to moderate the harsh conditions produced by adjacent disturbances (De Frenne et al., 2021). For instance, the accumulation of coarse woody debris from dead and fallen trees in proximity to disturbed sites enhances microhabitat heterogeneity and may locally recreate buffered microsites similar to those in undisturbed stands (Pedlar et al., 2002; De Frenne et al., 2021). Over time, these features may promote the partial recovery towards original microclimatic conditions, particularly where forest regeneration occurs under a partially closed canopy. Importantly, microclimatic gradients from the forest core to the edge can be substantial, extending up to 100 meters, depending on variables such as light, wind, and temperature (Hylander, 2005; Schmidt et al., 2017). This suggests that even areas not disturbed directly may still experience the effects of disturbance to a lesser extent, and this phenomenon highlights the significance of structural legacies in mitigating microclimatic shifts due to disturbances.

It is also important to note that the extent to which plant communities have an impact is driven by the spatial extent of these particular communities from the disturbance edge. For example, some previous studies in boreal ecosystems have reported that edge influences on understorey vegetation richness are generally weak but can extend at least up to 20 meters from the core disturbed area (Harper & Macdonald, 2002; Harper et al., 2015). However, in our study, the distance of sampling plots from disturbance edges was not explicitly measured, which may have limited our ability to fully capture potential edge-related effects on microhabitat conditions and understorey communities. This likely explains the lower impact of indirect disturbances observed in our study compared to the more pronounced effects associated with direct disturbances.

1.4.3 Time since disturbance

Time since disturbance is one of the important factors that influence vegetation dynamics, as it affects microhabitat conditions and successional processes. In the early stages following a disturbance, such as fire, understory diversity may be promoted due to the creation of conditions that support pioneer species adapted to colonize newly available substrates (Paquette et al., 2016). Over time, the interaction of fire with other disturbances, such as forest harvest or insect outbreaks, can enhance substrate heterogeneity through the delayed mortality of older trees, which contributes to the accumulation of coarse woody debris (Su et al., 2019). In our study, the time since fire was approximately 50 years, which is likely a key factor influencing the observed vegetation patterns. While fire can initially create harsh conditions such as high light exposure, low humidity, and limited microsite availability, these conditions gradually improve as the forest regenerates (Lavoie & Sirois, 1998). In addition to the natural recovery process, salvage harvest after fire can also contribute to structural complexity by adding coarse woody debris, which is a suitable substrate for the establishment and growth of colonist species, as it provides humid conditions even during dry periods (Tinker & Knight, 2000). It also increases the quantity of substrates that retain moisture, which can be an ideal shelter for understory species, as it can facilitate the persistence and recruitment of underground species to some extent. Therefore, our results are best interpreted as reflecting the cumulative effects of evenly aged disturbances.

1.4.4 Limitations and perspectives

Forest structural and compositional attributes form the ecological context through which disturbance influences understory diversity. As the effects of multiple disturbances cannot be fully understood by considering disturbance type alone, they are, thus, interpreted to the existing forest structures, specifically, the overstorey composition, canopy openness, and substrate heterogeneity that drive changes in light, humidity, and microhabitat quality. Moreover, many factors beyond what we considered can play a significant role in the disturbance and vegetation interaction. In this study, we focused on a defined set of variables, but future projects could incorporate key factors such as time since disturbance, organic layer thickness, and

canopy density to better capture their interactive effects on understorey plant communities.

1.5 *Conclusion*

Our study showed that multiple disturbances have different, yet significant, effects on the richness and composition of understorey plant communities in the boreal ecosystem. Liverworts, characterized by their narrow ecological tolerances and dependence on humid microhabitats, exhibited a pronounced decline in species richness, 18% per direct and 8% indirect disturbances. In contrast, vascular plant richness increased by 51% per direct disturbances but declined by 4% per indirect disturbances, reflecting the rapid colonization of disturbance-adapted and light-demanding species with the span of time. Moss richness generally remained unchanged, suggesting compensatory species turnover that maintained their overall diversity. Moreover, community composition analyses revealed that direct disturbances favoured the establishment of deciduous-associated species assemblages, while indirect disturbances maintained compositions associated with coniferous ecosystems.

This study demonstrated that the maintenance of understorey diversity within boreal ecosystems cannot solely rely on the mitigation of individual disturbance types. Effective conservation and management strategies must address the combined and interactive effects of multiple direct and indirect disturbances. The increasing frequency, spatial overlap, and cumulative nature of natural and anthropogenic disturbances underscore the critical need to enhance our understanding of how complex disturbance regimes affect forest resilience, biodiversity, and the provision of ecosystem services. The findings of this research recommend the integration of both direct and indirect disturbances, along with their cumulative and additive effects, within biodiversity conservation frameworks and forest management plans. This approach enables decision-makers to anticipate and manage the ecological consequences of future disturbances, which allows more accurate predictions of shifts in understorey biodiversity, vegetation structure, and ecosystem function. Furthermore, the increasing number of disturbances will lead to more parts of the landscapes being

exposed to indirect effects. Future research should evaluate how interactions between disturbance type, ecosystem type, and climate-driven vegetation change influence long-term biodiversity patterns and ecosystem services. Such studies should also examine how disturbance timing, sequence, and intensity affect recovery trajectories, providing critical insight for developing adaptive, multi-disturbance management strategies at regional and landscape scales.

GENERAL CONCLUSION

Our results suggest that sensitive taxa such as liverworts are particularly vulnerable, highlighting the importance of considering fine-scale habitat heterogeneity (Boudreault et al., 2018). Microhabitat conditions may buffer or exacerbate the effects of disturbances (Braithwaite & Mallik, 2012), and their inclusion in predictive models is critical to explain the patterns of species richness and composition across multiple disturbances. Furthermore, forest planners must account for both direct and indirect disturbance effects at the landscape scale to effectively maintain understorey biodiversity in the face of shifting disturbance regimes. This research predicts shifts in understorey plant community composition resulting from multiple disturbances, which supports the development of models aimed at enhancing long-term forest resilience and biodiversity conservation.

From a management perspective, the implications of the findings from this study are substantial. Current forest management plans treat disturbances such as forest harvest, fire, and insect outbreak independently, often ignoring the interactive and cumulative effects of multiple disturbances on biodiversity. However, our results indicate that such multiple disturbances can substantially alter community composition, reduce species richness, and disproportionately affect specialist species. Integrating a multi-disturbance framework into management strategies could, thus, improve predictions of biodiversity outcomes and inform adaptive interventions to enhance the resilience of understorey communities. Practical measures for achieving such goals include landscape-level monitoring to identify areas where disturbances co-occur or interact, retention of critical microhabitats such as shaded, moist microsites, and deadwood to support sensitive species, adaptive management guided by long-term monitoring to adjust harvesting schedules or controlled burns, and identification of ecological thresholds to prevent irreversible changes in community structure.

By implementing these strategies, forest managers can maintain functionally diverse and resilient understorey communities, even under an increased number of

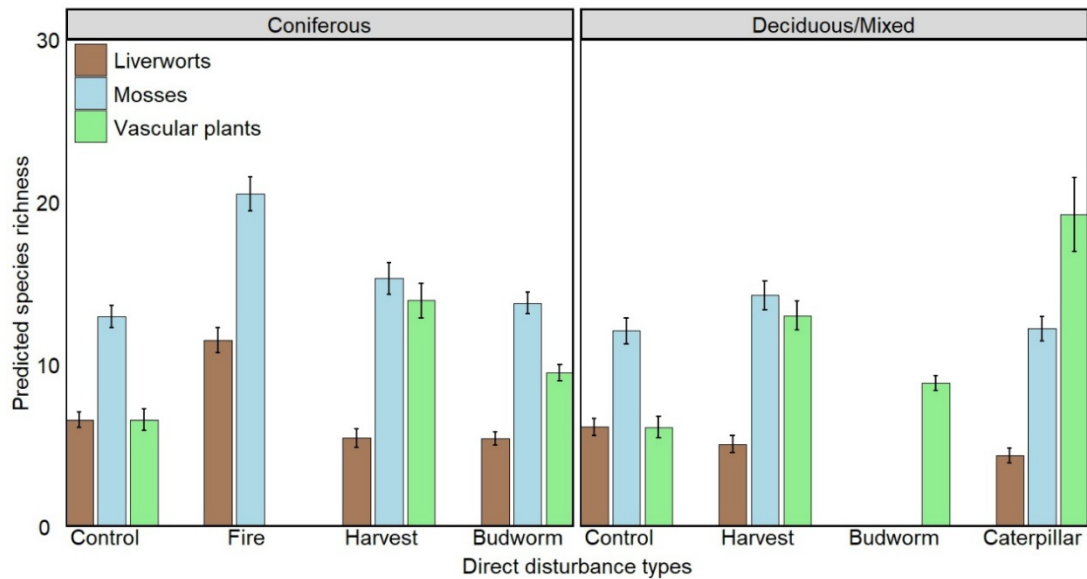
disturbances. Adopting a multi-disturbance perspective also supports the development of predictive models that incorporate interactions among disturbance types, enhancing the capacity to forecast shifts in species composition and ecosystem function under future scenarios. Importantly, these strategies align with ecosystem-based management principles, which aim to preserve structural and functional integrity while allowing for sustainable resource use. In conclusion, integrating knowledge of multiple disturbances into boreal forest management is critical for conserving understorey biodiversity and enhancing long-term ecosystem resilience. Hence, the incorporation of our insights for developing adaptive management plans and landscape-level ecological risk assessments will be critical for preserving the structural and functional integrity of boreal ecosystems in the face of increasing disturbance regimes.

Despite the novel insights provided by this study, substantial knowledge gaps remain. A key question that emerges is how environmental factors and time since multiple interacting disturbances influence the recovery trajectories and long-term resilience of bryophyte and vascular plant communities in boreal ecosystems. Addressing this question would clarify the temporal dynamics of species responses following complex multiple disturbances. Moreover, assessing microhabitat-scale variables such as substrate diversity, light availability, and humidity could provide a more mechanistic understanding of species-specific responses. Finally, a crucial aspect to determine would be to identify whether multiple disturbances push communities beyond ecological thresholds, potentially leading to irreversible shifts in forest structure and function.

ANNEX A - EXPLANATION OF SAMPLING DESIGN VARIATION AMONG DIFFERENT PROJECTS

The dataset used in this study was compiled from nine independent research projects. While there were slight variations in data collection methods across these projects, most of the bryophyte data were collected from rectangular 5 m × 10 m plots using modified floristic habitat sampling techniques. An exception is the project by Yin (2022), which employed a different design: at each mine site, 1-km-long 6 to 8 transects were established, depending on site size, along with 9 transects in undisturbed areas representing various ecosystem types. Along each transect, seven circular vegetation plots (3 m radius) were positioned at fixed distances from the mine edge, specifically at 0, 0.02, 0.05, 0.1, 0.2, 0.5, and 1 km. Within each plot, bryophytes were sampled from various microhabitats (ground, trees, logs, snags, stumps, and rocks). In another project, Noualhaguet (2023) applied a transect-based approach within permanent plots. From the center of each plot, a north–south transect measuring 11.28 m in length (equal to the plot radius) and 1 m in width was laid out. Along this transect, bryophytes were collected from distinct microhabitats such as tree bases, snags, fresh and decayed deadwood, stumps, and mineral soil. For our project, all plots across these studies were treated as independent sampling units. For vascular plant data, when multiple quadrats were presented within a plot, species richness was averaged.

ANNEX B - SPECIES RICHNESS ACROSS ECOSYSTEM TYPES FOR DIRECT DISTURBANCES



Figure

Results of the GLM for species richness of liverworts, mosses, and vascular plants across ecosystem types: coniferous and deciduous/mixed. Plots representing deciduous and mixed ecosystems were combined into a single category, as mixed stands in boreal forests are typically dominated by deciduous species. Notably, vascular plant plots were absent from coniferous ecosystems under fire disturbances, while liverwort and moss plots did not occur within deciduous/mixed ecosystems or in areas affected by spruce budworm disturbance.

ANNEX C - PLOT DISTRIBUTION ACROSS DIRECT DISTURBANCE AND ECOSYSTEM TYPES

Table

The number of plots according to direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar) and ecosystem types (coniferous and deciduous/mixed) for three plant groups. Plots fewer than five for each disturbance were excluded to ensure reliable representation.

Disturbances	Ecosystem types	Plant types	Number of plots
Undisturbed	Coniferous	Liverworts	53
		Mosses	53
		Vascular plants	26
	Deciduous/Mixed	Liverworts	17
		Mosses	17
		Vascular plants	13
Fire	Coniferous	Liverworts	46
		Mosses	46
Forest harvest	Coniferous	Liverworts	20
		Mosses	20
		Vascular plants	11
	Deciduous/Mixed	Liverworts	29
		Mosses	29
		Vascular plants	30
Spruce budworm	Coniferous	Liverworts	77
		Mosses	77
		Vascular plants	63
	Deciduous/Mixed	Vascular plants	75
	Forest tent caterpillar	Deciduous/Mixed	Liverworts
Mosses			52
Vascular plants			9

ANNEX D - ADDITIVE EFFECTS OF DIRECT DISTURBANCES ACROSS ECOSYSTEM TYPES

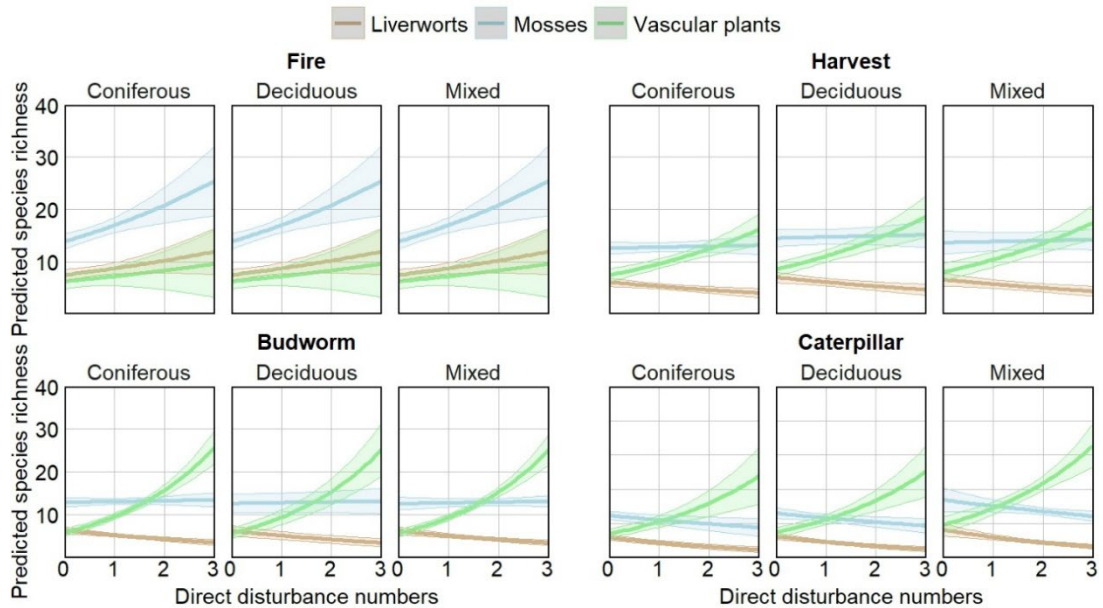


Figure
Predicted species richness of liverworts, mosses, and vascular plants in response to increasing disturbance numbers across different direct disturbances (fire, forest harvest, spruce budworm, and forest tent caterpillar) and ecosystem types (coniferous, deciduous, and mixed. The x-axis represents the number of disturbances, while the y-axis represents the predicted species richness. Brown, blue, and green lines correspond to the richness of liverworts, mosses, and vascular plants.

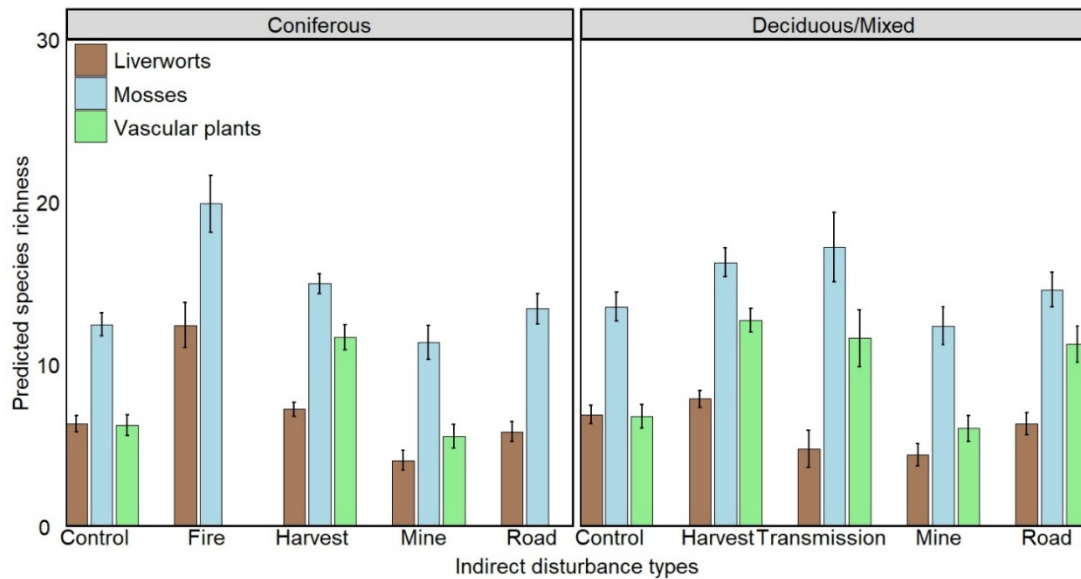
**ANNEX E - PLOT DISTRIBUTION BY NUMBER OF DIRECT DISTURBANCES
AND ECOSYSTEM TYPES**

Table

The distribution of plots across numbers of direct disturbances and ecosystem types (coniferous, deciduous, and mixed) for liverworts, mosses, and vascular plants. To ensure reliable representation, disturbances represented by fewer than five plots were excluded.

Ecosystem types	Plant types	Disturbance numbers	Number of plots
Coniferous	Liverworts	0	53
		1	143
		2	50
	Mosses	0	53
		1	143
		2	50
	Vascular plants	0	26
		1	74
		2	43
Deciduous	Liverworts	0	13
		1	79
	Mosses	0	13
		1	79
	Vascular plants	0	13
		1	31
Mixed	Liverworts	2	87
		3	21
	Mosses	2	87
		3	21
	Vascular plants	1	80
		2	63

ANNEX F - SPECIES RICHNESS ACROSS ECOSYSTEM TYPES FOR INDIRECT DISTURBANCES



Figure

The richness of liverworts, mosses, and vascular plants was assessed across ecosystem types: coniferous and deciduous/mixed for single indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, and transmission lines). Particularly, vascular plant plots were absent in coniferous ecosystems under fire indirect disturbances. Similarly, plots of all plant groups were absent from spruce budworm, forest tent caterpillar, and transmission line indirect disturbances in coniferous ecosystems, and no plant plots were recorded under fire, spruce budworm, and forest tent caterpillar indirect disturbances in deciduous/mixed ecosystems.

ANNEX G - PLOT DISTRIBUTION ACROSS INDIRECT DISTURBANCE AND ECOSYSTEM TYPES

Table

The number of plots based on indirect disturbances (fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, and transmission lines) and ecosystem types (coniferous and deciduous/mixed) for the three plant groups. Plots fewer than five for each disturbance were excluded to ensure reliable representation.

Disturbances	Ecosystem types	Plant types	Plot numbers
Undisturbed	Coniferous	Liverworts	53
		Mosses	53
		Vascular plants	26
	Deciduous/Mixed	Liverworts	17
		Mosses	17
		Vascular plants	13
Fire	Coniferous	Liverworts	17
		Mosses	17
Forest harvest	Coniferous	Liverworts	87
		Mosses	87
		Vascular plants	18
	Deciduous/Mixed	Liverworts	23
		Mosses	23
		Vascular plants	48
Mines	Coniferous	Liverworts	17
		Mosses	17
		Vascular plants	18
	Deciduous/Mixed	Liverworts	11
		Mosses	11
		Vascular plants	10
Forest roads	Coniferous	Liverworts	25
		Mosses	25
	Deciduous/Mixed	Liverworts	16
		Mosses	16
		Vascular plants	24
Transmission	Deciduous/Mixed	Liverworts	10
		Mosses	10
		Vascular plants	10

ANNEX H - ADDITIVE EFFECTS OF INDIRECT DISTURBANCES ACROSS ECOSYSTEM TYPES

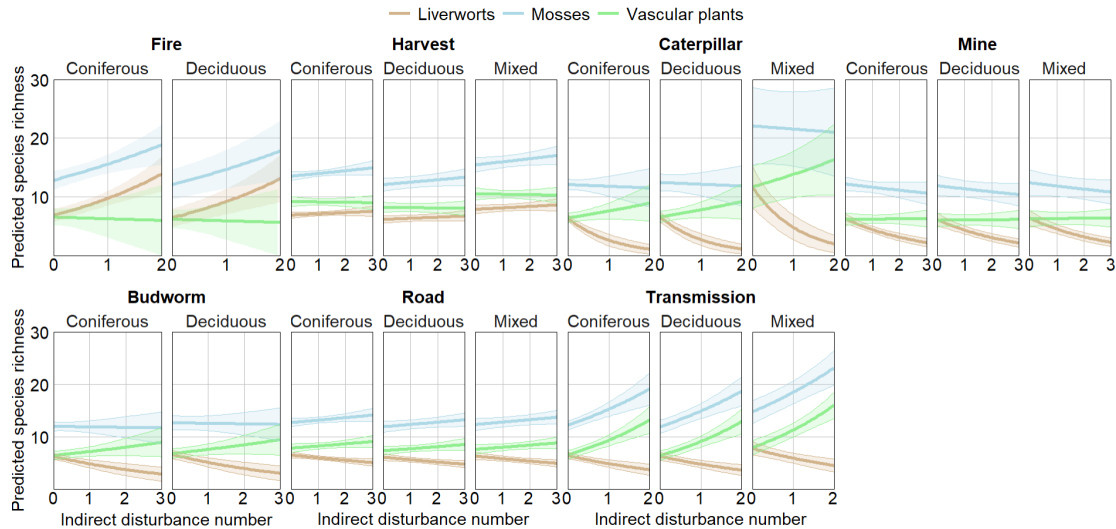


Figure
Predicted species richness of plant groups in response to increasing numbers of indirect disturbances across disturbance types (fire, forest harvest, spruce budworm, forest tent caterpillar, mines, forest roads, and transmission lines) and ecosystem types (coniferous, deciduous, and mixed), based on results from generalized linear models (GLM). The x-axis shows the number of disturbances, and the y-axis indicates the predicted species richness. Brown, blue, and green lines represent liverworts, mosses, and vascular plants, respectively.

**ANNEX I - PLOT DISTRIBUTION BY NUMBER OF INDIRECT
DISTURBANCES AND ECOSYSTEM TYPES**

Table

The number of plots across numbers of indirect disturbances and ecosystem types (coniferous, deciduous, and mixed) for liverworts, mosses, and vascular plants.

Ecosystem types	Plant types	Disturbance numbers	Number of plots
Coniferous	Liverworts	0	53
		1	161
		2	69
		3	6
	Mosses	0	53
		1	161
		2	69
		3	6
	Vascular plants	0	26
		1	46
		2	30
		3	10
Deciduous	Liverworts	0	13
		1	18
		2	22
		3	5
	Mosses	0	13
		1	18
		2	22
		3	5
	Vascular plants	0	13
		1	27
		2	18
Mixed	Liverworts	1	46
		2	27
	Mosses	1	46
		2	27
	Vascular plants	1	71
		2	32

ANNEX J - LIST OF BRYOPHYTES

Table

The species codes used in the bryophyte composition analysis with PCoA are provided in the table. The first letter of each code indicates the bryophyte guild: m for mosses, s for sphagnum, and h for liverworts. Following this, the code is generated by combining the guild letter with abbreviations of the genus and species names.

Species name	Code	Species name	Code
<i>Amblystegium serpens</i>	mAmbser	<i>Lophozia guttulata</i>	hLopgut
<i>Anastrophyllum hellerianum</i>	hAnahel	<i>Lophozia longiflora</i>	hLopven
<i>Anastrophyllum michauxii</i>	hAnamic	<i>Lophozia obtusa</i>	hLopobt
<i>Anastrophyllum minutum</i>	hAnamin	<i>Lophozia silvicola</i>	hLopsil
<i>Aneura pinguis</i>	hAnepin	<i>Lophozia sudetica</i>	hBarsude
<i>Atrichum altecristatum</i>	mAtralt	<i>Lophoziaopsis longidens</i>	hLoplongid
<i>Atrichum crispum</i>	mAtrcrispum	<i>Marchantia polymorpha</i>	hMarpol
<i>Atrichum tenellum</i>	mAtrten	<i>Meesia triquetra</i>	mMeetri
<i>Aulacomnium palustre</i>	mAulpal	<i>Mesoptychia heterocolpos</i>	hMeshet
<i>Barbilophozia attenuate</i>	hBaratt	<i>Mnium marginatum</i>	mMnimarg
<i>Barbilophozia barbata</i>	hBarbar	<i>Mnium spinulosum</i>	mMnispi
<i>Barbilophozia floerkei</i>	hBarflo	<i>Mylia anomala</i>	hMylano
<i>Barbilophozia hatcheri</i>	hBarhat	<i>Mylia taylorii</i>	hMyltay
<i>Barbilophozia kunzeana</i>	hBarkun	<i>Nowellia curvifolia</i>	hNowcur
<i>Barbilophozia reptans</i>	hBarrep	<i>Nowellia unifolia</i>	hNowuni
<i>Bazzania tricrenata</i>	hBaztric	<i>Odontoschisma denudatum</i>	hOdoden
<i>Bazzania trilobata</i>	hBaztril	<i>Oncophorus virens</i>	hOncvir
<i>Blepharostoma trichophyllum</i>	hBletri	<i>Oncophorus wahlenbergii</i>	mOncwah
<i>Blindia acuta</i>	mBliacu	<i>Orthotrichum anomalum</i>	mOrtanom
<i>Brachythecium acuminatum</i>	mBraacum	<i>Orthotrichum obtusifolium</i>	mNyhobtu
<i>Brachythecium acutum</i>	mBraact	<i>Orthotrichum ohioense</i>	mOrtohi
<i>Brachythecium campestre</i>	mBram	<i>Orthotrichum speciosum</i>	mOrtspe
<i>Brachythecium curtum</i>	mBracur	<i>Pallavicinia lyellii</i>	hPallye
<i>Brachythecium erythrorrhizon</i>	mBraery	<i>Paludella squarrosa</i>	mPalsqu
<i>Brachythecium falcatum</i>	mBrafal	<i>Palustriella falcata</i>	mCrafalc
<i>Brachythecium laetum</i>	mBralae	<i>Paraleucobryum longifolium</i>	mParlon
<i>Brachythecium plumosum</i>	mBraplu	<i>Pellia epiphylla</i>	hPeleph
<i>Brachythecium populeum</i>	mBrapop	<i>Pellia neesiana</i>	hPelnee

Species name	Code	Species name	Code
<i>Brachythecium reflexum</i>	mBraref	<i>Plagiochila porelloides</i>	hPlapor
<i>Brachythecium rivulare</i>	mBrariv	<i>Plagiomnium cuspidatum</i>	mPlacus
<i>Brachythecium rutabulum</i>	mBrarut	<i>Plagiomnium drummondii</i>	mPladru
<i>Brachythecium starkii</i>	mBrasta	<i>Plagiomnium ellipticum</i>	mPlaell
<i>Brachythecium velutinum</i>	mBravel	<i>Plagiomnium medium</i>	mPlamed
<i>Breidleria pratensis</i>	mBrepra	<i>Plagiomnium rostratum</i>	mPlaros
<i>Brotherella recurvans</i>	mBrorec	<i>Plagiothecium cavifolium</i>	mPlacav
<i>Bryhnia graminicolor</i>	mBrygra	<i>Plagiothecium denticulatum</i>	mPladen
<i>Bryhnia novae-angliae</i>	mBrynova	<i>Plagiothecium laetum</i>	mPlalae
<i>Bryoeruthrophyllum recurvirostrum</i>	mBryrecu	<i>Plagiothecium latebricola</i>	mPlalat
<i>Bryum caespiticium</i>	mBrycae	<i>Platydictya subtilis</i>	mPlasub
<i>Bryum capillare</i>	mBrycap	<i>Platygyrium repens</i>	mPlarep
<i>Bryum creberrimum</i>	mBrycreb	<i>Pleurozium schreberi</i>	mPlesch
<i>Bryum pallescens</i>	mBrypallesce ns	<i>Pogonatum dentatum</i>	mPogden
<i>Bryum pseudotriquetrum</i>	mBrypse	<i>Pohlia cruda</i>	mPohcruda
<i>Callicladium haldanianum</i>	mCalhal	<i>Pohlia elongata</i>	mPohelo
<i>Calliergon cordifolium</i>	mCalcor	<i>Pohlia filum</i>	mPohfil
<i>Calliergon giganteum</i>	mCalgig	<i>Pohlia nutans</i>	mPohnut
<i>Calliergon richardsonii</i>	mCalric	<i>Pohlia sphagnicola</i>	mPohsph
<i>Calypogeia integristipula</i>	hCalint	<i>Pohlia wahlenbergii</i>	mPohwahl
<i>Calypogeia muelleriana</i>	hCalmue	<i>Polytrichastrum alpinum</i>	mPolalpi
<i>Calypogeia neesiana</i>	hCalnee	<i>Polytrichastrum formosum</i>	mPolfor
<i>Calypogeia neogaea</i>	hCalneo	<i>Polytrichum commune</i>	mPolcom
<i>Calypogeia sphagnicola</i>	hCalsph	<i>Polytrichum juniperinum</i>	mPoljun
<i>Calypogeia suecica</i>	hCalsue	<i>Polytrichum longisetum</i>	mPollon
<i>Campyliadelphus chrysophyllus</i>	mCamchr	<i>Polytrichum pallidisetum</i>	mPolpal
<i>Campylium protensum</i>	mCampro	<i>Polytrichum piliferum</i>	mPolpil
<i>Campylium stellatum</i>	mCamste	<i>Polytrichum strictum</i>	mPolstr
<i>Campylophyllum helleri</i>	mCamhall	<i>Pseudobryum cinclidioides</i>	mPsecin
<i>Campylophyllum hispidulum</i>	mCamhis	<i>Pseudocampylium radicale</i>	mPserad
<i>Cephalozia ambigua</i>	hCepamb	<i>Pseudoleskeella nervosa</i>	mPsenerv
<i>Cephalozia bicuspidata</i>	hCepbic	<i>Pseudotaxiphyllum elegans</i>	mPseeleg
<i>Cephalozia catenulata</i>	hCepcat	<i>Ptilidium ciliare</i>	hPtCIL
<i>Cephalozia connivens</i>	hCepcon	<i>Ptilidium pulcherrimum</i>	hPtIPUL

Species name	Code	Species name	Code
<i>Cephalozia leucantha</i>	hCepleu	<i>Ptilium crista-castrensis</i>	mPticricas
<i>Cephalozia loitlesbergeri</i>	hCeploi	<i>Pylaisia intricata</i>	mPylint
<i>Cephalozia lunulifolia</i>	hCeplun	<i>Pylaisia polyantha</i>	mPylpol
<i>Cephalozia macrostachya</i>	hCepmac	<i>Pylaisia selwynii</i>	mPylselw
<i>Cephalozia pleniceps</i>	hCepple	<i>Racomitrium microcarpum</i>	mRacmicr
<i>Cephaloziella divaricate</i>	hCepdiv	<i>Radula complanata</i>	hRadcom
<i>Cephaloziella elachista</i>	hCepela	<i>Rhizomnium gracile</i>	mRhigra
<i>Cephaloziella hampeana</i>	hCepham	<i>Rhizomnium pseudopunctatum</i>	mRhipse
<i>Cephaloziella rubella</i>	hCeprub	<i>Rhizomnium punctatum</i>	mRhipun
<i>Cephaloziella spinigera</i>	hCepspi	<i>Rhodobryum ontariense</i>	mRhoont
<i>Ceratodon purpureus</i>	mCerpur	<i>Rhynchostegium serrulatum</i>	mRhyser
<i>Chiloscyphus coadunatus</i>	hChicoa	<i>Rhytidiadelphus subpinnatus</i>	mRhysub
<i>Chiloscyphus graveolens</i>	hChigra	<i>Rhytidiadelphus triquetrus</i>	mRhytri
<i>Chiloscyphus pallescens</i>	hChipal	<i>Riccardia latifrons</i>	hRiclat
<i>Chiloscyphus polyanthos</i>	hChipol	<i>Riccardia multifida</i>	hRicmult
<i>Chiloscyphus profundus</i>	hChipro	<i>Riccardia palmata</i>	hRicpal
<i>Cinclidium stygium</i>	mCinsty	<i>Riccardia vitrea</i>	hRicvitr
<i>Cladopodiella fluitans</i>	hClaflu	<i>Sanionia uncinata</i>	mSanunc
<i>Cladopodiella francisci</i>	hClafra	<i>Sarmentypnum exannulatum</i>	mSarexa
<i>Climacium dendroides</i>	mClidend	<i>Scapania apiculata</i>	hScaapi
<i>Dichodontium pellucidum</i>	mDicpell	<i>Scapania irrigua</i>	hScairr
<i>Dicranella heteromalla</i>	mDichet	<i>Scapania mucronata</i>	hScamuc
<i>Dicranella rufescens</i>	mDicruf	<i>Scapania paludicola</i>	hScapalc
<i>Dicranum acutifolium</i>	mDicacu	<i>Scapania uliginosa</i>	hScauli
<i>Dicranum flagellare</i>	mDicfla	<i>Schistidium agassizii</i>	mSchagas
<i>Dicranum fragilifolium</i>	mDicfra	<i>Schistochilopsis grandiretis</i>	hSchgra
<i>Dicranum fulvum</i>	mDicful	<i>Schistochilopsis incisa</i>	hSchinc
<i>Dicranum fuscescens</i>	mDicfus	<i>Scorpidium revolvens</i>	mScorev
<i>Dicranum groenlandicum</i>	mDicgro	<i>Scorpidium scorpioides</i>	mScosco
<i>Dicranum leioneuron</i>	mDiclei	<i>Solenostoma crenuliforme</i>	hSolcren
<i>Dicranum majus</i>	mDicmaj	<i>Sphagnum angustifolium</i>	sSphang
<i>Dicranum montanum</i>	mDicmon	<i>Sphagnum annulatum</i>	sSphann
<i>Dicranum ontariense</i>	mDicont	<i>Sphagnum balticum</i>	sSphbal
<i>Dicranum polysetum</i>	mDicpol	<i>Sphagnum capillifolium</i>	sSphcap

Species name	Code	Species name	Code
<i>Dicranum scoparium</i>	mDicsco	<i>Sphagnum centrale</i>	sSphcen
<i>Dicranum spurium</i>	mDicspu	<i>Sphagnum compactum</i>	sSphcom
<i>Dicranum undulatum</i>	mDicund	<i>Sphagnum contortum</i>	sSphcon
<i>Dicranum viride</i>	mDicvir	<i>Sphagnum cuspidatum</i>	sSphcus
<i>Ditrichum lineare</i>	mDitlin	<i>Sphagnum divinum</i>	sSphdiv
<i>Ditrichum pusillum</i>	mDitpus	<i>Sphagnum fallax</i>	sSphfal
<i>Drepanocladus aduncus</i>	mDreadu	<i>Sphagnum flexuosum</i>	sSphfle
<i>Drepanocladus polygamus</i>	mDrepol	<i>Sphagnum fuscum</i>	sSphfus
<i>Eurhynchiastrum pulchellum</i>	mEurpul	<i>Sphagnum girgensohnii</i>	sSphgir
<i>Fissidens bryoides</i>	mFisbry	<i>Sphagnum isoviitae</i>	sSphiso
<i>Fissidens osmundoides</i>	mFisosm	<i>Sphagnum lindbergii</i>	sSphlin
<i>Frullania eboracensis</i>	hFruebo	<i>Sphagnum magellanicum</i>	sSphmag
<i>Frullania inflata</i>	hFruinf	<i>Sphagnum majus</i>	sSphmaj
<i>Frullania oakesiana</i>	hFruoak	<i>Sphagnum palustre</i>	sSphpal
<i>Geocalyx graveolens</i>	hGeogra	<i>Sphagnum papillosum</i>	sSphpap
<i>Gymnocolea inflata</i>	hGyminf	<i>Sphagnum platyphyllum</i>	sSphpla
<i>Hamatocaulis vernicosus</i>	mHamver	<i>Sphagnum pulchrum</i>	sSphpul
<i>Hedwigia ciliata</i>	mHedcil	<i>Sphagnum quinquefarium</i>	sSphqui
<i>Helodium blandowii</i>	mHelbla	<i>Sphagnum riparium</i>	sSphrip
<i>Herzogiella striatella</i>	mHerstr	<i>Sphagnum rubellum</i>	sSphrub
<i>Herzogiella turfacea</i>	mHertur	<i>Sphagnum russowii</i>	sSphrus
<i>Homalia trichomanoides</i>	mHomtri	<i>Sphagnum squarrosum</i>	sSphsqu
<i>Hygroamblystegium varium</i>	mHygvar	<i>Sphagnum subfulvum</i>	sSphsubf
<i>Hygrohypnum eugyrium</i>	mHygeug	<i>Sphagnum subsecundum</i>	sSphsubs
<i>Hylocomium splendens</i>	mHylspl	<i>Sphagnum subtile</i>	sSphsubtile
<i>Hypnum cupressiforme</i>	mHypcup	<i>Sphagnum tenellum</i>	sSphtenellum
<i>Hypnum curvifolium</i>	mHypcur	<i>Sphagnum tenerum</i>	sSphtenr
<i>Hypnum fauriei</i>	mHypfau	<i>Sphagnum venustum</i>	sSphven
<i>Hypnum imponens</i>	mHypimp	<i>Sphagnum warnstorffii</i>	sSphwar
<i>Hypnum pallescens</i>	mHyppal	<i>Sphagnum wulfianum</i>	sSphwul
<i>Hypnum recurvatum</i>	mHyprec	<i>Sphenolobus hellerianus</i>	hSphhel
<i>Hypnum vaucher</i>	mHypvau	<i>Sphenolobus minutus</i>	sSphmin
<i>Isopterygiopsis muelleriana</i>	mIsomue	<i>Splachnum ampullaceum</i>	mSplamp
<i>Isopterygiopsis pulchella</i>	mIsopul	<i>Straminergon stramineum</i>	mStrstr
<i>Jamesoniella autumnalis</i>	hJamaut	<i>Tetraphis pellucida</i>	mTetpel
<i>Jamesoniella uncinata</i>	hJamunc	<i>Tetraplodon angustatus</i>	mTetang
<i>Jungermannia gracillima</i>	hJungra	<i>Thuidium delicatulum</i>	mThudeli

Species name	Code	Species name	Code
<i>Jungermannia leiantha</i>	hJunlei	<i>Thuidium recognitum</i>	mThurec
<i>Kindbergia praelonga</i>	mKinpra	<i>Tomentypnum falcifolium</i>	mTomfal
<i>Kurzia pauciflora</i>	hKurpau	<i>Tomentypnum nitens</i>	mTomnit
<i>Leiocolea rutheana</i>	hLeirut	<i>Tortella humilis</i>	mTorhumi
<i>Leiomylia anomala</i>	hLeiano	<i>Trematodon ambiguus</i>	mTreamb
<i>Lepidozia reptans</i>	hLeprep	<i>Tritomaria exsectiformis</i>	hTriexsecti
<i>Leptobryum pyriforme</i>	mLeppyr	<i>Tritomaria laxa</i>	hSchlax
<i>Leptodictyum riparium</i>	mLeprip	<i>Tritomaria quinquedentata</i>	hTriqui
<i>Leucobryum glaucum</i>	mLeugla	<i>Ulota coarctata</i>	mUlocoa
<i>Lophozia ascendens</i>	hLopasc	<i>Ulota crispa</i>	mUlocri
<i>Lophozia bicrenata</i>	hLopbic	<i>Warnstorfia fluitans</i>	mWarflu

ANNEX K - LIST OF VASCULAR PLANTS

Table

The species codes used in the vascular plant composition analysis with PCoA are provided in the table. Each code was generated by combining abbreviated forms of the genus and species names to ensure consistency and facilitate data analysis.

Species name	Code	Species name	Code
<i>Abies balsamea</i>	Abibal	<i>Lycopodium clavatum</i>	Lyccla
<i>Acer negundo</i>	Aceneg	<i>Lycopodium complanatum</i>	Lyccom
<i>Acer nigrum</i>	Acenig	<i>Lycopodium flabelliforme</i>	Lycfla
<i>Acer pensylvanium</i>	Acepen	<i>Lycopodium lucidulum</i>	Lycluc
<i>Acer rubrum</i>	Acerub	<i>Lycopodium obscurum</i>	Lycobs
<i>Acer saccharinum</i>	Acesac	<i>Lycopodium tristachyum</i>	Lyctri
<i>Acer saccharum</i>	Acesacc	<i>Lycopus uniflorus</i>	Lycuni
<i>Acer spicatum</i>	Acespi	<i>Lycopodium lagopus</i>	Lyl
<i>Achillea millefolium</i>	Achmil	<i>Lysimachia borealis</i>	Lysbor
<i>Actaea sp</i>	Act	<i>Lysimachia terrestris</i>	Lyster
<i>Actaea pachypoda</i>	Actpac	<i>Maianthemum canadense</i>	Maican
<i>Actaea rubra</i>	Actrub	<i>Maianthemum trifolium</i>	Maitri
<i>Adiantum pedatum</i>	Adiped	<i>Malus sp</i>	Mal
<i>Agrostis gigantea</i>	Agrgig	<i>Matteuccia struthiopteris</i>	Matstr
<i>Allium tricoccum</i>	Alltri	<i>Medeola virginiana</i>	Medvir
<i>Alnus alnobetula</i>	Alnaln	<i>Melilotus albus</i>	Melalb
<i>Alnus crispa</i>	Alncri	<i>Melampyrum lineare</i>	Mellin
<i>Alnus incana</i>	Alninc	<i>Mertensia paniculata</i>	Merpan
<i>Alnus rugosa</i>	Alnrug	<i>Mitella diphylla</i>	Mitdip
<i>Alnus viridis</i>	Alnvir	<i>Mitella nuda</i>	Mitnud
<i>Amelanchier sp</i>	Ame	<i>Mitchella repens</i>	Mitrep
<i>Amelanchier arborea</i>	Amearb	<i>Monotropa hypopitys</i>	Monhyp
<i>Amelanchier bartramiana</i>	Amebar	<i>Monotropa uniflora</i>	Monuni
<i>Amelanchier canadensis</i>	AmeCAN	<i>Monoses uniflora</i>	Monunif
<i>Amelanchier laevis</i>	Amelae	<i>Myrica gale</i>	Myrgal
<i>Anaphalis margaritacea</i>	Anamar	<i>Nemopanthus mucronatus</i>	Nemmuc
<i>Andromeda glaucophylla</i>	Andgla	<i>Oclemena nemoralis</i>	Ocnem
<i>Anemone canadensis</i>	Anecan	<i>Oenothera biennis</i>	Oenbie
<i>Anemone quinquefolia</i>	Anequi	<i>Onoclea sensibilis</i>	Onosen
<i>Apocynum androsaemifolium</i>	Apoand	<i>Orthilia secunda</i>	Ortsec
<i>Aralia hispida</i>	Arahis	<i>Osmunda cinnamomea</i>	Osmcin
<i>Aralia nudicaulis</i>	Aranud	<i>Osmorhiza claytoni</i>	Osmcla

Species name	Code	Species name	Code
<i>Aralia racemosa</i>	Ararac	<i>Osmunda claytoniana</i>	Osmclay
<i>Arctostaphylos uva-ursi</i>	Arcuva	<i>Osmunda regalis</i>	Osmreg
<i>Arisaema atrorubens</i>	Ariatr	<i>Ostrya virginiana</i>	Ostvir
<i>Aronia melanocarpa</i>	Aromel	<i>Oxalis acetosella</i>	Oxaace
<i>Asarum canadense</i>	Asacan	<i>Oxalis montana</i>	Oxamon
<i>Asclepias syriaca</i>	Ascsyr	<i>Oxalis stricta</i>	Oxastr
<i>Aster sp</i>	Ast	<i>Parthenocissus quinquefolia</i>	Parqui
<i>Aster acuminatus</i>	Astacu	<i>Petasites frigidus</i>	Petfri
<i>Aster macrophyllus</i>	Astmac	<i>Petasites palmatus</i>	Petpal
<i>Aster puniceus</i>	Astpun	<i>Phegopteris connectilis</i>	Phecon
<i>Athyrium filix-femina</i>	Athfil	<i>Picea abies</i>	Picabi
<i>Athyrium thelypteroides</i>	Aththe	<i>Picea glauca</i>	Picgla
<i>Betula alleghaniensis</i>	Betall	<i>Picea mariana</i>	Picmar
<i>Betula glandulosa</i>	Betgla	<i>Picea rubens</i>	Picrub
<i>Betula papyrifera</i>	Betpap	<i>Pilosella aurantiacum</i>	Pilaur
<i>Betula populifolia</i>	Betpop	<i>Pilosella caespitosum</i>	Pilcae
<i>Betula pumila</i>	Betpum	<i>Pinus banksiana</i>	Pinban
<i>Botrychium virginianum</i>	Botvir	<i>Pinus resinosa</i>	Pinres
<i>Calypso bulbosa</i>	Calbul	<i>Pinus rigida</i>	Pinrig
<i>Calamagrostis canadensis</i>	Calcan	<i>Pinus strobus</i>	Pinstr
<i>Caltha palustris</i>	Calpal	<i>Pinus sylvestris</i>	Pinsyl
<i>Capnoides sempervirens</i>	Capsem	<i>Plantago major</i>	Plamaj
<i>Carex sp</i>	Car	<i>Poa sp</i>	Poa
<i>Carpinus caroliniana</i>	Carcar	<i>Poa compressa</i>	Poacom
<i>Carya cordiformis</i>	Carcor	<i>Polygonum sp</i>	Pol
<i>Carex disperma</i>	Cardis	<i>Polystichum acrostichoides</i>	Polacr
<i>Carex magellanica</i>	Carmag	<i>Polystichum braunii</i>	Polbra
<i>Carex oligosperma</i>	Caroli	<i>Polygonum cilinode</i>	Polcil
<i>Carya ovata</i>	Carova	<i>Polygonatum pubescens</i>	Polpub
<i>Carex platyphylla</i>	Carpla	<i>Polypodium virginianum</i>	Polvir
<i>Carex retrorsa</i>	Carret	<i>Populus sp</i>	Pop
<i>Carex stipata</i>	Carsti	<i>Populus balsamifera</i>	Popbal
<i>Carex tenara</i>	Carten	<i>Populus deltoides</i>	Popdel
<i>Cassandra calyculata</i>	Cascal	<i>Populus grandidentata</i>	Popgra
<i>Caulophyllum thalictroides</i>	Cautha	<i>Populus tremuloides</i>	Poptre
<i>Celtis occidentalis</i>	Celocc	<i>Poryla elliptica</i>	Porell

Species name	Code	Species name	Code
<i>Chamaenerion angustifolium</i>	Chaang	<i>Potentilla fruticosa</i>	Potfru
<i>Chamaedaphne calyculata</i>	Chacal	<i>Potentilla norvegica</i>	Potnor
<i>Chimaphila umbellata</i>	Chiumb	<i>Potentilla palustris</i>	Potpal
<i>Chrysanthemum leucantemum</i>	Chrleu	<i>Potentilla simplex</i>	Potsim
<i>Cicuta bulbifera</i>	Cicbul	<i>Prenanthes sp</i>	Pre
<i>Cinna latifolia</i>	Cinlat	<i>Prunus pensylvanica</i>	Prupen
<i>Cirsium sp</i>	Cir	<i>Prunus serotina</i>	Pruser
<i>Circaea alpina</i>	Ciralp	<i>Prunus virginiana</i>	Pruvir
<i>Circaea lutetiana</i>	Cirlut	<i>Prunella vulgaris</i>	Pruvul
<i>Claytonia caroliniana</i>	Clacar	<i>Pteridium aquilinum</i>	Pteaqu
<i>Claytosmunda claytoniana</i>	Clacla	<i>Pyrola sp</i>	Pyr
<i>Clematis virginiana</i>	Clevir	<i>Pyrola asarifolia</i>	Pyrasa
<i>Clintonia borealis</i>	Clibor	<i>Pyrola elliptica</i>	Pyrell
<i>Comandra livida</i>	Comliv	<i>Pyrola minor</i>	Pyrmin
<i>Comarum palustre</i>	Compal	<i>Pyrola rotundifolia</i>	Pyrrot
<i>Comptonia peregrina</i>	Comper	<i>Pyrola secunda</i>	Pyrsec
<i>Coptis groenlandica</i>	Copgro	<i>Pyrola verens</i>	Pyrver
<i>Coptis trifolia</i>	Coptri	<i>Quercus alba</i>	Quealb
<i>Cornus alternifolia</i>	Coralt	<i>Quercus bicolor</i>	Quebic
<i>Corylus americana</i>	Corame	<i>Quercus macrocarpa</i>	Quemac
<i>Cornus canadensis</i>	Corcan	<i>Quercus rubra</i>	Querub
<i>Corylus cornuta</i>	Corcor	<i>Ranunculus sp</i>	Ran
<i>Corallorhiza maculata</i>	Cormac	<i>Ranunculus abortivus</i>	Ranabo
<i>Cornus sericea</i>	Corser	<i>Ranunculus acris</i>	Ranacr
<i>Cornus stolonifera</i>	Corsto	<i>Rhamnus alnifolia</i>	Rhaaln
<i>Crataegus sp</i>	Cra	<i>Rhamnus cathartica</i>	Rhacat
<i>Cylactis pubescens</i>	Cylpub	<i>Rhododendron canadense</i>	Rhocan
<i>Cypripedium acaule</i>	Cypaca	<i>Rhododendron groenlandicum</i>	Rhogro
<i>Cypripedium calceolus</i>	Cypcal	<i>Rhus radicans</i>	Rhurad
<i>Cyperus esculentus</i>	Cypesc	<i>Rhus typhina</i>	Rhutyp
<i>Cypripedium reginae</i>	Cypreg	<i>Ribes americanum</i>	Ribame
<i>Cystopteris bulbifera</i>	Cysbul	<i>Ribes cynosbati</i>	Ribcyn
<i>Dalibarda repens</i>	Dalrep	<i>Ribes glandulosum</i>	Ribgla
<i>Danthonia compressa</i>	Dancom	<i>Ribes hirtellum</i>	Ribhir
<i>Delphinium carolinianum</i>	Delcar	<i>Ribes hudsonianum</i>	Ribhud
<i>Dendrolycopodium dendroideum</i>	Denden	<i>Ribes lacustre</i>	Riblac

Species name	Code	Species name	Code
<i>Dentaria diphylla</i>	Dendip	<i>Ribes ruizii</i>	Ribrui
<i>Dendrolycopodium obscurum</i>	Denobs	<i>Ribes triste</i>	Ribri
<i>Dennstaedtia punctilobula</i>	Denpun	<i>Rosa acicularis</i>	Rosaci
<i>Dicentra sp</i>	Dic	<i>Rosa blanda</i>	Rosbla
<i>Dicentra canadensis</i>	Diccan	<i>Rubus alleghaniensis</i>	Ruball
<i>Dicentra cucullaria</i>	Diccuc	<i>Rubus chamaemorus</i>	Rubcha
<i>Diervilla lonicera</i>	Dielon	<i>Rubus idaeus</i>	Rubida
<i>Dirca palustris</i>	Dirpal	<i>Rubus occidentalis</i>	Rubocc
<i>Drosera sp</i>	Dro	<i>Rubus odoratus</i>	Rubodo
<i>Drosera rotundifolia</i>	Drorot	<i>Rubus pubescens</i>	Rubpub
<i>Dryopteris carthusiana</i>	Drycar	<i>Rumex sp</i>	Rum
<i>Dryopteris cristata</i>	Drycri	<i>Salix sp</i>	Sal
<i>Dryopteris disjuncta</i>	Drydis	<i>Salix balsamifera</i>	Salbal
<i>Dryopteris goldiana</i>	Drygol	<i>Salix bebbiana</i>	Salbeb
<i>Dryopteris intermedia</i>	Dryint	<i>Sambucus canadensis</i>	Samcan
<i>Dryopteris marginalis</i>	Drymar	<i>Sambucus pubens</i>	Sampub
<i>Dryopteris noveboracensis</i>	Drynov	<i>Sambucus racemosa</i>	Samrac
<i>Dryopteris phegopteris</i>	Dryphe	<i>Sanguinaria canadensis</i>	Sancan
<i>Dryopteris spinulosa</i>	Dryspi	<i>Sanguisorba canadensis</i>	Sancana
<i>Elymus canadensis</i>	Elycan	<i>Sarracenia purpurea</i>	Sarpur
<i>Elymus repens</i>	Elyrep	<i>Scheuchzeria palustris</i>	Schpal
<i>Empetrum nigrum</i>	Empnig	<i>Scirpus microcarpus</i>	Scimic
<i>Epilobium angustifolium</i>	Epiang	<i>Scirpus pendulus</i>	Scipen
<i>Epipactis helleborine</i>	Epihel	<i>Scutellaria epilobiifolia</i>	Screpi
<i>Epilobium leptophyllum</i>	Epilep	<i>Scutellaria lateriflora</i>	Sclrat
<i>Epilobium palustre</i>	Epipal	<i>Scutellaria galericulata</i>	Scugal
<i>Epigaea repens</i>	Epirep	<i>Senecio sp</i>	Sen
<i>Epifagus virginiana</i>	Epivir	<i>Shepherdia canadensis</i>	Shecan
<i>Equisetum sp</i>	Equ	<i>Smilacina racemosa</i>	Smirac
<i>Equisetum arvense</i>	Equarv	<i>Smilacine stellata</i>	Smiste
<i>Equisetum fluviatile</i>	Equflu	<i>Smilacina trifolia</i>	Smitri
<i>Equisetum pratense</i>	Equipra	<i>Solidago sp</i>	Sol
<i>Equisetum sylvaticum</i>	Equsyl	<i>Solidago brendae</i>	Solbre
<i>Eriophorum sp</i>	Eri	<i>Solidago canadensis</i>	Solcan
<i>Eriophorum vaginatum</i>	Erivag	<i>Solidago flexicaulis</i>	Solfle
<i>Erythronium americanum</i>	Eryame	<i>Solidago hispida</i>	Solhis
<i>Eupatorium maculatum</i>	Eupmac	<i>Solidago macrophylla</i>	Solmac
<i>Eupatorium rugosum</i>	Euprug	<i>Solidago rugosa</i>	Solrug

Species name	Code	Species name	Code
<i>Eurybia macrophylla</i>	Eurmac	<i>Solidago uliginosa</i>	Soluli
<i>Fagus grandifolia</i>	Faggra	<i>Sonchus sp</i>	Son
<i>Fallopia cilinodis</i>	Falcil	<i>Sonchus oleraceus</i>	Sonole
<i>Fragaria sp</i>	Fra	<i>Sorbus americana</i>	Sorame
<i>Fraxinus americana</i>	Fraame	<i>Sorbus decora</i>	Sordec
<i>Fraxinus nigra</i>	Franig	<i>Sparganium americanum</i>	Spaame
<i>Fraxinus pensylvanica</i>	Frapen	<i>Spinulum annotinum</i>	Spiann
<i>Fragaria vesca</i>	Fraves	<i>Spiraea latifolia</i>	Spilat
<i>Fragaria virginiana</i>	Fravir	<i>Spiranthes romanzoffiana</i>	Spirom
<i>Galium sp</i>	Gal	<i>Spiraea tomentosa</i>	Spitom
<i>Galium aparine</i>	Galapa	<i>Stellaria sp</i>	Ste
<i>Galium asprellum</i>	Galasp	<i>Streptopus amplexifolius</i>	Stramp
<i>Galeopsis bifida</i>	Galbif	<i>Streptopus lanceolatus</i>	Strlan
<i>Galium labradoricum</i>	Gallab	<i>Streptopus roseus</i>	Strros
<i>Galium sylvaticum</i>	Galsyl	<i>Symphyotrichum ciliolatum</i>	Symcil
<i>Galium trifolium</i>	Galtri	<i>Symplocarpus foetidus</i>	Symfoe
<i>Gaultheria hispidula</i>	Gauhis	<i>Symphyotrichum puniceum</i>	Sympun
<i>Gaultheria procumbens</i>	Gaupro	<i>Taraxacum officinale</i>	Taroff
<i>Gentiana linearis</i>	Genlin	<i>Taxus canadensis</i>	Taxcan
<i>Geocaulon lividum</i>	Geoliv	<i>Thalictrum dioicum</i>	Thadio
<i>Geranium sp</i>	Ger	<i>Thalictrum pubescens</i>	Thapub
<i>Geum macrophyllum</i>	Geumac	<i>Thuja occidentalis</i>	Thuocc
<i>Geum rivale</i>	Geuriv	<i>Tiarella cordifolia</i>	Tiacor
<i>Glyceria striata</i>	Glystr	<i>Tilia americana</i>	Tilame
<i>Goodyera sp</i>	Goo	<i>Trifolium sp</i>	Tri
<i>Goodyera repens</i>	Goorep	<i>Trientalis borealis</i>	Tribor
<i>Gramineae sp</i>	Gra	<i>Trillium cernuum</i>	Tricer
<i>Gymnocarpium dryopteris</i>	Gymdry	<i>Trillium erectum</i>	Triere
<i>Habenaria sp</i>	Hab	<i>Trillium grandiflorum</i>	Trigra
<i>Habenaria orbiculata</i>	Haborb	<i>Trifolium pratense</i>	Triptra
<i>Hepatica acutiloba</i>	Hepacu	<i>Trifolium repens</i>	Trirep
<i>Heracleum maximum</i>	Hermax	<i>Trillium undulatum</i>	Triund
<i>Hieracium sp</i>	Hie	<i>Tsuga canadensis</i>	Tsucan
<i>Huperzia lucidula</i>	Hupluc	<i>Tussilago farfara</i>	Tusfar
<i>Hypericum perforatum</i>	Hyper	<i>Typha latifolia</i>	Typlat
<i>Ilex mucronata</i>	Ilemuc	<i>Ulmus americana</i>	Ulmame
<i>Ilex verticillata</i>	Ilever	<i>Ulmus rubra</i>	Ulmrub
<i>Impatiens sp</i>	Imp	<i>Ulmus thomasii</i>	Ulmtho

Species name	Code	Species name	Code
<i>Impatiens capensis</i>	Impcap	<i>Uvularia grandiflora</i>	Uvugra
<i>Iris setosa</i>	Iriset	<i>Uvularia sessifolia</i>	Uvuses
<i>Iris versicolor</i>	Iriver	<i>Vaccinium spp</i>	Vac
<i>Juglans cinerea</i>	Jugcin	<i>Vaccinium angustifolium</i>	Vacang
<i>Juniperus sp</i>	Jun	<i>Vaccinium cespitosum</i>	Vacces
<i>Juniperus communis</i>	Juncom	<i>Vaccinium corymbosum</i>	Vaccor
<i>Juncus effusus</i>	Juneff	<i>Vaccinium myrtilloides</i>	Vacmyr
<i>Juniperus horizontalis</i>	Junhor	<i>Vaccinium oxycoccos</i>	Vacoxy
<i>Juniperus virginiana</i>	Junvir	<i>Vaccinium uliginosum</i>	Vaculi
<i>Kalmia angustifolia</i>	Kalang	<i>Vaccinium vitis-idaea</i>	Vacvit
<i>Kalmia microphylla</i>	Kalmic	<i>Veronica officinalis</i>	Veroff
<i>Kalmia polifolia</i>	Kalpol	<i>Veratrum viride</i>	Vervir
<i>Lactuca canadensis</i>	Laccan	<i>Viburnum alnifolium</i>	Vibaln
<i>Laportea canadensis</i>	Lapcan	<i>Viburnum cassinoides</i>	Vibcas
<i>Larix decidua</i>	Lardec	<i>Viburnum edule</i>	Vibedu
<i>Larix laricina</i>	Larlar	<i>Viburnum lentago</i>	Viblen
<i>Larix leptolepis</i>	Larlep	<i>Viburnum nudum</i>	Vibnud
<i>Ledum groenlandicum</i>	Ledgro	<i>Viburnum trilobum</i>	Vibri
<i>Leucanthemum vulgare</i>	Leuvul	<i>Vicia cracca</i>	Viccra
<i>Linnaea borealis</i>	Linbor	<i>Viola sp</i>	Vio
<i>Linaria vulgaris</i>	Linvul	<i>Viola canadensis</i>	Viocan
<i>Listera cordata</i>	Liscor	<i>Viola macloskeyi</i>	Viomac
<i>Lonicera caerulea</i>	Loncae	<i>Viola pallens</i>	Viopal
<i>Lonicera canadensis</i>	Loncan	<i>Viola renifolia</i>	Vioren
<i>Lonicera hirsuta</i>	Lonhir	<i>Viola rostrata</i>	Vioros
<i>Lonicera villosa</i>	Lonvil	<i>Viola sensylvanica</i>	Viosen
<i>Lotus corniculatus</i>	Lotcor	<i>Vitis riparia</i>	Vitrip
<i>Lycopus americanus</i>	Lycame	<i>Waldsteinia fragarioides</i>	Walfra
<i>Lycopodium annotium</i>	Lycann		

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