Université du Québec en Abitibi-Témiscamingue

# LE PAYSAGE COMME MODULATEUR DE LA DIVERSITÉ DES BRYOPHYTES BORÉALES

Thèse
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# ÉPIGRAPHE

*« Je vais recueillir des plantes et des fossiles, et faire des observations astronomiques avec les meilleurs instruments. Cependant, ce n'est pas le but principal de mon voyage. Je chercherai à comprendre comment les forces de la nature agissent les unes sur les autres, et de quelle manière l'environnement géographique influence les animaux et les plantes. En résumé, je dois apprendre l'harmonie de la nature »*.

Alexander von Humboldt

## AVANT-PROPOS

Cette thèse de doctorat s’inscrit dans un cadre de cotutelle entre l’Institut de recherche sur les forêts de l’Université du Québec en Abitibi-Témiscamingue (UQAT) et l’Institut de biologie intégrative et des systèmes de l’Université Laval. Elle a été réalisée sous la supervision conjointe de la professeure Nicole J. Fenton (UQAT) et du professeur Juan Carlos Villarreal Aguilar (Université Laval). Ce projet a bénéficié du soutien financier du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), du ministère des Ressources naturelles et des Forêts du Québec, ainsi que de la compagnie Resolute Forest Products.

L’ensemble du travail présenté ici est le fruit de mes propres démarches scientifiques, menées en collaboration étroite avec mes codirecteurs et divers partenaires de recherche. Mes directeurs m’ont accompagné à chaque étape du projet, depuis sa conception jusqu’à l’échantillonnage sur le terrain, l’analyse des données et la rédaction des articles scientifiques.

La thèse est structurée en cinq chapitres. Le premier introduit le contexte général de la recherche. Les chapitres II, III et IV forment le noyau scientifique du projet, rédigés sous forme d’articles scientifiques destinés à des revues spécialisées. Le chapitre final présente une synthèse et une discussion globale des résultats. Le chapitre II a déjà été publié dans une revue à comité de lecture, tandis que le chapitre III est actuellement en cours d’évaluation, et le chapitre IV en préparation. L’inclusion de ces manuscrits dans la thèse a été autorisée par l’ensemble des coauteurs.

Ci-dessous sont présentés les coauteurs de chaque chapitre, ainsi que les contributions spécifiques et partagées de chacun, conformément aux critères d’attribution de l’autorité scientifique.

Chapitre II : Enrique Hernández-Rodríguez a contribué à la rédaction de la première version du manuscrit ainsi qu’à sa révision et à son édition. Il a également participé à la visualisation, à la validation, au développement de logiciels, à la méthodologie, à l’investigation, à l’analyse formelle et à la curation des données.

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Chapitre III : Enrique Hernández-Rodríguez et Nicole J. Fenton ont conçu l'idée de recherche et développé la méthodologie. Xiangbo Yin, Marion Noualhaguet, Marc-Frédéric Indorf, Marion Barbé et Enrique Hernández-Rodríguez ont réalisé le travail de terrain et l'identification des espèces. La gestion des données des échantillons de bryophytes a été effectuée par Enrique Hernández-Rodríguez, Xiangbo Yin, Carlos Cerrejón, Marion Barbé et Marion Noualhaguet.

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Enrique Hernández-Rodríguez et Nicole J. Fenton ont rédigé les premières versions du manuscrit, avec des contributions de Carlos Cerrejón, Varina E. Crisfield et Juan C. Villarreal A. Tous les auteurs ont participé à la révision et à l'édition du manuscrit et ont approuvé la version finale pour publication.

Chapitre IV : Enrique Hernández-Rodríguez, Nicole J. Fenton et Juan C. Villarreal A. ont conçu l'idée de recherche. Enrique Hernández-Rodríguez, Adriel Michel Sierra et Marta Alonso-García ont réalisé les analyses statistiques et génétiques, ainsi que la visualisation des données.

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Ce parcours doctoral a donné lieu à plusieurs contributions à la communauté scientifique, notamment une publication, trois communications orales et cinq présentations par affiche lors de colloques et congrès nationaux et internationaux. La liste suivante présente les principales productions issues de ce travail :

Article de revues avec comité de lecture:

- Hernández-Rodríguez, E., Villarreal Aguilar, J.C., Fenton, N. (2024). Patch level boreal bryophyte diversity driven by landscape heterogeneity. Forest Ecology and Management, 563, 121978. https://doi.org/10.1016/j.foreco.2024.121978

Présentations orales :

- Composition et configuration du paysage et leur rôle dans la diversité des bryophytes boréales. 2022 – XXIIIe Symposium international de botanique cryptogamique, Espagne.
- Portrait du niveau de perturbation à l'échelle du paysage dans la forêt de l'épinette noire. 2021 – Colloque « Maintien de la biodiversité en milieu forestier », Canada.
- Fragmentation de l'habitat et diversité des bryophytes : étude dans la forêt boréale. 2021 – Conférence BL2021, Canada.

Présentations par affiche :

- Les plantes forestières discrètes révèlent comment aménager le paysage pour protéger la biodiversité. 2022 – 24e Colloque annuel de la Chaire UQAT-UQAM, Canada.

- Composition et configuration du paysage et leur rôle dans la diversité des bryophytes boréales. 2022 – Conférence annuelle de la Société Écologique d'Amérique, Canada.
- Définir la rareté et la fréquence des bryophytes boréales. 2022 – Conférence annuelle de l'Association Botanique du Canada, Canada.
- Fragmentation du paysage boréal et diversité des bryophytes. 2021 – 14e Colloque du Centre d'étude de la Forêt (CEF), Canada.
- Effets de la fragmentation sur la diversité bryophytique des forêts boréales. 2020 – Conférence annuelle de l'Association Botanique du Canada, Québec, Canada.

## RÉSUMÉ

Les types de couvertures du sol et leur disposition spatiale sont des facteurs qui modèlent les communautés biologiques. Actuellement, les biomes de la planète subissent des transformations drastiques dans les schémas de composition et de configuration de leurs paysages, ce qui affecte directement la biodiversité native. Cette situation souligne l'urgence de comprendre comment ces changements influencent les espèces, en particulier dans les régions qui conservent encore de vastes étendues de territoires naturels, mais qui sont de plus en plus soumises à la pression des activités productives.

Cette thèse aborde cette problématique en adoptant une approche multi-échelle du paysage et multidimensionnelle de la biodiversité, dans le but de comprendre comment la structure du paysage influence la richesse spécifique, la composition des communautés et la diversité génétique des bryophytes boréales dans l'est du Canada. À travers l'analyse de 92 paysages de 10 km de rayon, il a été observé que l'expansion des forêts jeunes dans l'environnement réduit la richesse en mousses et hépatiques, avec des effets particulièrement marqués lorsque cette couverture dépasse 40 %. Il a également été constaté que l'agrégation des parcelles de conifères peut avoir un impact négatif sur certains groupes fonctionnels comme les hépatiques et les sphaignes. Ces résultats démontrent que, même dans des paysages boréaux relativement peu altérés, la qualité de la matrice paysagère exerce une influence significative sur la diversité des bryophytes. En guise de mesure de conservation, il est proposé d'éviter que la couverture de forêts jeunes dépasse le seuil critique de 40 % et de réduire leur agrégation spatiale.

En explorant la composition des communautés, les patrons de rareté de 282 espèces de bryophytes ont été caractérisés dans deux domaines bioclimatiques aux couvertures forestières dominantes et régimes de perturbation différents : le domaine de la pessière à mousse (SPMO) et celui de la sapinière à bouleau blanc (BFWB). En appliquant l'approche de rareté de Rabinowitz, les espèces ont été classées selon leur distribution géographique, leur spécificité d'habitat et leur abondance locale. Il a été constaté que la majorité des espèces étaient rares, caractérisées par de petites populations et spécialisées dans des habitats tels que les forêts de conifères et les tourbières. Un gradient richesse-rareté a révélé une plus grande richesse et concentration d'espèces rares dans le SPMO, où plusieurs espèces communes se sont avérées rares dans le BFWB. Ce schéma est lié à des traits fonctionnels tels que la taille des spores et la stratégie sexuelle dioïque, indiquant une capacité de dispersion plus faible. Ces résultats soulignent le rôle crucial des forêts matures de conifères dans la conservation des bryophytes et l'importance des traits biologiques et des contextes régionaux dans la structuration des patrons de rareté.

Parallèlement, l'effet de la structure du paysage sur la diversité génétique de la mousse *Dicranum flagellare* Hedw., une espèce à reproduction majoritairement asexuée et à dispersion limitée, typique des forêts matures, a été analysé. À l'aide de données génomiques (SNPs) issues de 191 tiges collectées dans 12 fragments de forêt mature, il a été démontré que la configuration du paysage — notamment l’agrégation des zones non forestières — a un impact plus marqué que la composition sur la diversité et la structure génétique de l’espèce, avec des effets détectables jusqu’à 8 km. De façon inattendue, les paysages présentant une fragmentation modérée des vieilles forêts ont favorisé le flux génétique, homogénéisant la structure génétique entre les populations. De plus, les forêts d’âge intermédiaire et les zones non forestières adjacentes aux vieilles forêts ont contribué à accroître à la fois la diversité génétique et la différenciation entre populations. Ces résultats soulignent que la connectivité fonctionnelle dans les paysages boréaux peut être maintenue non seulement par des fragments conservés, mais aussi par des habitats complémentaires. Des seuils spatiaux importants ont été identifiés, comme la nécessité de maintenir environ 3 km de vieille forêt autour des parcelles clés, qui devraient être intégrés dans les plans de conservation.

Dans l’ensemble, cette thèse démontre que la diversité taxonomique et génétique des bryophytes boréales répond de manière sensible à la structure du paysage, et ce, à des échelles plus larges que ce qui avait été reconnu auparavant. Les résultats mettent en évidence l’importance d’intégrer la configuration spatiale de l’habitat dans les stratégies de conservation, en tenant compte non seulement de la quantité d’habitat résiduel, mais aussi de sa disposition, de sa complémentarité et de sa qualité fonctionnelle. Ainsi, cette recherche offre des contributions concrètes à une planification territoriale qui concilie conservation de la biodiversité et gestion responsable du paysage dans un contexte de changement global.

Mots-clés : écologie du paysage, espèces communes, espèces rares, génétique du paysage, modèle en mosaïque, plantes non vasculaires, seuils de gestion forestière.

Keywords: common species; forest management thresholds; landscape ecology; landscape genetics; mosaic model; non-vascular plants; rare species

# ABSTRACT

Land cover types and their spatial arrangement are key factors shaping biological communities. Currently, the world's biomes are undergoing drastic transformations in the composition and configuration of their landscapes, directly affecting native biodiversity. This situation highlights the urgency of understanding how these changes influence species, particularly in regions that still retain vast natural areas but are increasingly subjected to pressure from productive activities.

This thesis addresses this issue by adopting a multi-scale landscape approach and a multidimensional perspective on biodiversity, with the aim of understanding how landscape structure influences species richness, community composition, and genetic diversity of boreal bryophytes in eastern Canada. Through the analysis of 92 landscapes with a 10 km radius, it was observed that the expansion of young forests in the surrounding environment reduces the richness of mosses and liverworts, with particularly strong effects when this cover exceeds 40%. It was also found that the aggregation of coniferous stands can negatively impact certain functional groups such as liverworts and sphagnum mosses. These results demonstrate that even in relatively undisturbed boreal landscapes, the quality of the landscape matrix exerts a significant influence on bryophyte diversity. As a conservation measure, it is proposed to avoid exceeding the critical threshold of 40% young forest cover and to reduce its spatial aggregation.

By exploring community composition, rarity patterns of 282 bryophyte species were characterized in two bioclimatic domains with different dominant forest covers and disturbance regimes: the spruce–moss domain (SPMO) and the balsam fir–white birch domain (BFWB). Using Rabinowitz's rarity framework, species were classified according to their geographic distribution, habitat specificity, and local abundance. It was found that most species were rare, characterized by small populations and specialization in habitats such as coniferous forests and peatlands. A richness–rarity gradient revealed greater richness and a higher concentration of rare species in the SPMO, where several common species were found to be rare in the BFWB. This pattern is associated with functional traits such as spore size and dioicous sexual strategy, indicating lower dispersal capacity. These findings highlight the crucial role of mature coniferous forests in bryophyte conservation and the importance of biological traits and regional contexts in structuring rarity patterns.

In parallel, the effect of landscape structure on the genetic diversity of the moss Dicranum flagellare Hedw., a species with predominantly asexual reproduction and limited dispersal typical of mature forests, was analyzed. Using genomic data (SNPs) from 191 stems collected in 12 mature forest fragments, it was shown that landscape configuration—particularly the aggregation of non-forested areas—has a stronger impact than composition on the species' genetic diversity and structure, with detectable effects up to 8 km. Unexpectedly, landscapes with moderate fragmentation of old-growth forests promoted gene flow, homogenizing genetic structure among populations. Additionally, intermediate-aged forests and non-forested areas adjacent to old-growth forests contributed to increasing both genetic diversity and differentiation among populations. These results emphasize that functional connectivity in boreal landscapes can be maintained not only through conserved fragments but also through complementary habitats. Important spatial thresholds were identified, such as the need to maintain approximately 3 km of old-growth forest around key patches, which should be incorporated into conservation planning.

Overall, this thesis demonstrates that the taxonomic and genetic diversity of boreal bryophytes responds sensitively to landscape structure, at broader scales than previously recognized. The results highlight the importance of integrating spatial habitat configuration into conservation strategies, considering not only the quantity of remaining habitat but also its arrangement, complementarity, and functional quality. This research thus provides concrete contributions to land-use planning that reconciles biodiversity conservation with responsible landscape management in a context of global change.

Keywords: common species; forest management thresholds; landscape ecology; landscape genetics; mosaic model; non-vascular plants; rare species

## TABLE DES MATIÈRES

2. RÉVÉLER LES PATRONS DE RARETÉ DES PLANTES À SPORES ET LES PROCESSUS QUI LES FAÇONNENT À TRAVERS DES PAYSAGES CONTRASTÉS

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# INTRODUCTION

**Contexte et enjeux écologiques contemporains**. Comprendre comment les espèces réagissent à l'échelle locale aux changements paysagers est une préoccupation centrale en écologie et une nécessité contemporaine pour améliorer la gestion des écosystèmes tout en conservant la biodiversité (Arroyo-Rodríguez et al., 2020; Fahrig, 2003a, 2017; Tscharntke et al., 2012). En raison des activités humaines au cours des 12 000 dernières années, au moins les trois quarts de la surface terrestre ont été modifiés (Ellis et al., 2021). Cette transformation historique, qui s'est accélérée récemment, a entraîné la réduction et la fragmentation des paysages naturels, ainsi que la conversion des biomes naturels en biomes anthropiques, ou anthromes (Ellis, 2013; Ellis et al., 2021). Parallèlement, les perturbations naturelles et leurs régimes ont façonné la structure des paysages restants (Harvey & Enright, 2022; Turner, 2010). Ainsi, l'interaction entre les perturbations anthropiques et naturelles a modifié l'hétérogénéité et les structures spatiales des paysages (Harvey & Enright, 2022), affectant à la fois leur composition (les types de couvert végétal) et leur configuration (la répartition spatiale de ces types de couvert).

La disponibilité, le type et la répartition spatiale des habitats au sein d'un paysage ont un impact direct sur l'écologie des espèces (With, 2019). Ces facteurs influencent des processus tels que la dispersion et les déplacements des organismes, affectant la répartition spatiale des populations et, par conséquent, leur flux génique et leur structure génétique. Puisque plusieurs espèces sont intégrées dans cette dynamique, le paysage façonne également la structure et la dynamique des communautés biologiques (With, 2019).

**Perte d'habitat et fragmentation: Perspectives actuelles et lacunes dans les connaissances.** Une façon d'évaluer l'impact des changements dans la composition ou la configuration du paysage consiste à étudier la perte et la fragmentation de l'habitat. La perte d'habitat correspond à une diminution de la quantité d'habitat dans un paysage, et il existe un large consensus quant à ses effets négatifs sur la biodiversité (Fahrig, 2003; Hanski, 2011; Watling et al., 2020). En revanche, la fragmentation est un concept plus complexe, ayant été défini de diverses manières, ce qui alimente un débat continu sur ses impacts. Initialement, elle a été décrite comme la division d’un habitat en plusieurs fragments, sans perte d’habitat (Curtis, 1956). Toutefois, avec le temps, le terme a été mal interprété et a acquis plusieurs significations, ce qui a contribué à une perception principalement négative de ses effets sur la biodiversité (Riva et al., 2024).

Au cours des dernières décennies, des efforts ont été faits pour rétablir le sens original de la fragmentation afin de mieux comprendre ses effets et promouvoir des paysages favorables à la conservation et à la gestion de la biodiversité (Arroyo-Rodríguez et al., 2020; Fahrig, 2003a). Pour distinguer les effets de la fragmentation de ceux liés à la perte d’habitat, Fahrig (2003) a proposé le terme *fragmentation per se* (ci-après *fragmentation*). Cette réinterprétation du concept a mené à la réévaluation de nombreuses conclusions antérieures. Plus tard, Fahrig (2017) a démontré que la fragmentation a en réalité des effets majoritairement positifs sur la biodiversité.

Malgré ces avancées, le débat persiste, soulignant la nécessité d’études qui analysent indépendamment les patrons de perte et de fragmentation (Fahrig et al., 2019; Fletcher et al., 2018). Cette nécessité est d’autant plus pressante lorsqu’on considère les implications de ces patrons pour la conservation et la gestion des ressources naturelles. Par exemple, pour identifier les structures spatiales maintenant une connectivité fonctionnelle entre populations, pour décider s’il est préférable de préserver plusieurs petits fragments forestiers ou une grande zone continue, ou pour orienter les stratégies de restauration fondées sur l’agencement spatial de l’habitat (Arroyo-Rodríguez et al., 2020; Fahrig, 2020; Riva et al., 2025).

Les études sur les effets de la perte et de la fragmentation de l’habitat ont porté sur une ou plusieurs espèces, principalement des vertébrés et des plantes vasculaires (Fahrig, 2017; Gonçalves-Souza et al., 2025). Toutefois, des aspects écologiques supplémentaires ont récemment été explorés, tels que le rôle de ces patrons dans le recrutement d’espèces spécialistes et généralistes (Arasa-Gisbert et al., 2021), leurs traits fonctionnels liés à la dispersion, la persistance et l’établissement (Arasa-Gisbert et al., 2022; Zambrano et al., 2019), ainsi que leur diversité génétique (Lino et al., 2019). Malgré ces progrès, la réponse des taxons moins charismatiques à la structure du paysage demeure incertaine aux différents niveaux de diversité, tels que la diversité communautaire et génétique. Ces taxons pourraient pourtant fournir des éléments clés pour répondre à des questions fondamentales et tester des hypothèses en écologie du paysage. Les bryophytes en sont un exemple clair.

**Les bryophytes et les forêts boréales**. Les bryophytes regroupent les mousses, les hépatiques et les anthocérotes, des plantes non vasculaires comptant environ 19 000 espèces, ce qui en fait le deuxième groupe végétal terrestre le plus diversifié après les angiospermes (Rousk & Villarreal A, 2024). Ces plantes se distinguent par leur petite taille, leur phase haploïde dominante et l'absence de tissus vasculaires spécialisés. Elles occupent des milieux terrestres variés et jouent des rôles écologiques majeurs (Fenton et al., 2024; Longton, 1988; Scott, 1982). Bien qu'on les retrouve dans divers écosystèmes, elles sont particulièrement abondantes et diversifiées dans les forêts tropicales et boréales. Dans ces dernières, elles dominent la flore, amplifiant leur importance écologique. Leurs fonctions incluent la régulation du cycle hydrologique, la fixation de l'azote et du carbone, et leur contribution aux flux d'énergie et aux réseaux trophiques, avec parfois des implications à l'échelle mondiale (Slate et al., 2024). De plus, leur sensibilité aux changements environnementaux en fait d'excellents bioindicateurs pour évaluer les impacts des perturbations humaines sur l'intégrité forestière (Frego, 2007). Ainsi, les bryophytes sont des organismes clés pour évaluer les transformations des paysages forestiers boréaux, soumis à des perturbations naturelles et anthropiques menaçant leur biodiversité et les services écosystémiques associés.

Les forêts boréales représentent le biome ayant le plus vaste territoire sauvage encore intact (Gauthier et al., 2015). Toutefois, bon nombre de ces territoires sont influencés par des perturbations telles que les feux et l'aménagement forestier (Hansen et al., 2013). Le Canada en offre un exemple marquant : des centaines d'hectares de paysages boréaux sont façonnés par les incendies, les épidémies d'insectes et les tempêtes. De plus, 35 % à 40 % de ces paysages sont vulnérables aux modifications anthropiques, car désignés pour la production forestière (Gauthier et al., 2015;

Shorohova et al., 2011). Puisque la conservation de la biodiversité et des services écosystémiques dans ces forêts, tout en soutenant les activités économiques essentielles à la société, est cruciale pour le bien-être du pays (Brandt et al. 2013), étudier les effets de la perte et de la fragmentation de l'habitat représente une stratégie pertinente pour identifier des mécanismes d'action à grande échelle conciliant ces deux impératifs.

**Objectifs de la thèse**. Dans cette thèse, je vise à analyser les effets de la composition et de la configuration du paysage, en définissant le paysage comme une entité physique délimitée spatialement et possédant des caractéristiques distinctes (Francis & Antrop, 2021). Plus précisément, j'examinerai les effets de la perte d'habitat, de son remplacement et de la fragmentation afin de comprendre comment la biodiversité des bryophytes boréaux répond à ces patrons à l'échelle du paysage. Pour ce faire, je traiterai diverses questions portant sur l'influence de la structure du paysage sur les bryophytes boréaux, en considérant deux niveaux de diversité biologique : la diversité communautaire et la diversité génétique.

1. Tout d'abord, afin de contribuer au débat actuel sur les effets de la fragmentation (Fahrig et al., 2019; Fletcher et al., 2018; Riva et al., 2025), j'analyserai comment les changements dans les patrons paysagers (à l'intérieur d'un rayon de 10 km) influencent la diversité et la structure des communautés de bryophytes boréales dans des fragments de forêts anciennes. En utilisant des variables explicites de composition (selon l'âge de la forêt et la végétation dominante) et de configuration (densité des fragments forestiers), je chercherai à :
    i) déterminer si la composition ou la configuration du paysage est le principal moteur de la diversité taxonomique des bryophytes à l'échelle des fragments,
    ii) évaluer si l'âge des habitats ou la composition en espèces arborées du paysage influence les patrons de diversité observés,
    iii) analyser si certains groupes de bryophytes (mousses, hépatiques ou *Sphagnum*) sont plus sensibles aux changements paysagers,

    iv) identifier si les patrons du paysage expliquent le remplacement d'espèces (turnover) à l'échelle des fragments

2. Ensuite, puisque l'interaction entre les espèces et les processus spatiaux influence leur abondance locale et leurs aires de répartition, façonnant leurs patrons de rareté (Crisfield et al., 2024), j'adopterai une approche métacommunautaire et la définition de la rareté de Rabinowitz (1981) pour analyser comment la composition du paysage peut agir comme un filtre en fonction des traits fonctionnels des espèces, influençant leurs patrons de rareté. En élargissant l'échelle paysagère du niveau local à celui du domaine bioclimatique, j'examinerai :
    i) si les métacommunautés de deux domaines bioclimatiques diffèrent en termes de composition spécifique et de rareté,
    ii) si elles sont similaires, si leurs patrons de rareté le sont également,
    iii) si des différences sont observées, si elles peuvent être expliquées par les régimes de perturbation et les statuts de conservation contrastés des domaines,
    iv) le rôle des traits fonctionnels dans ces différences.
3. Enfin, bien qu'il soit bien établi que la répartition des habitats dans le paysage influence la variation génétique et la structure des populations (Jackson & Fahrig, 2016; Keyghobadi, 2007), on sait peu de choses sur la manière dont la quantité et la configuration de l'habitat contribuent à la divergence génétique (Jackson & Fahrig, 2016). Pour combler cette lacune, je reviendrai à l'échelle du paysage de 10 km et me concentrerai sur la mousse *Dicranum flagellare*, une espèce associée aux forêts anciennes qui pourrait être affectée par la perte d'habitat à cette échelle. Dans ce chapitre, j'évaluerai :
    i) si une réduction de la superficie de forêts anciennes dans le paysage entraîne une diminution de la diversité génétique de *D. flagellare* à l'échelle des fragments,
    ii) si la fragmentation de l'habitat a un effet négatif sur la diversité génétique, comme on le suppose généralement,

iii) si l'hétérogénéité du paysage, incluant la présence de forêts plus jeunes, peut contribuer positivement à la conservation de la diversité et de la structure génétique de cette mousse boréale.

Par cette thèse, je souhaite éclairer les effets de la perte et de la fragmentation des forêts boréales sur l'un de leurs groupes botaniques les plus représentatifs, dans le but de fournir des pistes concrètes aux décideurs pour la planification de la gestion des paysages au Canada.

# 1. DIVERSITÉ DES BRYOPHYTES BORÉALES À L'ÉCHELLE DE LA PARCELLE INFLUENCÉE PAR L'HÉTÉROGÉNÉITÉ DU PAYSAGE

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**Résumé**

Bien que l'influence des paysages boréaux sur les plantes ait été étudiée dans les paysages fortement modifiés d'Europe, nous manquons de connaissances sur la façon dont les paysages relativement intacts d'Amérique du Nord influencent les communautés locales de bryophytes. En adoptant une approche « patch-paysage », nous avons évalué les effets de la composition du paysage (en tenant compte de l'âge et du type forestier des peuplements) et de sa configuration (densité de peuplements) sur la diversité des bryophytes (richesse, espèces communes et dominantes) dans des peuplements cibles de vieilles forêts. Les effets de la composition et de la configuration du paysage (dans 92 paysages d'un rayon de 10 km) ont été évalués à la fois pour l'ensemble des bryophytes et selon les guildes (mousses, hépatiques et Sphagnum). La richesse des mousses était négativement corrélée à l'expansion des jeunes forêts dans le paysage. De plus, la richesse des hépatiques, ainsi que celle de leurs espèces communes, diminuait de manière significative lorsque les jeunes forêts occupaient plus de 40 % du paysage. L'effet de la proportion de forêts mélangées variait selon les guildes, mais la diversité des hépatiques et des Sphagnum était négativement associée à une densité accrue de peuplements résineux. Même dans les forêts boréales nord-américaines relativement peu perturbées, les jeunes forêts ont un impact significatif sur la diversité des vieux peuplements. Afin de conserver la diversité des bryophytes dans les vieux peuplements forestiers situés en régions aménagées, nous suggérons que la proportion de jeunes forêts ne dépasse pas 40 % du paysage environnant, et que leur agrégation soit évitée. Les seuils de perte d'espèces détectés ici peuvent être utilisés dans la planification du territoire pour atténuer les effets négatifs des changements d'usage des terres sur la biodiversité boréale.

Mots clés : Composition du paysage, configuration du paysage, hypothèse de la quantité d'habitat, modèle en mosaïque, perte d'habitat, qualité de la matrice

## Abstract

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

Keywords: Habitat amount hypothesis, habitat loss, landscape composition, landscape configuration. matrix quality, mosaic model

## *1.1 Introduction*

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

North American boreal forests face increasing land transformation by natural (e.g., wildfires, insect outbreaks) and anthropogenic disturbances (e.g., harvesting, urban development) (Bradshaw et al., 2009; Erb et al., 2018), which are exacerbated by climate change (Macias Fauria & Johnson, 2008). These disturbances put at risk one of the planet's largest and most important carbon sinks and its biodiversity (Bradshaw et al., 2009; Olson et al., 2001; Velasco Hererra et al., 2022). Also, natural and anthropogenic disturbances have combined effects that impact ecological processes related to biogeochemical cycles and the structure of the forest community (Artaxo et al., 2022; Shao et al., 2023). In addition, climate change-mediated landscape fragmentation is predicted to reduce suitable niches and lead to the extinction of characteristic trees, birds, and mammals of the North American boreal forests (Murray et al., 2017). Despite these advances, little is known about the response of various plants and animals in these forests to landscape-level changes (Brandt et al., 2013; Venier et al., 2014), particularly of the understory species that are the main diversity driver in these environments (Hart & Chen, 2006). A clear example of one of these least understood groups of the understory concerning landscape effects is the bryophytes.

Bryophytes (here, mosses, liverworts, and sphagna guilds) are a conspicuous group in boreal forests due to their diversity and biomass (Longton, 1992). Their dominance makes them the primary plants driving ecosystem functions such as primary productivity, water relations, carbon and nitrogen cycles, and as habitat for small invertebrates and a wide diversity of microorganisms (DeLuca et al., 2002; Turetsky et al., 2010; Williams & Rastetter, 2001). In old boreal forests, bryophyte diversity is characterized primarily by the presence of specialist species that are susceptible to off-site disturbances (Barbé et al., 2017). Bryophytes in general, but particularly liverworts, are sensitive to environmental changes because they depend on specific microhabitats conditions (humidity and substrate) (Cole et al., 2008; Frego, 2007). These microhabitat conditions are related to the local habitat characteristics, such as the type of vegetation cover and the patch size (Barbé et al., 2017; Gignac & Dale, 2005). Thus, bryophytes can be influenced by landscape disturbances that modify and fragment their habitat. In addition, these changes may affect the maintenance of their populations in the long term, since some species are dispersal limited and might not be able to reach the next suitable habitat after disturbance (Lönnell & Hylander, 2018; B. Yin et al., 2019).

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

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

## *1.2 Materials and methods*

### 1.2.1 Study area

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

### 1.2.2 Study design

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

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

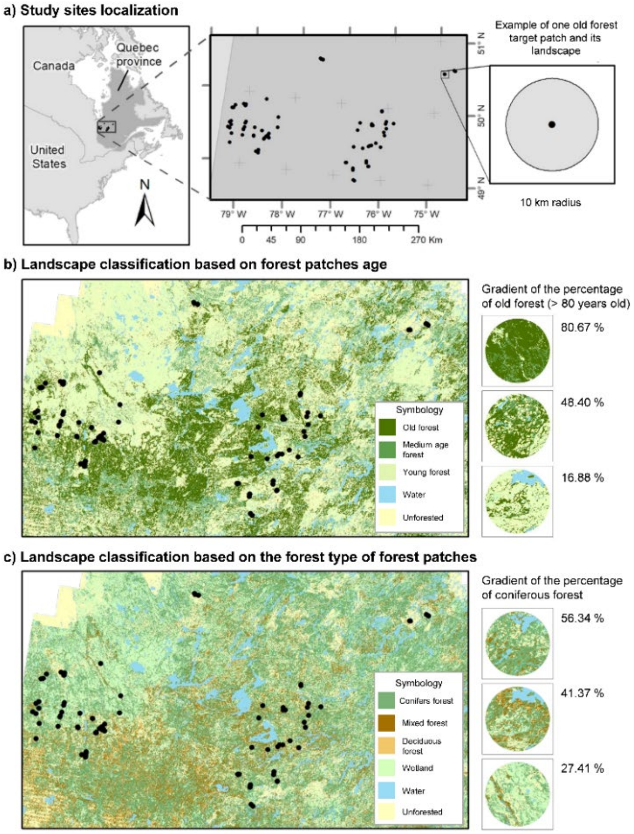

**Figure 1**
**a) Study area in Western Quebec, Canada, showing 92 old forest target patches (black dots) around which, we circumscribe landscapes with a 10 km radius. The landscapes can be classified based on the b) age and c) forest type of their forest patches, which show a gradient in the percentage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

### 1.2.3 Bryophyte taxonomic diversity

First, we used the number of occurrences per target patch as an abundance measure for our analyses. In the case of patches with two or three plots, we combined the data per patch to avoid pseudoreplication (Arasa-Gisbert et al., 2021). We then evaluated the bryophyte sampling completeness of each target patch using the sample coverage estimator where values close to one means complete data (Chao & Jost, 2012). Thus, we ensured that our target patches had equally complete species communities, representing all the species in the patch, and avoided the risk of assuming landscape influence based on communities with incomplete sampling. Two of 92 target patches had sample coverage values below 0.70, and we removed these two patches from the subsequent analyses. Also, because our bryophyte sample coverage varied among patches from 0.77 to 0.99, we estimated species diversity using observed and expected data based on the extrapolation approach to ensure target patches were equivalent in sampling effort for the analyses (Chao & Jost, 2012).

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

### 1.2.4 Spatial data and landscape metrics

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

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

### 1.2.5 Statistical analyses

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

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

### *1.3 Results*

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

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

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

**Tableau 1**
**Generalized additive models assessing the landscape composition and configuration effects based on the a) age and b) forest type using expected bryophyte diversity (q0=richness, q1=number of common species). Edf = estimated degrees of freedom for each model parameter. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.**

a) Age landscape classification

| Response variables | Explanatory variable | edf | p-value |
|---|---|---|---|
| Mosses *q0* | Percentage of young forest area | 1 | 0.04 * |
| | Percentage of medium age forest area | 4.28 | <0.00 ** |
| | Percentage old forest area | 1 | 0.06 (.) |
| | Density of young forest patches | 1 | 0.36 |
| Liverworts *q0* | Percentage of young forest area | 5.05 | 0.01 ** |
| | Percentage of young forest area (threshold) | 3.37 | 0.03* |
| | Percentage of medium age forest area | 2.93 | 0.31 |
| | Percentage old forest area | 1 | 0.08 |
| | Density of young forest patches | 2.65 | 0.05 * |
| Liverworts *q1* | Percentage of young forest area | 5.86 | 0.01 ** |
| | Percentage of young forest area (threshold) | 3.28 | 0.03* |
| | Percentage of medium age forest area | 1 | 0.64 |
| | Percentage old forest area | 2.75 | 0.17 |
| | Density of young forest patches | 3.86 | <0.00 *** |
| Sphagna *q0* | Percentage of young forest area | 1 | 0.68 |
| | Percentage of medium age forest area | 3.924 | 0.13 |
| | Percentage old forest area | 1 | 0.47 |
| | Density of young forest patches | 1 | 0.87 |

**Tableau 1**
**(continued) Generalized additive models assessing the landscape composition and configuration effects based on the a) age and b) forest type using expected bryophyte diversity (q0=richness, q1=number of common species). Edf = estimated degrees of freedom for each model parameter. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.**

| b) Forest type landscape classification | | | |
|---|---|---|---|
| Response variables | Explanatory variable | edf | p-value |
| Mosses *q0* | Percentage of conifers area | 2.61 | 0.05 (.) |
| | Density of conifer forest patches | 2.79 | 0.18 |
| | Percentage of mixed forest area | 1 | 0.06 (.) |
| | Percentage of deciduous forest area | 1 | 0.43 |
| | Target patch size | 1.97 | 0.00 *** |
| Liverworts *q0* | Percentage of conifers area | 1.83 | 0.09 (.) |
| | Density of conifer forest patches | 1 | <0.00 ** |
| | Percentage of mixed forest area | 1 | 0.28 |
| | Percentage of deciduous forest area | 3.06 | 0.07 (.) |
| | Target patch size | 1 | 0.07 (.) |
| Liverworts *q1* | Percentage of conifers area | 1.94 | 0.07 (.) |
| | Density of conifer forest patches | 2.07 | <0.00 *** |
| | Percentage of mixed forest area | 1 | 0.02 * |
| | Percentage of deciduous forest area | 1.94 | 0.05 (.) |
| | Target patch size | 1.15 | 0.52 |
| Sphagna *q0* | Percentage of conifers area | 1.83 | 0.09 (.) |
| | Density of conifer forest patches | 1 | <0.00 ** |
| | Percentage of mixed forest area | 1 | 0.28 |
| | Percentage of deciduous forest area | 3.06 | 0.07 (.) |
| | Target patch size | 1 | 0.07 (.) |

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

Landscape variables explaining bryophyte diversity also influenced community composition. The percent cover of medium age forest in the landscape is the most significant contributing variable to bryophyte community composition in general (r2 = 0.10, $p < 0.01$), followed by the coniferous patch density (r2=0.18, $p < 0.01$) (Figure 4A). This pattern is the same when the community of bryophytes is analyzed by guild (Figure 4, Table 2). The liverwort community composition, unlike mosses and sphagna, was more influenced by the amount of young forest in the surrounding landscape than the medium age forest percent cover. Community composition changes were consistent with the results of liverwort diversity (q0 and q1) in the GAMs. For example, we observed that changes in liverwort community composition were associated with an increase in species richness as the percent cover of young forest and conifer patch density decreased in the landscape (Figure 4D). Thus, we observed that the changes in community composition are related to a gradient in bryophyte species richness influenced by LCC (Figure 4). For sphagna, only the density of conifer forest patches was significant negative.

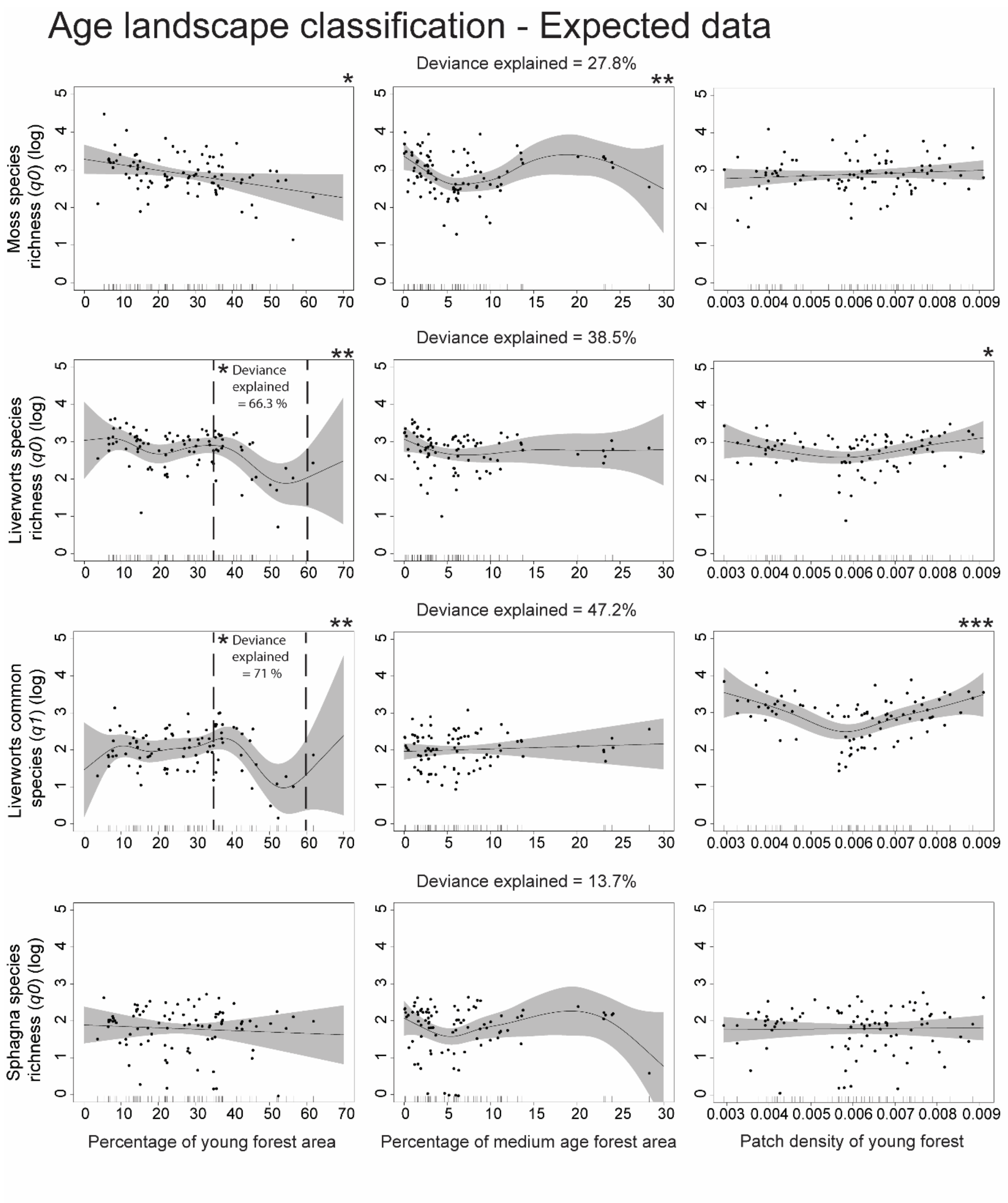

**Figure 2**

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

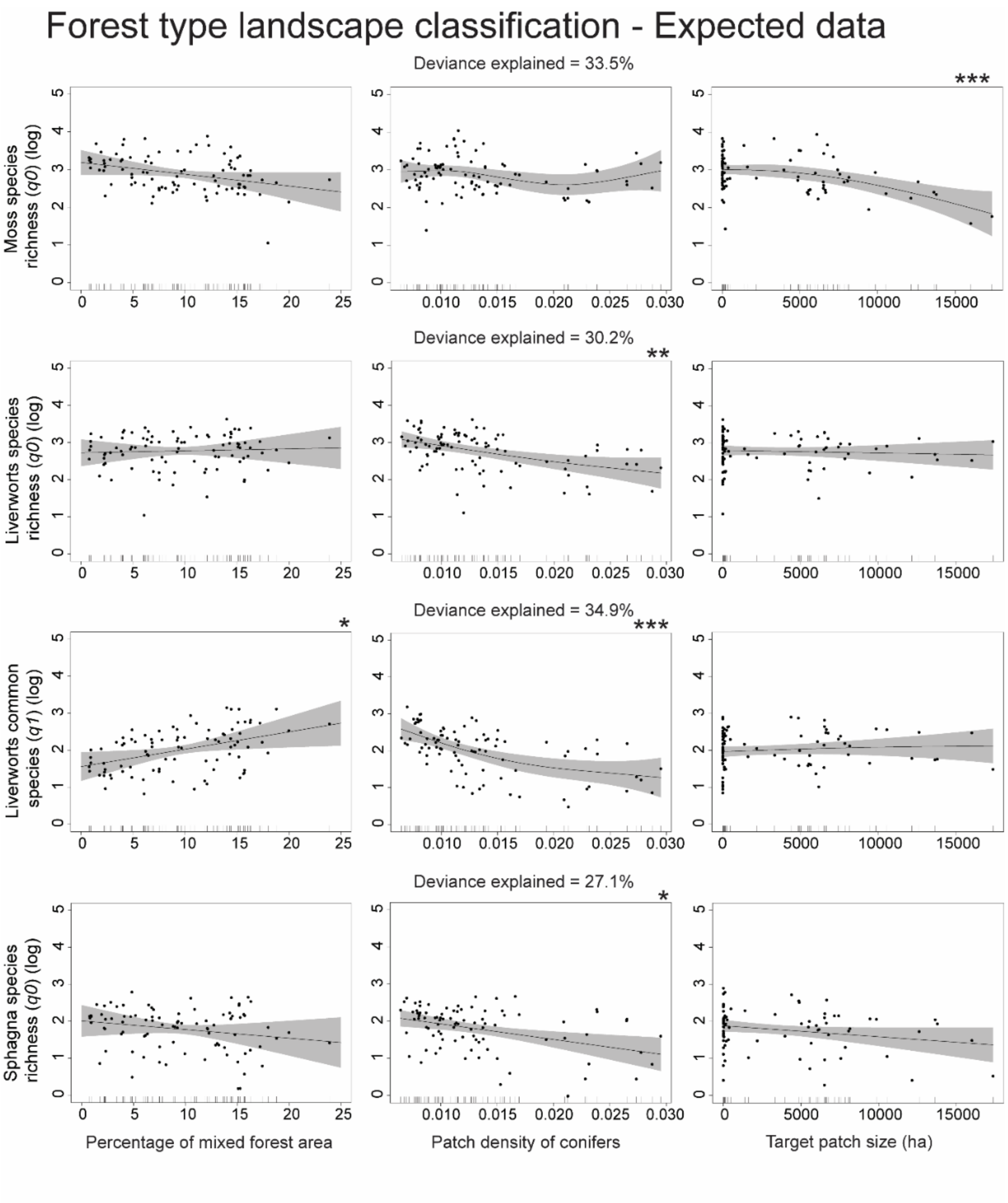

**Figure 3**
**Effect of the composition and configuration of the landscape classified according to the forest type of its patches for mosses (q0), liverworts (q0 and q1), and sphagna (q0) based on expected data. Asterisk on chart tops indicates the significance level of the variable: *** = p <0.0001, ** = p <0.001, * = p <0.05.**

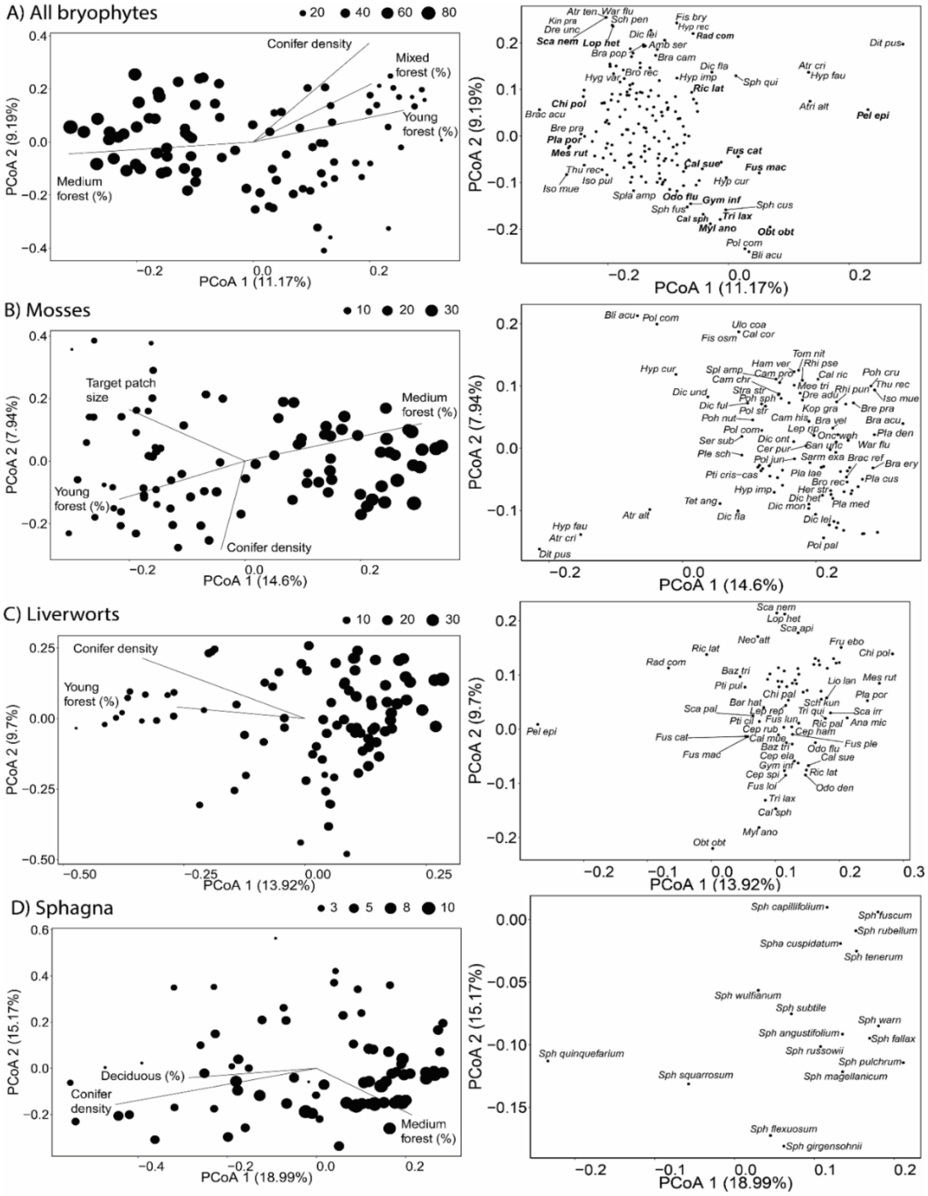

**Figure 4**

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

**Tableau 2**
**Generalized additive models assessing the landscape composition and configuration effects based on the a) age and b) forest type using expected bryophyte diversity (q0=richness, q1=number of common species). Edf = estimated degrees of freedom for each model parameter. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.**

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

## *1.4 Discussion*

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

### 1.4.1 Landscape context explains bryophyte diversity at the local scale

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

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

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

With respect to the young forest effect, Barbé et al. (2017) found that patches of residual old forest left over from wildfires have higher richness than continuous old forest. However, because young forests harbor different species than those found in old forests, their dispersal into old forest patches affects the species composition of the latter. Furthermore, the authors also found that the community composition of the remnant patches was characterized by specialist species loss and the inclusion of disturbance-adapted species. Consequently, it is important to consider that although young forest can act as a source of propagules for old forest patches, the excessive increase in the area of the former can cause the loss of specialist species in the old forest patches due to source-sink dynamics (Holt, 1985; Pulliam, 1988). If the old forest patches are immersed in landscapes dominated by young forests, the former will not have an incoming flow of propagules of their characteristic species to allow them to maintain their richness and community structure. Other studies have also found that the surrounding matrix influences the loss of local vascular plants species (e.g., Metzger, 2000, Williams et al., 2006). Thus, our study contributes to demonstrate the influence of non-dominante land cover on the local diversity of non-vascular plants.

Our results support the idea that habitat loss is the main driver of species loss (Fahrig, 2003a, 2017). We also note that fragmentation, measured here as patch density, affects bryophyte diversity and community structure. In addition to the amount of young forest in the landscape, we observed that the density of its patches affects liverwort diversity (q0 and q1). Furthermore, we found that the number of species fluctuates depending on the distance between the patches of young forest.

Specifically, we found that liverwort diversity decreases when young forest patches become closer together but increases when the young forest patches start to form defined group patches in the landscape. This represents a process of species loss and gain (Socolar et al., 2016), affecting the structure of the liverwort community. These findings support the beta diversity dominance hypothesis, which posits that local-scale species loss can be offset by an increase in beta diversity in the landscape. This, in turn, helps to maintain original values of gamma diversity in the landscape (Arroyo-Rodríguez et al., 2019; Socolar et al., 2016; Tscharntke et al., 2012). According to Arroyo-Rodríguez et al. (2019), these effects are typical of landscapes with low or moderate disturbances. Although the effects result in local species loss, their impact on beta diversity promotes the maintenance of landscape diversity.

Changes in the liverwort community can also be attributed to forest composition. An increase in mixed forest percentage results in an increase in common liverwort species (q1). This change may be the result of increased dispersal pressure in target old forests by common generalist species associated with mixed forests (Hernandez-Rodriguez et al. submitted). Factors such as natural and anthropogenic disturbances decrease the presence of conifers and promote the emergence of deciduous species (Marchais et al., 2020), potentially resulting in altered composition of boreal bryophyte species over time. Our study is limited to landscapes with approximately 20% mixed forest coverage. Further research on landscapes dominated by this forest type can offer a more comprehensive understanding of its role as a source of species for other vegetation types.

Landscape classification based on forest types also enables detection of the impact of other LCC attributes. We found that larger target patches (>5000 ha) tend to have fewer moss species than smaller patches. This may be due to the dispersal of species from the matrix of young forest or mixed forest, which increases their distribution and probability of colonizing old forest small patches (Nordén & Larsson, 2000). In contrast, larger patches that maintain structural connectivity (connectedness, Baudry and Merriam 1988) may possess characteristic old forest species due to more extensive homogeneous conditions (Löbel et al., 2018a). These results are related to the decrease in the diversity of liverworts (q0 and q1) and sphagna (q0) when the density of coniferous patches increases. This may be because an increase in coniferous patch density could maintain the structural connectivity of the old forest through patch connectivity, thus allowing for species persistence (Baudry & Merriam, 1988; Tischendorf & Fahrig, 2000b, 2000a). Therefore, when conifer density is lower, species from other forest types, such as mixed forests, can colonize the target patches.

### 1.4.2 Species driven by landscape composition and configuration

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

### 1.4.3 Considerations for forest management and future studies

Although our study demonstrates the impact of LCC on bryophyte diversity in old forest patches, we did not rule out the influence of local factors on their diversity. (Martin et al., 2018) found that old forests can be differentiated based on their structural diversity defined by the influence of environmental and temporal factors (such as slope, time since the last fire, and depth of the organic horizon) on variables such as tree density and the basal area of the site. The effect of temporal factors is reinforced by works such as that of Fenton and Bergeron (2013), which also demonstrate that the severity of fires, as founder effects of the habitat, influences the current composition of bryophytes in old forests.

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

### *1.5 Conclusions*

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

### 1.6 Funding

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### 1.8 Supporting information (Appendix A)

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

# 2. RÉVÉLER LES PATRONS DE RARETÉ DES PLANTES À SPORES ET LES PROCESSUS QUI LES FAÇONNENT À TRAVERS DES PAYSAGES CONTRASTÉS

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*Revealing rarity patterns of spore producing plants and the processes driving them across contrasting landscapes*

**Résumé**

Identifier les mécanismes écologiques qui contribuent à la rareté ou à la commonalité des espèces est essentiel pour comprendre leur répartition régionale et assurer leur conservation. Les bryophytes dominent les domaines bioclimatiques boréaux, mais leurs schémas de rareté et les processus qui les sous-tendent sont encore peu explorés. Nous avons étudié la répartition de 282 espèces de bryophytes (à partir d'environ 60 000 enregistrements) dans deux domaines bioclimatiques (épinette-mousse et sapin-bouleau) de l'est du Canada, caractérisés par des régimes de perturbation différents. Nos objectifs étaient : 1) classifier les schémas de rareté des espèces (selon Rabinowitz), 2) identifier les variations de ces schémas entre les domaines, et 3) déterminer comment les traits fonctionnels liés à la dispersion et au cycle de vie, en synergie avec les régimes de perturbation bioclimatiques, influencent ces schémas. Nous avons constaté que la plupart des espèces de bryophytes sont rares ; le groupe dominant était constitué de spécialistes à populations clairsemées, associés aux forêts de conifères et aux tourbières. Un gradient richesse-rareté a été observé, avec une plus grande richesse spécifique et le plus grand nombre d'espèces rares dans le domaine épinette-mousse. De nombreuses espèces communes dans l'épinette-mousse étaient rares dans le sapin-bouleau. Les grandes spores et une stratégie sexuelle dioïque étaient associées aux espèces rares, suggérant un potentiel de dispersion plus faible. Nous soulignons l'importance des forêts de conifères dans l'épinette-mousse pour la conservation de la diversité des bryophytes et confirmons que les traits fonctionnels des espèces et les régimes régionaux de perturbation sont des facteurs clés façonnant leurs schémas de rareté.

Mots clés : connectivité paysagère, cryptogames, dynamique des métapopulations, espèces communes, plantes non vasculaires, traits fonctionnels.

## Abstract

Identifying the ecological mechanisms contributing to species rarity or commonness are crucial for understanding their regional distributions and ensuring their conservation. Bryophytes are dominant plants in boreal bioclimatic domains, but their rarity patterns and the processes driving them are poorly explored. We studied the distribution patterns of 282 bryophyte species (from ~60k records) in two bioclimatic domains (spruce-moss and fir-birch) in Eastern Canada with different disturbance regimes. Our aim was to 1) classify species rarity patterns (based Rabinowitz), 2) identify variations in rarity patterns among domains, and 3) determine how dispersal and life-history functional traits, in synergy with bioclimatic disturbance regimes, drive rarity patterns. We found that most bryophyte species are rare, the dominant group were sparse population specialists associated with coniferous forests and peat bogs. A richness-rarity gradient was observed, with greater richness and the highest number of rare species in the spruce-moss. Many common species in the spruce-moss were rare in the fir-birch. Large spores and a dioicous sexual strategy were associated with rare species, suggesting lower dispersal potential. We highlight the importance of coniferous forests in spruce-moss for conserving bryophyte diversity and confirm that species' functional traits and regional disturbance regimes are key drivers shaping their rarity patterns.

Keywords: common species, cryptogams, functional traits, landscape connectivity, metapopulation dynamics, non-vascular plants.

## *2.1 Introduction*

Amid the current biodiversity crisis, landscapes are increasingly shaped by natural and anthropogenic disturbances. These disturbances alter habitat availability and spatial arrangement, driving local biodiversity patterns at the landscape scale (Fahrig, 2017; Martin et al., 2019). Consequently, landscapes differing in functional connectivity, habitat dominance, or heterogeneity can support different community compositions under similar patch conditions (Alves et al., 2020; Arasa-Gisbert et al., 2022). Species' interaction with spatial processes affects their abundance and range, shaping their patterns of rarity and commonness (Crisfield et al., 2024). However, linking disturbances to rarity patterns at the metacommunity scale remains difficult due to multiscale complexity, and challenges in analyzing large-scale, spatially explicit biodiversity data.

Rarity lacks a precise definition, but it generally refers to species with limited distribution, low abundance, or both (Crisfield et al., 2024; Kunin & Gaston, 1993, 1996). Rabinowitz (1981) proposed that a combination of these attributes, along with the type of habitat where the species occurs, can lead to a species being common or exhibiting various forms of rarity (hereafter rarity patterns). Thus, rarity patterns can increase species' vulnerability to extinction, especially under pressures like climate change and human activity (Foden et al., 2019; Jablonski, 1986). Common species, although widespread and abundant, are also at risk due to overexploitation and habitat alteration, which can shift them to rarity (Jansen et al., 2020; Lindenmayer et al., 2011). Therefore, understanding the drivers of rarity patterns in metacommunities is urgent to support conservation under accelerating habitat loss (Gaston, 2010; Mateo-Tomás et al., 2017).

Studying functional traits is a key approach to understanding and predicting how species and communities respond to their environment (Funk et al., 2017), including how they respond to disturbances and how rarity patterns emerge across different spatiotemporal scales (Cleavitt, 2005; Crisfield et al., 2024). Yet, for many small, non-charismatic organisms, rarity patterns and the traits driving them remain unknown, limiting our ability to detect changes and prioritize overlooked endangered species

(Coe et al., 2024; Deane-Coe & Stanton, 2017). In bryophytes, traits related to life history and dispersal predict metacommunity assembly (Frahm, 2008; A. M. Sierra et al., 2019) but their link to rarity patterns has not been studied at this scale.

Bryophytes (mosses, liverworts, and hornworts) occupy diverse ecosystems worldwide (Fenton et al., 2015; Longton, 1988; Scott, 1982), and are especially dominant in boreal forests (Möls et al., 2013; Turetsky et al., 2012). There, they play key ecological roles, regulating water, carbon, and nitrogen cycles, moderating soil conditions and providing habitat for microorganisms (Slate et al., 2024). While a few species (e.g., feather mosses, sphagna) dominate, rare species drive overall richness (Fenton & Bergeron, 2013; Frisvoll, 1997). Bryophyte metacommunity structure is influenced by climatic gradients represented by boreal bioclimatic domains (Barbé et al. 2020), zones defined by distinct vegetation, climate, topography and disturbance regimes (Barbé et al., 2020; Gagnon, 2004; Grondin et al., 2014). The vegetation, climate, and disturbance dynamics produce differences in landscape composition and configuration, and, thus in bryophyte metacommunity structure. However, how rarity patterns of bryophyte metacommunities are influenced by landscapes and contrasting disturbance regimes has not been investigated.

The spruce-moss and balsam fir-white birch (fir-birch hereafter) bioclimatic domains in eastern Canada differ markedly in dominant vegetation, climatic conditions, and disturbance regimes. Spruce-moss also retains larger areas of natural forest compared to fir-birch (Duchesne & Ouimet, 2009), making these domains ideal for exploring bryophyte rarity patterns at the metacommunity scale. Using 60,000 systematically collected records covering 310, 000 km2, we integrate dispersal-linked functional traits and apply a novel computational tool developed in R software that operationalizes Rabinowitz's (1981) rarity framework, to test the following hypotheses:

Given the demonstrated influence of climate and landscape patterns on bryophyte community composition and the divergent disturbance regimes as contingencies shaping landscapes and rarity process across bioclimatic domains (Barbé et al., 2020; Crisfield et al., 2024), we hypothesize that (H1) bryophyte metacommunities will differ in species composition and rarity patterns between domains. Furthermore, since rarity is influenced by environmental contingencies (Crisfield et al., 2024), we propose that (H2) even when metacommunity compositions are similar, shared species will exhibit different rarity patterns across domains. In addition, because forest spatial arrangement and composition in bioclimatic domains reflect distinct disturbance regimes (Bergeron et al., 2004a), and rare habitat specialist are associated with old-growth forests (Barbé et al., 2017), we hypothesize (H3) that rare species will be more strongly associated with the domain characterized by longer fire return intervals. Finally, given that bryophyte metacommunity composition is shaped by functional traits related to dispersal and life history (Frahm, 2008; Sierra et al., 2019), we expect (H4) traits such as sexual condition, asexual reproduction, and spore size dictate changes in rarity patterns across bioclimatic domains.

## *2.2 Methods*

### 2.2.1 Contrasting bioclimatic domains

Our study area spans the transition between the spruce-moss and fir-birch bioclimatic domains in Eastern Canada (Supplementary material Figure B1). Each domain is defined by dominant tree species and forest stand types with similar tree density and floristic composition, shaped by homogeneous climate and disturbance regimes (Saucier & Meidinger, 2010). The spruce-moss is characterized by coniferous stands with black spruce (*Picea mariana*), white spruce (*P. glauca*), and balsam fir (*Abies balsamea*) (Messaoud et al., 2007). Mixedwood and deciduous stands also occur, with hardwoods like white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). In contrast, the fir-birch, is dominated by mixedwood stands with balsam fir, white birch, and white spruce stands (Bérard & Côté, 1996). Both domains also include open ecosystems such as peatlands and recently harvested or burned forest areas.

Although similar in seasonal rainfall (419.06 vs 396.93 mm) and wind speed (10.37 vs 10.46 m/s), spruce-moss and fir-birch differ in mean annual temperature (-2.5-0°C vs. 0-1°C), mean annual precipitation (700-1000 mm vs. 800-1200 mm), proportion of snowfall (25-50% vs. 40-45%), and relative humidity (59.04 vs 56.5 %) (Bergeron et al., 2004a; Messaoud et al., 2007). These differences lead to contrasting wildfire regimes.

Fire is the main natural disturbance in boreal forests (Bergeron et al. 2001, 2004) with spruce-moss shaped by large fires and fir-birch by frequent small ones (mean fire size 17,660 ha vs 969 ha, respectively; Belleau et al. (2007)). Smaller, less intense fires in the fir-birch have favored fire-sensitive species typical of mixedwood forests, such as balsam fir and eastern white cedar (*Thuja occidentalis*) (Bergeron et al., 2004a). Other disturbances include severe spruce budworm outbreaks in fir-birch due to the high abundance of its host, balsam fir (Bergeron, 2000; Bergeron & Leduc, 1998; MacLean, 1980). Succession also differs: In spruce-moss, succession is influenced by shifts in forest structure and understory bryophyte composition, whereas in fir-birch, it involves shifts in tree dominance from broadleaf to conifers (Bergeron & Fenton, 2012). Over the last 50 years, both domains have also been affected by industrial logging.

### 2.2.2 Bryophyte dataset

We used 966 sampling sites (50m2 plots) distributed across eastern Canada: 575 in the spruce-moss and 391 in the fir-birch, representing 48,300 m2 sampled. Of these, 421 sites were from previous studies (Barbé et al., 2017, 2020; Castonguay, 2016), and 545 were established during fieldwork between 2017-2019 (Supplementary material, Figure B1). All sites were established within well-defined coniferous, mixed, or deciduous forests stands, classified by dominant tree species at a minimum scale of 0.5 ha (Gouvernement du Québec, 2020). Sites also included open ecosystems, primarily peatlands and areas with trees of low DBH (< 10 cm) (Yin et al., 2022). Site distribution by bioclimatic domain and forest type is detailed in the Supplementary material (Table A1).

Bryophyte were sampled from all available microhabitats within sites, ground, logs, trees, snags, stumps, and rocks, while avoiding forest edge effects (Newmaster et al., 2005). Specimens from each microhabitat were stored in paper bags with site information. Species occurrences were recorded per site, and identification to species level was conducted at the Laboratoire de Bryologie, Université du Quebec en Abitibi-Témiscamingue.

To explain bryophyte rarity patterns, we constructed a database of species' functional traits from literature (Supplementary material Methods 1) including: 1) sexual condition (dioicous/monoicous), 2) asexual reproduction presence (gemmae, branchlets, deciduous leaves or tubers or none), and 3) spore size (< 25 um = small, > 25 um = large (Söderström & During, 2005)). Sexual condition and asexual reproduction were considered life-history traits, while spore size as dispersal trait (Crisfield et al., 2024).

### 2.2.3 Data analysis

*Sample coverage and species diversity*. To accurately understand rarity patterns, inventories must integrate both richness and species abundance to avoid underestimating common species and overestimating rare ones. We evaluated inventory completeness using sample coverage analysis, which estimates the proportion of species represented in the sample (Hsieh et al., 2016). This method standardizes samples by completeness rather than size, enabling accurate comparisons of species richness across different sample sizes (Chiu, 2023).

To ensure adequate representation of richness and abundance, we performed sample coverage analysis for key taxonomic diversity dimensions (species richness, and frequent and dominant species, i.e., Hill's numbers) across forest types (coniferous, deciduous, mixedwood forest, and open ecosystems) nested within each bioclimatic domain and bryophyte lineage (mosses, liverworts, sphagnum). Sphagnum was treated separately due to of its specialized morphological and physiological adaptations that promote peat accumulation, and its diversity is influenced by environmental factors different from the rest of the boreal forest bryophytes (Cerrejón et al., 2020; van de Koot et al., 2021). We performed sample coverage and diversity analyses using the iNEXT package (Hsieh et al., 2016) in R software 4.1.2 (R Development Core Team, 2021). High sample coverage values (mean SC = 0.97 out of 1.0; Supplementary material Table 2) indicated low to negligible probability of missing species from any bryophyte lineages in any forest type, supporting robust inferences about species rarity patterns.

*Rarity analysis*. We assessed bryophyte rarity using the Rare7 R package (Maciel & Arlé, 2020), based on Rabinowitz's (1981) classification. This framework addresses the continuous and complex nature of rarity, while allowing for the addition of explanatory ecological power to elucidate the causes of rarity (Cerrejón et al., 2021; Crisfield et al., 2024). The analysis combines three parameters, namely geographical range, population size, and habitat specificity across spatial scales, to classify species as common or as one of seven rarity patterns (Maciel & Arlé, 2020). The Rabinowitz classification is based on three axes: population size, habitat specificity, and geographic range size. Each of these axes are dichotomised, forming eight different combinations (Table 3.3). Seven of these combinations represent different types of rarity (Patterns 1-7; Table 3.3), whereas the eighth group is considered common.

To determine whether a species had a restricted or wide geographic range, we calculated the total distribution of each species across latitudinal degree belts in our dataset. Species occurring in <10 % of the total latitudinal extent were considered geographically restricted (Broennimann et al., 2005; Saetersdal & Birks, 1997).

**Tableau 3**
**Seven patterns of rarity based on the geographic distribution range, habitat preference, and population size of the species (Modified from Rabinowitz 1981, Maciel and Arlé 2020).**

| Geographic distribution | Wide | | Restricted | |
|---|---|---|---|---|
| Habitat specificity | Generalist | Specialist | Generalist | Specialist |
| Abundant population | Common | Pattern 2: wide abundant specialists | Pattern 4: restricted abundant generalists | Pattern 6: restricted abundant specialists |
| Sparse population | Pattern 1: wide sparse population generalists | Pattern 3: wide sparse population specialists | Pattern 5: restricted sparse population generalists | Pattern 7: restricted sparse population specialists |

While population size is generally estimated based on the number of individuals, the clonal growth form of bryophytes and their lack clear individual boundaries led us to estimate population size based on the number of occurrences per sampling site. Populations were defined sparse if a species occurred once or twice within a site, and abundant if it occurred three or more times (Caiafa & Martins, 2010; Pitman et al., 1999).

Habitat specificity was determined based on the four forest stands types where bryophytes were sampled: coniferous, deciduous, and mixedwood forests, and open ecosystems. These forests were selected because they represent the dominant land cover types in the boreal forest. Less frequent habitats (e.g., rocky hills or streams) were excluded in our study. Habitat specificity reflects a species' ecological requirements and tolerances and is therefore considered a trait that induces rarity rather than a rarity pattern itself (Crisfield et al., 2024). Nevertheless, we considered habitat specificity, instead of occupancy (Crisfield et al., 2024), to underscore the role of forest habitat types in the conservation of rare bryophytes and to explain part of the rarity patterns among bioclimatic domains. In the rarity analysis, species occurring in a single forest type were classified as a specialist, while those occurring in more than one as a generalist.

After determining the rarity pattern of each species in each bioclimatic domain, we calculated the total number of rare and common species at the sampling site scale. Similarly, we calculated the number of rare species per rarity pattern for each site. We also identified exclusive and shared species across domains. For shared species, we checked if their rarity patterns changed between domains. Both the exclusivity/shared status and changes in rarity pattern were included as rarity-related variables in our functional trait database. These two rarity variables, along with the life history and dispersal traits, we used to calculated community-weighted mean (CWM) traits at the site scale (Laliberte & Legendre, 2010). CWM refers to trait values weighted by species relative abundance in a community (Lavorel et al., 2008; Muscarella & Uriarte, 2016) and were calculated using the FD R package (Laliberté et al., 2014; Laliberte & Legendre, 2010).

To determine if the metacommunities of the bioclimatic domains differed in species composition, we constructed a distance matrix based on species abundances at each site using Sørensen's dissimilarity index (ade4 R package; Dray and Dufour (2007)). We then applied Nonmetric Multidimensional Scaling (NMDS) with 999 permutations to visualize compositional dissimilarities (vegan R package; Oksanen et al. (2022)). Differences in species composition among domains were tested using permutational multivariate analysis of variance (PERMANOVA) through the adonis2 function. Additionally, we employed the Envfit() function to determine if variations in community composition were ordinated with species rarity patterns and/or functional traits.

### *2.3 Results*

We documented 282 species (86 liverworts, 164 mosses, 32 sphagna) across the spruce-moss and fir-birch bioclimatic domains in Eastern Canada (Supplementary material Figure B2; Table 3). Species richness was higher in the spruce-moss than in the fir-birch (267 spp. vs 161 spp., Supplementary material Figure B2, Table 5).

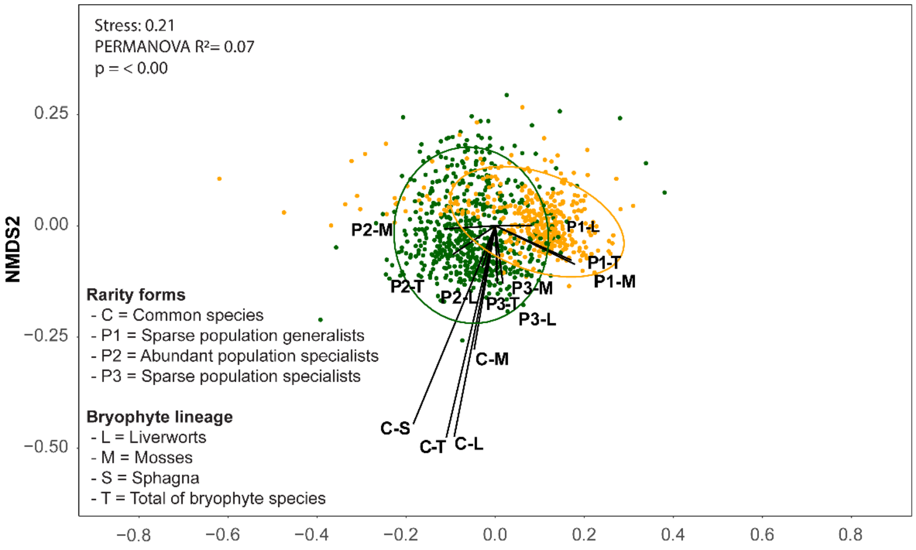
We did not identify species with restricted ranges in your dataset (patterns 4-7). Thus, all rare species were widely distributed across domains, occurring either as generalists with sparse populations (rarity pattern 1) or as specialists with abundant and sparse populations (patterns 2 and 3; Table 3.3; Supplementary material Figure B2). In the spruce-moss we found 134 common species, 49 sparse generalists, 16 abundant specialists, and 68 sparse specialists (Supplementary material Figure B2). In the fir-birch we found 70 common species, 43 sparse generalists, 4 abundant specialists, and 44 sparse specialists.

At the lineage level, the spruce-moss had considerably more common liverworts (47) than the fir-birch (18), while rare liverwort richness was similar across domains. For mosses, the spruce-moss hosted more common and rare species (patterns 2 and 3) than fir-birch. Common sphagna were more numerous in the spruce-moss than in the fir-birch, thought sparse generalists (pattern 1) were similar in both domains. Specialist sphagna, whether sparse or abundant, were exclusive to the spruce-moss (Supplementary material Figure B2).

Beyond richness differences, we detected significant disparities in metacommunity compositions between domains (Figure 5, Supplementary material Table 4). The spruce-moss had markedly more common species across all bryophyte lineages and more rare specialists with both sparse and abundant populations. In contrast, sparse generalists were more frequent in the fir-birch, primarily among mosses and liverworts.

Of the 282 species identified, 43% (121 spp.) and 5% (15 spp.) were exclusive to the spruce-moss and fir-birch respectively, while 52% (146 spp.) occurred in both domains. Rarity patterns shifted among domains for shared species (Figure 6): 42 species common in the spruce-moss became rare in the fir-birch, whereas 11 rare species in the spruce-moss became common in the fir-birch. For example, *Cladopodiella fluitans* and *Tomentypnum nitens* were common in the spruce-moss but became rare abundant specialists in the fir-birch, occurring in only one forest type. *Anastrophyllum minutum* and *Calypogeia integristipula* were common in the spruce-moss but became sparse population specialists in the fir-birch. Overall, 65 of the 146 shared species changed rarity patterns, including a third of mosses (36/93), two-thirds of sphagna (8/12), and half of liverworts (20/41).

a) Bryophyte rarity patterns across bioclimatics domains



b) Life history and dispersal traits driving bryophyte rarity patterns

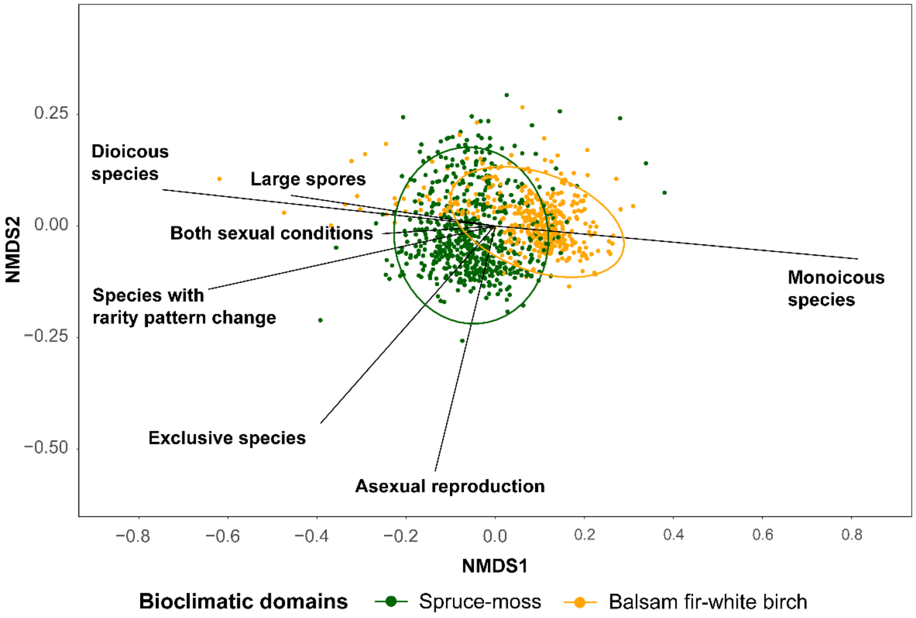


**Figure 5**
**Non-metric multidimensional scaling (NMDS) of bryophyte metacommunities by a) rarity patterns and b) life history and dispersal traits driving them in spruce-moss and balsam fir-white birch bioclimatic domains in Eastern,**

**Canada. Dots represent sampling sites. Codes in the section a) indicate the rarity pattern and bryophyte lineage, e.g., P2-M = abundant specialists mosses.**

Rarity patterns across domains corresponded closely with the functional traits exhibited by their metacommunities (Figure 5b). Dioicous species were associated with the spruce-moss, while monoicous species dominated in the fir-birch. Species with large spores, or both sexual and asexual reproduction, exhibited a preference for the spruce-moss, notably among abundant specialist mosses. Conversely, asexual reproduction and common species occurred all three lineages.

Trait-based analyses revealed further shifts rarity patterns across domains (Figure 7). First, in monoicous species, ~50% of common spruce-moss species became rare in the fir-birch, mainly as sparse generalists and, to a lesser extent, as sparse specialists. Most monoicous rare species in the spruce-moss retained their status in the fir-birch; only three became common. In contrast, over half of the common dioicous species in the spruce-moss remained common in the fir-birch; the rest became sparse generalists or specialists, and a few abundant specialists. Only five dioicous rare species in spruce-moss became common in fir-birch (Figure 7a). Species proportion by sexual condition (monoicous, dioicous, or both) was constant for common and sparse specialists and generalist among domains. Only abundant specialists were mainly dioicous in both domains (6 mosses and 2 liverworts). Of these abundant specialists, only two were common in one domain, the rest were sparse specialists or generalists. No uniform rarity shifts were explained exclusively by sexual condition.

Secondly, most of the shared species lacked specialised asexual reproduction (Figure 7b). Among common species in spruce-moss without specialised asexual reproduction, over half remained common in fir-birch; others became sparse generalists or specialists with sparse or abundant populations. Half of the rare species without asexual reproduction in the spruce-moss retained their status; the rest changed or became common in the fir-birch. For species with asexual reproduction, half of the common ones in the spruce-moss remained common in the fir-birch; others became sparse specialists or generalists. Of the six rare species with asexual reproduction in the spruce-moss, four maintained or changed their rarity pattern, and two became common in the fir-birch.

Thirdly, small spores dominated among common and rare shared species (Figure 7c). From 15 common species in the spruce-moss producing large spores, only a third remained common in the fir-birch; the rest became sparse specialist or generalist species.

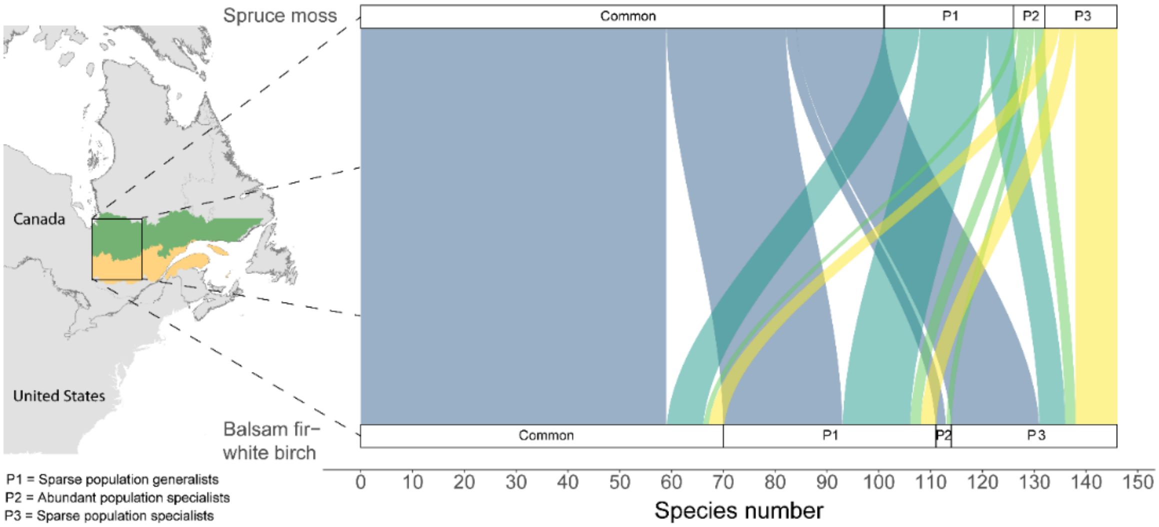


**Figure 6**
**Alluvial diagram indicating the 145 bryophyte species found in both bioclimatic domains and their change in commonness and rarity patterns between the spruce-moss and fir-birch domains in Eastern Canada (Supplementary material Table 3). The colors are given by the commonness and the different rarity patterns of species in the spruce-moss domain.**

Finally, among exclusive species, none of the fir-birch restricted species were common (Figure 7). Most exclusive species in both domains were sparse population specialists, contrasting with shared species, which were primarily common or sparse generalists.

Spruce-moss exclusive species included a greater proportion of dioicous species in both common and rare categories (Figure 7a). In the fir-birch, dioicous and dual sexual species were better represented by sparse specialists while monoicous taxa dominated other rarity types (Figure 7b). Asexual reproduction was mostly absent in restricted species. In the spruce-moss, its presence was evenly distributed across all rarity patterns, while in the fir-birch, only two sparse specialist species and one abundant specialist species had asexual reproduction (Figure 7b). Most rare restricted spruce-moss species had large or unknown spore sizes, while nearly all fir-birch exclusive species had small spores.

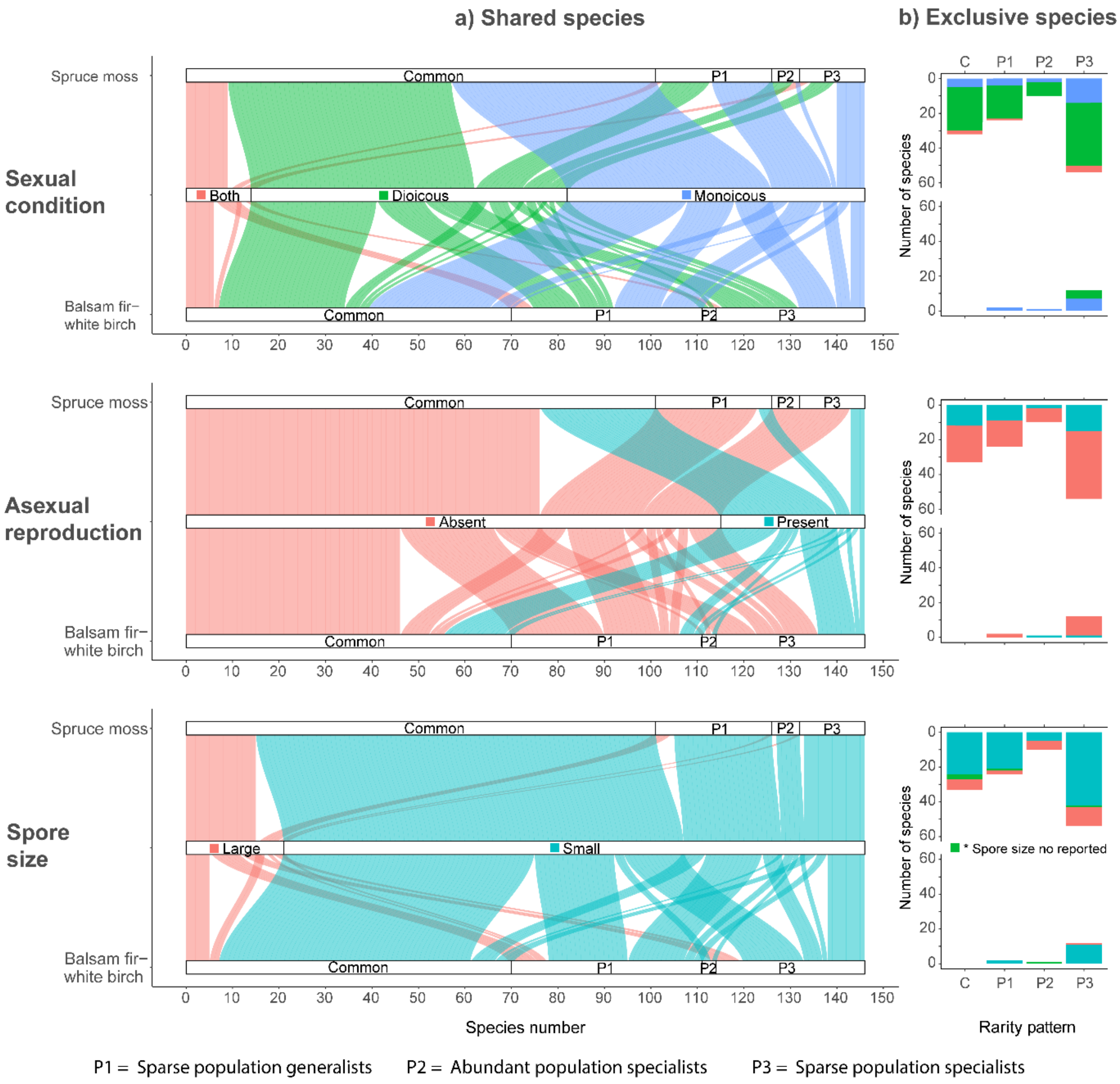


**Figure 7 a) Shared and b) exclusive bryophytes species by sexual condition, asexual reproduction, and their spore size in the spruce-moss and fir-birch bioclimatic domains in Eastern Canada (Supplementary material Table 3). Alluvial graphs show the rarity pattern shifts among shared species. Bar graphs represent exclusive species displaying the species number by rarity pattern and functional trait within each bioclimatic domain. Colors represent trait levels.**

## *2.4 Discussion*

Bryophyte metacommunities in boreal forests show distinct richness and composition patterns across bioclimatic domains, related with landscape composition and disturbance regimes. These differences are closely tied to rarity patterns, which are linked to dispersal and life history traits.

### 2.4.1 Rarity patterns and their underlying processes

Although most species are generally rare (Raunkier's Law; Gleason (1929)), we found a similar proportion of rare and common bryophytes in both bioclimatic domains (spruce-moss: 51% rare, 49% common; fir-birch: 58% rare, 42% common). This contrasts with previous bryophyte studies where rare species dominate (Birks et al., 1998; Gabriel et al., 2011; Longton & Hedderson, 2000; Söderström, 2006), likely due to differences in how rarity is defined using Rabinowitz's approach. Our findings highlight the significant role of common species in bryophyte richness, challenging the view that rare species are the primary contributors to boreal forest richness (Fenton & Bergeron, 2008).

A key feature of eastern Canada rare bryophytes is their wide distribution ranges. The persistency of forest types and microhabitats allow broad biogeographic range, assuming adequate long-distance dispersal (Barbé et al., 2016; Kyrkjeeide et al., 2016; Vanderpoorten et al., 2019). This pattern of wide biogeographic ranges aligns with findings in the boreal flora for vascular plants and bryophytes in the only continent-scale biogeographic studies to date (La Roi 1967, La Roi and Stringer 1976). Consequently, the above explains the absence of geographically restricted rare species (Storch & Gaston, 2004). However, we did find that most rare species were limited to certain forest types, especially with sparse populations.

As predicted, metacommunities differ in rarity patterns between domains, supporting our first hypothesis. The fir-birch had lower richness and fewer exclusive species compared to the spruce-moss domain. Unlike the spruce-moss, the fir-birch landscapes are dominated by mixed forest stands, are more naturally fragmented, experience severe insect defoliation (Huang et al., 2008), have a history of more frequent wildfires, and face more anthropogenic activities, particularly clearing for agriculture (12% of the landscape (Bergeron et al., 2004a; Valeria et al., 2012)). Studies in regions with varying patterns of land use change have shown that areas with high to intermediate levels of disturbance have less diverse communities with different compositions compared to those with low levels of disturbance (Arasa-Gisbert, et al., 2021). In our case, the differences in cumulative effects of landscapes composition and configuration of fir-birch, derivative of dominant forest stands and disturbance regimes, may have shaped the structure of the current bryophyte metacommunity, resulting in a more depauperate and disturbance-adapted flora, characterized by rare generalists (Arasa-Gisbert, et al., 2021; Löbel, Snäll, et al., 2006; Pharo & Zartman, 2007a).

Landscape composition defined by forest type also plays a role. Preference of rare generalists for the fir-birch can be due to the dominance of mixed forest stands compared to the coniferous in spruce-moss which influences differences in bryophyte metacommunities due to the impact of climate on the microhabitat specialist species (Barbé et al., 2020). Bryophytes associated with tree bases and dead wood are more sensitive to climatic variations in mixed forest stands than in coniferous ones (Barbé et al., 2020). Furthermore, the presence of old-growth coniferous stands in spruce-moss increases microhabitats diversity and, consequently, bryophyte richness (Fenton et al., 2015; Hylander et al., 2005). This reinforces the role of forest types in filtering species based on their traits and altering rarity patterns.

### 2.4.2 Changes in species rarity across domains

Supporting our second hypothesis, we found that 58% of shared species maintained their rarity pattern, indicating that broad environmental and consistent habitat allow population stability across domains. However, for the remaining species, contrasting landscapes altered population sizes and habitat specificity. Some rare species with sparse populations restricted to a specific forest type in one domain were however common in the other. Rare-common shifts (diffusive rarity; Schoener (1987)) can be attributed to the species' ability to achieve high abundance opportunistically across forest types due to potential combined effect of spore size and output, and colonization ability for a niche fulfillment (Murray & Lepschi, 2004).

Opportunistic behavior was more prevalent in fir-birch. Several specialists from fir-birch became common in the spruce-moss, while the reverse was less frequent. This asymmetry, combined with the generalist-dominated flora of fir-birch, could suggest that rarity pattern shifts reflect distributional limits. We identified taxa that are common species in one domain but become sparse population generalists or specialists in the other (Hanski, 1982; Söderström & Soderstrom, 1989). Therefore, some species may become rare where their ranges terminate. Further studies should examinate contiguous bioclimatic domains to whether rarity shifts align with regional limits.

Spruce-moss domain appears to function as a host for different rarity patterns due to the presence of a variety of ecological niches in its forests. According to the species-sorting model (Holyoak et al., 2005; Logue et al., 2011), the higher number of species, as well rarity patterns, in the spruce-moss, is due to each species having a competitive advantage in its preferred habitat (With, 2019). As we mentioned, the spruce-moss provides a wide variety of microhabitats (Fenton et al., 2015) increasing bryophyte richness by expanding the ecological niches availability allowing more specialist species than fir-birch (Barbé et al., 2020). At the same time, in addition to coniferous forests the presence of mixed, deciduous forests and open ecosystems increases habitat diversity, contributing to greater heterogeneity in rarity patterns across the landscape compared to the fir-birch domain (Barbé et al., 2020; With, 2019). Thus, mixed forest dominance in fir-birch seems to favor homogeneous generalist assemblages, mainly mosses and liverworts with sparse populations. These differences confirm our third hypothesis and point to the joint influence of forest type, time since disturbance, and microhabitat availability on bryophyte metacommunities and rarity patterns (Barbé et al., 2020).

The species regional filter through functional traits shapes metacommunity assembly, and in the case of bryophytes, traits are crucial for their distribution and response to landscape factors (Löbel et al., 2018b; Tscharntke et al., 2012). In our study, roles of spruce-moss as a favorable environment and the fir-birch as an environmental filter shaping bryophyte rarity patterns were more evident when analyzing functional traits confirming our fourth hypothesis. Considering dioicous species, they tend to be either restricted to spruce-moss or shift from being common in the spruce-moss to rare in the fir-birch by the reduction in their population size and in the variety of occupied forest types across domains. Roads and Longton (2003) demonstrated that dioicous species face greater sexual reproductive limitations than monoicous species due to the distance between male and female plants. Considering the influence of microhabitats of dominant forest stands in each bioclimatic domains, our results suggest that spruce-moss possess favorable microhabitat-landscape conditions for dioicous and specialized species niche fulfillment contrasting with the fir-birch which harbor primarily monoicous and generalist species. The same bioclimatic conditions can be applied to explain the preferences of species with asexual reproduction for the spruce-moss due to their association to dioicous species (Longton & Schuster, 1983). Finally, we showed that many common species with large spores in the spruce-moss have become rare in the fir-birch. Species with large spores or asexual propagules are less capable of wind dispersal compared to those with small spores (Söderström & During, 2005; Zanatta et al., 2016), and therefore are restricted to small population sizes in landscapes with distant optimal forest stands.

### 2.4.3 Considerations on rarity patterns

Identifying rarity patterns and the processes underlying them between bioclimatic domains is crucial for understanding future changes in the composition of boreal bryophyte communities. For example, climate change is predicted to increase the proportion of mixed wood forests in boreal coniferous landscapes (Molina et al., 2022). This could lead the reduction or extinction of species typical of the spruce-moss. Unfortunately, this hypothesis is supported by recent predictions of the decline and fragmentation of animal and plant niches in our study area (Murray et al., 2017).

This is the first assessment of bryophyte rarity at the landscape scale spanning two bioclimatic domains. However, a caveat of our work is that we cataloged and classified the species according to dominant forest types in the bioclimatic domain’s landscapes

(Vitt et al., 1997). We consequently exclude less prevalent habitats such as streams and cliffs that could harbor other rare habitat-specific species (Heinlen & Vitt, 2003) and, which could include species with restricted geographic ranges. Incorporating these habitats into the rare species assessment will enable the development of more effective conservation strategies. For instance, it would help determine whether prioritizing areas exclusively for their conservation is necessary or if existing conservation areas for other rare species already safeguard them (Grittz et al., 2024). Thus, our results represent a baseline for stand-scale conservation purposes because the forest types studied here are of valuable interest for forest management and conservation initiatives. Particularly, we highlight the importance of forest stands in spruce-moss due to their high richness of rare specialist species and those that are dispersal limited.

Rare habitat preservation should be a priority to safeguard rare species at landscape and regionals scales (Cleavitt, 2005). However, large extensions of dominant habitats and their inhabitants suffer the pronounced impacts of disturbances in the Anthropocene. Here we evaluate for the first time both rare and common bryophyte patterns, using extensive systematic sampling and analyses, in two boreal bioclimatic domains. More importantly, we proposed how disturbance regimes in synergy with functional traits drive rarity patterns in bryophyte metacommunities at the bioclimatic domain scale. Also, our study provides information about traits associated with species rarity. Thus, our systematized bryophyte common-rare classification can be used to monitor target species, protect zones where they live, and integrate their conservation with other biodiversity management objectives in boreal forest.

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### *2.7 Data accessibility*

The data and code supporting our methods and findings are openly available at https://github.com/BryoSeneca/Rare-Species/tree/main.

### *2.8 Authors contributions*

EHR and NJF conceived the research idea and developed the methodology. XY, MN, M-FI, MB and EHR did fieldwork and species identification. EHR, XY, CC, MB and MN performed the data management of bryophyte samples. EHR, XY, and MN constructed the species functional traits data base. EHR and CC did the diversity analyses and data visualization. NJF and JCV acquired the research funding. EHR and NJF wrote the first drafts with contributions from CC, VC and JCV. All authors participated in the writing-review & editing and approved the document for its publication.

# 3. AU-DELÀ DE LA VIEILLE FORÊT : COMMENT LES MOSAÏQUES DE LA FORÊT BORÉALE INFLUENCENT-ELLES LE FLUX GÉNÉTIQUE D'UNE PLANTE DÉPENDANTE DE LA REPRODUCTION ASEXUÉE?

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**Résumé**

Les types d'habitats et leur organisation spatiale influencent la distribution des populations biologiques, affectant leur flux génétique et, par conséquent, des processus clés pour leur survie. Avec l'augmentation rapide de la fragmentation des paysages, il devient essentiel de comprendre comment la perte d'habitat et la fragmentation per se affectent la biodiversité, notamment la diversité génétique, encore peu étudiée dans un contexte d'écologie du paysage. Dans cette étude, nous avons évalué les effets de la composition et de la configuration des paysages boréaux sur la génétique des populations de *Dicranum flagellare* Hedw., une mousse à reproduction principalement asexuée et à faible capacité de dispersion, caractéristique des forêts anciennes. Nous avons pris en compte les types de forêts d'âges différents ainsi que les zones non forestières (composition) et leur agrégation spatiale (configuration). Nous avons utilisé des polymorphismes mononucléotidiques (SNP) issus de 191 tiges de *D. flagellare* échantillonnées dans 12 fragments de forêts matures dans l'est du Québec, au Canada. Une approche multi-échelle basée sur les relations site-paysage et l'inférence de modèles fondée sur l'information a été appliquée pour évaluer les liens entre la diversité et la structure génétique de la mousse et les motifs paysagers. Nos résultats indiquent que la diversité génétique et le flux génique de *D. flagellare* sont influencés par le paysage jusqu'à une distance de 8 km de la colonie, la configuration ayant un impact plus important que la composition. Nous avons observé que la présence de forêts intermédiaires et de zones non forestières autour des fragments de forêts anciennes augmente la diversité génétique de *D. flagellare* tout en favorisant la différenciation des populations. De plus, la fragmentation per se des forêts anciennes est positivement associée au flux génique de l'espèce, ce qui renforce sa diversité et homogénéise sa structure génétique. Cette étude démontre que la perte d'habitat et l'agrégation des zones non forestières affectent la diversité génétique et la structure spatiale de l'espèce. Ces résultats permettent d'identifier des seuils critiques à partir desquels les changements paysagers peuvent influencer la biodiversité du sous-bois (jusqu'à 8 km), et soulignent l'importance de maintenir des fragments de forêts anciennes (~3 km) autour des zones de conservation pour assurer la connectivité de l'habitat. Enfin, ils mettent en évidence le rôle crucial des habitats complémentaires, comme les forêts intermédiaires, dans le maintien de la connectivité fonctionnelle à l'intérieur des paysages boréaux.

Mots clés : capacité de dispersion, échelle d'effet, faibles disperseurs, fragmentation per se, hétérogénéité de l'habitat, qualité de la matrice.

## Abstract

Habitat types and their spatial arrangement influence the distribution of biological populations, affecting their genetic flow and, consequently, key processes for their survival. With the rapid increase in landscape fragmentation, understanding how habitat loss and fragmentation per se impact biodiversity becomes essential to predict species' responses to environmental change—particularly genetic diversity, that has been less studied in a landscape ecology context. In this study, we evaluated the effects of boreal landscape composition and configuration on the population genetics of *Dicranum flagellare* Hedw., a moss with dominant asexual reproduction and limited dispersal capacity, characteristic of old-growth forests. We considered the types of forests of different ages, as well as non-forest areas (composition) and their aggregation (configuration). We used single nucleotide polymorphisms from 191 *D. flagellare* stems sampled across 12 mature boreal forest fragments in eastern Quebec, Canada. We applied a multiscale approach based on site-landscape relationships and information-theoretic model inference to assess the relationship between moss genetic diversity and structure, and landscape patterns. Our results indicate that the genetic diversity and gene flow of *D. flagellare* are influenced by landscape up to 8 km from the colony, with configuration exerting a greater impact than composition. We found that mid-aged forests and non-forest areas around old forest patches increase *D. flagellare*'s genetic diversity while also promoting population differentiation. Additionally, we observed that old-growth forest fragmentation per se is positively associated with the species' gene flow, enhancing its diversity and making more homogeneous its genetic structure. Our study demonstrates that habitat loss and the aggregation of non-forest areas affect the genetic diversity and spatial structure of the species. These findings contribute to identifying critical thresholds at which landscape changes may influence understory biodiversity (up to 8 km). They also highlight that keeping old-growth forest patches (~3 km) around conservation patches is key for habitat connectivity. Moreover, they underscore the importance of complementary habitats, such as mid-aged forests, in maintaining functional connectivity within boreal forest conservation areas.

Keywords: dispersal capacity, fragmentation per se, habitat heterogeneity, matrix quality, scale of effect, poor dispersers.

### *3.1 Introduction*

Wildlands worldwide are experiencing changes in both their spatial extent and the way they are distributed across the landscape (Ellis, 2013). These changes are due to increasing anthropogenic activities and natural disturbances resulting in habitat loss, emergence of new land covers, and the fragmentation and spatial reconfiguration of remanent patches (Curtis et al., 2018; Loehman et al., 2021). Consequently, this landscape composition and configuration (LCC) dynamic impacts biodiversity at multiple dimensions (from genetic to community structure), even within forest patches designated for conservation (Mori et al., 2017).

Empirical research has documented the different LCC impacts on species richness, and community structure (Fahrig 2003, 2017; Arroyo-Rodríguez et al. 2020). However, to gain a more comprehensive understanding of how landscape changes shape biodiversity, it is essential to also consider their effects on genetic diversity—a diversity dimension that has received comparatively less attention (Lino et al. 2019; González-Fernández et al. 2019, Lanes et al. 2018; Carvalho et al. 2019). A landscape composed of small, isolated patches can reduce dispersal opportunities, altering species colonization and extinction dynamics (Thrall et al., 2000). As a result, shifts in population genetic structure can serve as an early warning system for extinction debt in species experiencing prolonged landscape disturbances (Gargiulo et al., 2025). In highly fragmented landscapes, reduced connectivity increases genetic drift, potentially accelerating genetic erosion (Pinto et al., 2023). A major challenge remains in predicting the landscape scale at which these genetic changes begin to significantly impact population viability.

Boreal forests represent one of the biomes with the largest areas of pristine land on the planet (Gauthier et al., 2015; Ruckstuhl et al., 2008). However, habitat loss and changes in forest structure are increasingly altering its biodiversity (DiLeo & Wagner, 2016; Gibb et al., 2006; Xi et al., 2024). Bryophytes are a dominant component of boreal forest biodiversity, participating in nutrient cycling, water retention, and soil formation (Slate et al., 2024). They are considered as highly vagile organisms due to their rather small airborne propagules, yet evidence of dispersal limitation between local habitats and across regional landscape have been observed (Barbé, Fenton, et al., 2016; Hernández-Rodríguez et al., 2024; Vanderpoorten et al., 2019). Besides, the typically short generation times and dominant haploid phase of bryophytes make them an ideal taxon for studying the ecological and evolutionary impacts of landscape changes (Pharo & Zartman, 2007b).

Although studies have assessed bryophyte genetic diversity in disturbed landscapes (see Wang et al. 2012), few have explicitly considered the distinct roles of LCC to elucidate the effects of patterns as fragmentation and habitat loss (for example DiLeo and Wagner, 2016). This is due to study designs conducted in fragmented environments, where analyses often overlook the difference between habitat loss (landscape composition) and fragmentation per se (landscape configuration). Additionally, genetic consequences observed at the patch scale are often extrapolated to the landscape scale, leading to potential confounding conclusions of broader ecological processes (Riva et al., 2024). As a result, the specific LCC effects and related patterns of fragmentation and habitat loss per se on gene flow remain unclear.

Distinguishing between fragmentation and habitat loss is necessary because both patterns have different ecological implications, influencing how ecosystems are managed and conserved. According to Fahrig (2003), habitat loss refers to the reduction in the total amount of available habitat, directly impacting the space available for species that depend on that habitat. Fragmentation per se, on the other hand, refers to the division of a continuous habitat into smaller, isolated fragments, but without necessarily implying a reduction in the total amount of habitat. Although habitat loss reliably leads to biodiversity declines, the effects of fragmentation per se are generally weaker and may even be positive in some cases (Arasa-Gisbert & Andresen, 2021; Fahrig, 2003a). Understanding these contrasting effects is key to designing conservation actions that address the right drivers of biodiversity change (Arasa-Gisbert et al., 2021a). Therefore, studies are needed to elucidate the effects of habitat loss and fragmentation per se as patterns of LCC. Especially in boreal forests, where there is a significant lack of information on how the distribution and spatial arrangement of conservation areas affect biodiversity conservation (Kyaschenko et al., 2024).

In this study, we evaluated the effects of landscape composition (habitat loss and role of forests with different ages) and landscape configuration (fragmentation per se) on the gene flow of the common moss *Dicranum flagellare* Hedw. (Bryophyta) in boreal forests of eastern Canada. *Dicranum flagellare* colonizes decaying wood, a resource that is more abundant and diverse in old-growth forests (Linder and Ostlund 1998; Brassard and Chen 2006). Additionally, species with large propagules, like *D. flagellare*, generally disperse over shorter distances than those with smaller propagules, making it more dependent on habitat continuity (Frey & Kürschner, 2011; Laaka-Lindberg et al., 2003). Based on this, we predict that 1) the genetic diversity of *D. flagellare* will decrease as the surrounded area of old-growth forest declines, given that habitat loss is a key driver of biodiversity loss (Fahrig, 2003b, 2017). 2) Fragmentation of old-growth boreal forests will not necessarily reduce genetic diversity of *D. flagellare* and may even have a neutral or positive effect due to increased habitat connectivity (Fahrig, 2017; Fahrig et al., 2019). 3) Although medium-age and young-growth forests offer lower structural quality than old-growth forests (Ekbom et al., 2006), they may still provide suitable microhabitats for *D. flagellare*, serving as a high-quality matrix (Arroyo-Rodríguez et al., 2020) and increase its genetic diversity.

## *3.2 Material and methods*

### 3.2.1 Study area

Our sampling covered boreal forests in Western Quebec, Canada (from 76° W to 80° W and from 48° N to 50° N) (Figure 8a). The forest is dominated by the tree species black spruce (*Picea mariana* Mill.) and balsam fir (*Abies balsamea* L. Mill.) (Robitaille & Saucier, 1998). Other tree species present in smaller proportions are jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* Moench, Voss), paper birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.) (Robitaille & Saucier, 1998). The terrain is mostly flat, with soils predominantly composed of organic matter and clay deposits (Bergeron et al., 2004b). Disturbances in the region include insect outbreaks, wildfires and logging activities (Bergeron et al., 2001, 2002; Cyr et al., 2009; Nguyen-Xuan et al., 2000). Natural and human-induced disturbances, include insect outbreaks, wildfires and logging activities, have created heterogeneous landscapes, with non-forest areas (e.g., agricultural areas, and urban zones) and forest cover varying in age (old forest >80 years, medium age forest >40 to <80 years, young forests <40 years). Vegetation types in the region include open ecosystems, conifer, deciduous, and mixed forest.

### 3.2.2 Study species

*D. flagellare*, is a common boreal moss that typically grows in tufts ranging from 0.5 to 5.5 cm in height (FNAEC (Flora of North America Editorial Committee), 2007). This dioecious species has male and female plants of similar size. In boreal forests, it commonly occurs on decaying logs, at the base of tree trunks, on the ground, or on stones. While it reproduces sexually, asexual reproduction via propagules is predominant (Kimmerer, 1994) (Fig 8e). These propagules, located at the distal end of the stem, are rigid and cylindrical, with small, tightly pressed, short, ovate leaves (Faubert, 2013). Dispersal of the propagules has been documented to occur through vectors like slugs and likely squirrels (Kimmerer and Young 1995; Faubert 2013).

### 3.2.3 Study design and landscape variables

To assess the influence of landscape composition and configuration on *D. flagellare*'s populations genetics, we used a patch-landscape approach (Mcgarigal & Cushman, 2002). We estimated response variables (genetic diversity) within target patches (Figure 8b-d), and calculated landscape variables (composition and configuration) within concentric buffers of varying sizes around the geographic center of each patch (Figure 8c). Fieldwork was conducted during the summers of 2018 and 2019 to collect samples.

First, we selected old forest patches based on the presence of *D. flagellare* (Figure 8d). To increase sample size and study area coverage, we also incorporated herbarium specimens from recent community ecological studies by our group (Barbé et al., 2017, 2020; Castonguay, 2016; Chaieb et al., 2015), which followed the same sampling protocol as our fieldwork. Within each forest patch, one to three plots (5 ×

10 m, spaced 10 m apart) were surveyed, and where the focal species was collected (Figure 8e). This approach yielded between 1 and 22 colonies of *D. flagellare* per patch, totaling 217 individuals (single stems) from 12 old forest patches (Fig 1b,f). Colonies from each forest patch represent our study populations.

Second, we used a multiscale approach to identify the scale at which LCC most strongly influences *D. flagellare*' population genetics. We established 10 concentric buffers (from 1 to 10 km radii) around each patch (12 yellow dots in Figure 8b, c) to assess the strongest response-landscape relationship (scale of the effect; Jackson and Fahrig 2015; McGarigal et al. 2016). The maximum buffer size (10 km) and scale intervals were established based on typically accepted bryophyte dispersal capacity (Vanderpoorten et al., 2019), the effects of landscape heterogeneity at community patch level (Hernández-Rodríguez et al., 2024), and the size of managed areas in boreal forests (Gouvernement du Québec, 2020).

Third, we classified the landscape surrounding each forest patch harboring *D. flagellare* populations into four forest classes: i) young forest (<40 years), ii) medium forest (40–80 years), iii) old forest (>80 years), and iv) non-forest land. This classification was based on silvicultural harvesting criteria for forest age categories and land use for non-forest areas. To perform landscape classification, we used forest information from the (Gouvernement du Québec, 2020) treated in ArcGis 10.8 (ESRI, 2010). For each forest class, we calculated composition and configuration variables for the 10 buffer sizes. The composition was measured as the percent area of each forest class. The configuration was evaluated based on patch density, referred to the number of patches of each forest class within the landscape divided by the area of the landscape (n/ha) (Arasa-Gisbert, et al., 2021). To estimate these measures, we used the Patch Analyst extension (Rempel et al., 2012) in ArcMap 10.8 (ESRI, 2010). We had two landscape variables (composition and configuration, measured as percent area and patch density, respectively) for four forest classes (three age classes + non-forest land) totalling 8 variables. We performed a correlation analysis between the 8-landscape variables at the different scales using the Hmisc package (Harrell, 2022) in the R software version 4.4.1 (R Core Team, 2024). We measured landscape variable autocorrelation and removed those sets of variables that were autocorrelated ($r >= 0.4$, $p < 0.05$; Table S1). Patch density of medium and non-forest land were consequently excluded. We finally retained for the subsequent analyses the percentage of old, medium, young forests and non-forest land and the patch density of old and young forests.

### 3.2.4 Library preparation and sequencing

Genomic DNA was extracted from ~30 mg pulverized tissue using the standard protocol of the cetyl trimethylammonium bromide (CTAB) method (Murray & Thompson, 1980) from 217 individuals. Genomic DNA concentration was evaluated using a Nanodrop 1000 spectrophotometer (ThermoFisher, Waltham, USA). After, a double-digest genotyping-by-sequencing (GBS) library (enzymes PstI/MspI) was prepared for Ion Torrent sequencing (Mascher et al., 2013). Single-end sequencing was performed on an ion proton machine at the Plateforme d’analyses génomiques (Institut de Biologie Intégrative et des Systèmes), at Laval University (Quebec City, QC, Canada).

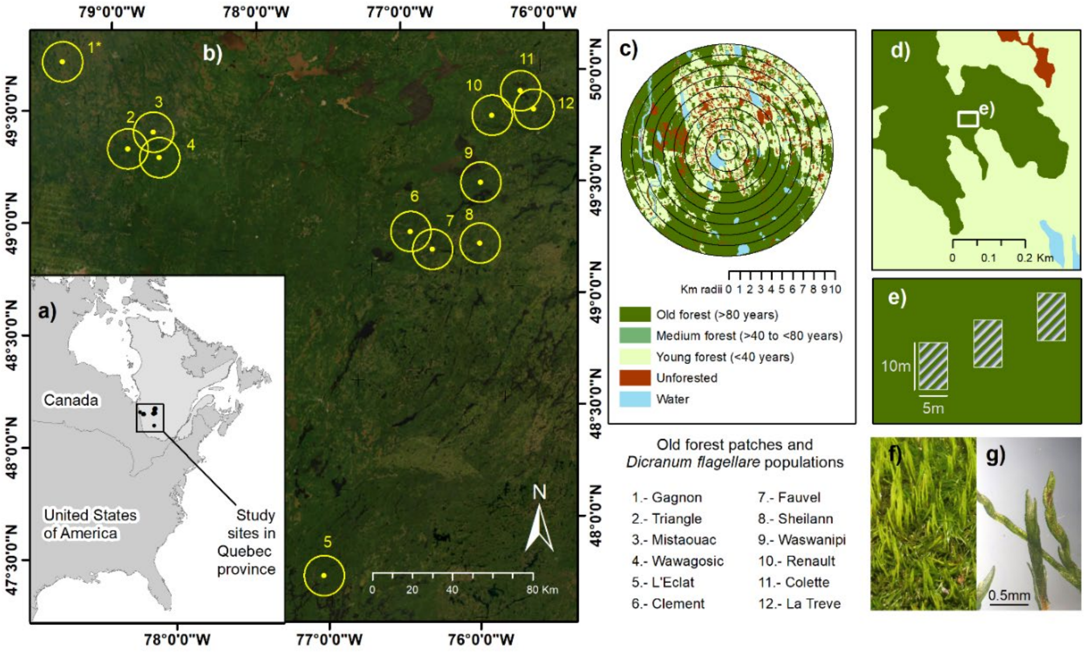


**Figure 8**
**a) Location of the study patches in eastern Canada. b) Yellow dots indicate old forest patches where D. flagellare populations were sampled. Yellow buffers around each point represent the largest spatial scale considered for landscape analysis (10 km radius). c) Example of a study landscape, showing the 10 concentric buffers (1 to 10 km radii) surrounding an old forest patch used to calculate landscape metrics. d) Detailed view of an old forest patch where sampling plots were established to collect D. flagellare colonies, shown more closely in panel f. g) Illustration of D. flagellare propagules. Panels f and g adapted from images by Hermann Schachner (Wikimedia Commons).**

### 3.2.5 Generating genomic data sets and Population genetic diversity

The Stacks v2.5 pipeline was used to demultiplex the libraries and cluster loci using the function process_radtaqs (Rochette et al., 2019). Raw sequence reads were demultiplexed for each individual sample based on their specific barcode. All reads were trimmed to 130 base pairs representing the best quality length distribution observed in FastQC v0.11 .3 (Andrews, 2010). Quality scores were encoded using the default parameter 'phred33'. To demultiplex the libraries and cluster loci we used a minimal percentage of identity of 90% within and among individuals.

We used the mapping to a reference approach for the construction of loci and the identification of SNPs (single nucleotide polymorphisms). The resulting SNP dataset was then used to infer population structure and estimate genetic diversity.

We selected loci present in at least 75% (-r 75) of the individuals from a population. We used population in Stacks (Catchen et al., 2013) and the poppr 2.9.3 R package (Kamvar et al., 2014, 2015) to estimate the following genetic diversity variables: allelic diversity, expected number of multi-locus genotypes, Shannon-Weiner diversity index (H), percentage of polymorphic sites, percentage of variant sites, and nucleotide diversity (πT).

### 3.2.6 Genetic diversity and landscape metrics

To assess the scale of the effect of each landscape variable (composition and configuration, measured as percent area and patch density, respectively) on each of six genetic diversity variables, we used generalized linear models (GLMs) and the multifit function (Huais, 2018) in R software. The continuous response variables (Shannon-Wiener index, percentage of variant sites, percentage of polymorphic loci, and nucleotide diversity) were assessed with a Gaussian distribution error, and those count response variables (Expected number of multi-locus genotypes and allelic diversity) were tested with a Poisson distribution error (Crawley, 2012). For each GLM, we determined the lowest AIC (Akaike information criterion) as an indicator of the model's goodness-of-fit. We then selected the model with the lowest AIC value across the 10 spatial scales assessed for each genetic diversity variable.

We tested for multicollinearity among landscape variables with the variance inflation factors (VIF) using the car package for R version 3.0.1 (Fox & Weisberg, 2020). We detected significant collinearity between the percentage of young forest and the rest of the landscape variables (VIF > 4). Therefore, we removed the young forest percentage from subsequent analyses.

To identify LCC patterns that contribute to explaining the genetic flow of *D. flagellare*, but that are not necessarily detectable, we used an information-theory approach combined with multi-model inference (Burnham & Anderson, 2004; Castilho & Prado, 2021). Then, to reduce uncertainty, we applied GLMs to identify LCC patterns with direct influence on *D. flagellare* genetic diversity.

To apply the Information-theory approach we followed the workflow outlined by (Arasa-Gisbert et al., 2021). We began by constructing 32 models for each genetic variable, which included all possible combinations of five landscape variables (percentage of area covered by old, medium forest, and non-forest land, along with patch density of old and young forest), and the null model (intercept only). A sample-corrected Akaike Information Criterion (AICc) for each model was assessed, ranking them from the lowest (best-fitting model) to the highest AICc values. We then summed the Akaike weights (∑▒w_i ) for each landscape metric appearing in the models. This sum indicates the likelihood that a given landscape variable would be included in the best model if the data were to be collected again under similar conditions, serving as an indicator of each variable’s relative importance (Burnham & Anderson, 2004; Giam & Olden, 2016). We examined the presence of overdispersion in the data by comparing the residual deviance with the residual degrees of freedom of each model. In all cases, the ratio was less than 2, suggesting that our models did not exhibit overdispersion. We conducted all model testing using the glmulti package in R version 3.3.2 (Calcagno & Mazancourt, 2010). To adopt a conservative approach, we considered a landscape variable significant for a given response variable only if it met the following three criteria: i) it had a relatively high ∑▒w_i , ii) the model-averaged unconditional variance was smaller than the model-averaged parameter estimate; Burnham and Anderson 2004), and ii) the metric was included in a full model with a relatively high percentage of explained deviance (Crawley, 2012).

Since the multi-model averaging approach evaluates all combinations of predictor variables, the averaged impact of fragmentation (here patch density) cannot be interpreted as fragmentation per se (Fahrig, 2003b). Some models involved in this averaged effect (e.g., genetic variable ~ fragmentation, genetic variable ~ fragmentation + old forest percentage) do not statistically control the influence of each landscape pattern (composition and configuration). To address this, we also applied multiple regression models (GLMs) that included both forest class percentage and patch density as explanatory variables for each response. Thus, we estimated fragmentation effects independently from habitat amount effects (Fahrig, 2017; Smith et al., 2009).

### 3.2.7 Population structure analyses using individual-based clustering

For subsequent analyses, we imputed missing genotypes within populations based on the mean allele frequency of the known genotype observed as a reference. Imputing missing genotypes helps to prevent inflation in Type I error rates and ordination bias (Yi & Latch, 2022). We inferred the genetic relatedness of the individuals within populations in old growth forest patches using a multivariate statistical approach. We used the Discriminant Analysis of Principal Components (DAPC) to partition the genetic variance into between-group and within-group components, to maximize discrimination between groups without making assumptions of panmixia (Jombart et al., 2010). This approach is more convenient for populations assumed to be partially clonal and genetically related due to relatively recent isolation events. DAPC integrates principal component analysis (PCA) identified through discriminant analysis (DA) to infer the optimal number of clusters in the metapopulation. We performed a stratified cross-validation of DAPC to select the optimal number of principal components (PCs) to retain, considering most sources of variation. Following cross-validation, we performed a DAPC assigning samples to their populations corresponding to their geographical site as cluster population priors (n = 12), with the optimal number of PCs axes and using the five first axes retained in the DAPC.

We investigated whether LCC influenced the genetic structure of *D. flagellare* populations by examining the relationship between the significant landscape metrics from our GLMs and the population patterns in the DAPC. To assess this, we used the envfit function in R with 999 permutations (Oksanen et al., 2022).

To assess whether populations exhibit significant genetic differentiation within and between populations, we computed a pairwise genetic differentiation index for each population pair (FST: Weir & Clark 1984), using the R-package hierfstat (Goudet & Jombart, 2022). Furthermore, we applied the hierarchical analysis of molecular variance (AMOVA) with 999 permutations to the FST calculations. We evaluated differences in the total genetic variation observed between assigned populations. All calculations were performed using R-packages hierfst (Goudet & Jombart, 2022), and poppr (Kamvar et al., 2014),

### *3.3 Results*

Our results indicated that the genetic diversity of *D. flagellare* is influenced by the composition and configuration of the landscape within a radius of up to 8 km around a population (Figure 8, 9). The scale of effect (GLMs) of each composition and configuration variable varied depending on the genetic diversity measure analyzed. For instance, according to the analyses based on the information-theoretic approach with multimodel inference, allelic diversity showed a strong and positive association (Akaike weight = 1) with LCC metrics at scales ranging from 1 to 8 km involving the four forest classes. In contrast, the remaining measures of genetic diversity were influenced more moderately (Akaike weight < 0.5) and at narrower scales compared to allelic diversity. For example, the Shannon-Wiener index was associated with the percent cover of non-forest land and mid-aged forest at a scale of 2 km. Meanwhile, the expected number of multilocus genotypes was influenced by the same forest classes but at scales of 2 and 3 km, respectively (Figure 9). Nucleotide diversity, on the other hand, was primarily associated with the percent cover of old forest and mid-aged forest at scales of 4 and 6 km, respectively. Finally, the metric of percentage of variant sites was determined by the percent cover of old forest at 5 km and non-forest land at 1 km. These patterns were consistent when jointly modeling the effects of composition (forest class percent) and configuration (patch density) as well as when evaluating these factors independently (Figure 9).

Outside of allelic diversity, landscape composition variables had a relatively low contribution to explaining the observed patterns in the genetic diversity variables. Nevertheless, despite their moderate relative effect, they were the only metrics that exhibited a detectable influence, as landscape configuration metrics showed no relative effect on the other variables analyzed.

When analyzing the effects of the landscape variables in our GLMs, we found that allelic diversity was significantly associated with the composition and configuration patterns of the landscape at the scales identified as most explanatory by the information-theoretic approach. Specifically, allelic diversity decreased with increasing percent of old forest within 1 km landscapes but increased with increasing percent of mid-aged forests and non-forest land at scales of 8 and 5 km, respectively (Figure 10). Similarly, allelic diversity was positively influenced by an increase in patch density of old forest at 4 km and young forest at 5 km (Figure 10a). In contrast, the percent and patch density of old forest showed the opposite effect on the Shannon-Wiener index. While a higher percent of old forest in 2 km landscapes reduced the diversity, an increase in the patch density of old forest at the same scale resulted in an increase in diversity.

The DAPC analysis revealed that individuals from spatially close populations tended to be genetically similar (e.g., Renault and Colette populations). However, cases of geographically proximate but genetically differentiated populations were also identified (e.g., Fauvel and Triangle; Figure 11). These results were consistent with those obtained through the Fst analysis values (Figure 12).

According to our ordination and envfit analysis, the genetic similarity and differentiation of *D. flagellare* populations in the landscape were influenced by the amount and spatial arrangement of habitat. The density of old-growth forest patches (between 2 and 4 km) and the percent of mid-aged forest (at 8 km) were strongly associated with five genetically similar populations. In contrast, non-forest percent and the density of young forest patches (at 5 km) were related to the genetic differentiation of some populations.

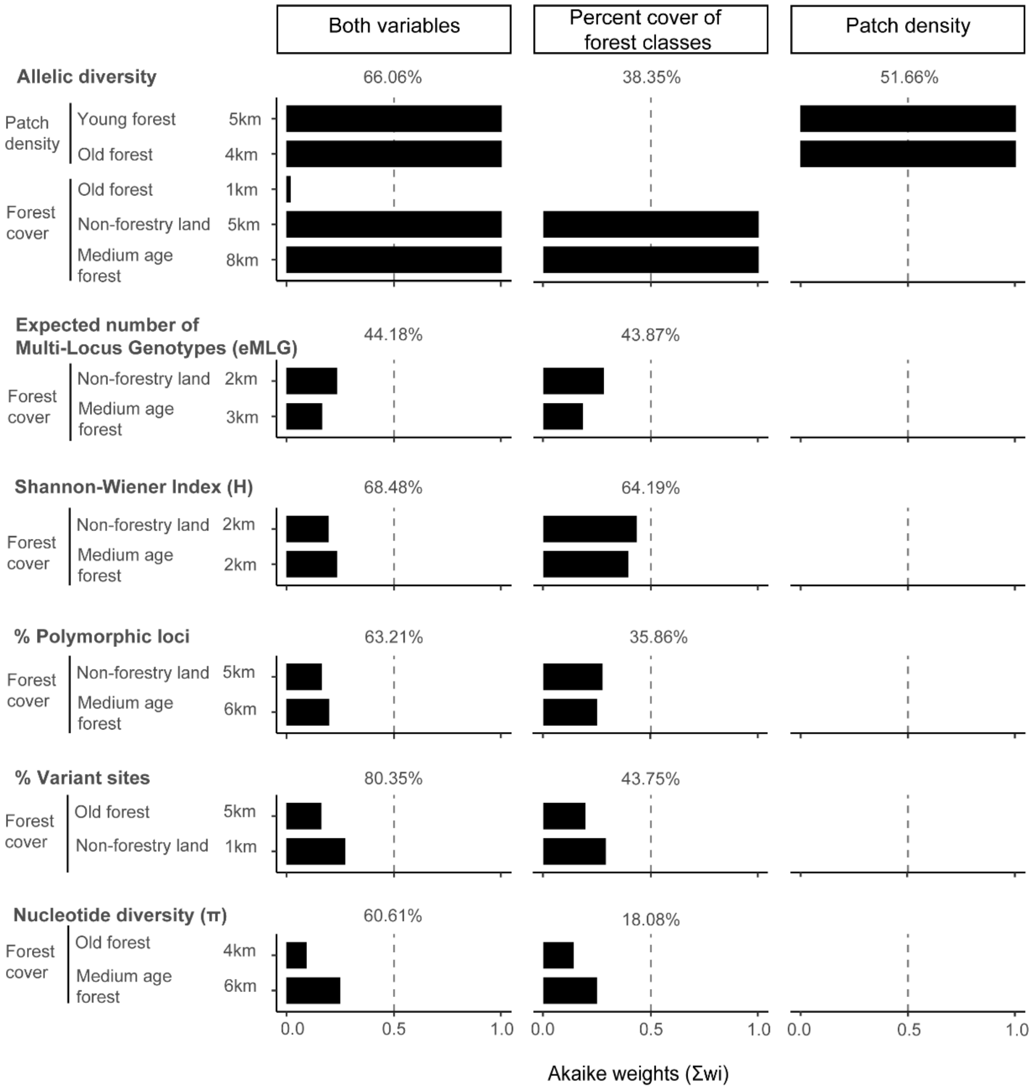

Both variables
Percent cover of forest classes
Patch density
Allelic diversity
66.06%
38.35%
51.66%
Patch density
Young forest 5km
Old forest 4km
Forest cover
Old forest 1km
Non-forestry land 5km
Medium age forest 8km
Expected number of Multi-Locus Genotypes (eMLG)
44.18%
43.87%
Forest cover
Non-forestry land 2km
Medium age forest 3km
Shannon-Wiener Index (H)
68.48%
64.19%
Forest cover
Non-forestry land 2km
Medium age forest 2km
% Polymorphic loci
63.21%
35.86%
Forest cover
Non-forestry land 5km
Medium age forest 6km
% Variant sites
80.35%
43.75%
Forest cover
Old forest 5km
Non-forestry land 1km
Nucleotide diversity (π)
60.61%
18.08%
Forest cover
Old forest 4km
Medium age forest 6km
0.0
0.5
1.0
Akaike weights (Σwi)

**Figure 9**
**Relationship between landscape composition metrics (percent cover of cover classes) and configuration metrics (patch density) with standard measures of genetic diversity in D. flagellare in eastern Canada. In each panel, the length of the bars along the x-axis represents the sum of the Akaike weights (∑wi). These values indicate the relative importance of each landscape predictor for the different response variables. The first panel shows the results of the models that include both composition and configuration variables. The second panel presents the results of models considering only composition variables, while the third panel includes only configuration variables. The percentage of variation explained by the models (pseudo-R²) is shown at the top of each graph. Landscape predictors were excluded when unconditional variance exceeded the average parameter estimates obtained through modeling. The scale effects of each landscape metric is showed on the left side of the panels.**

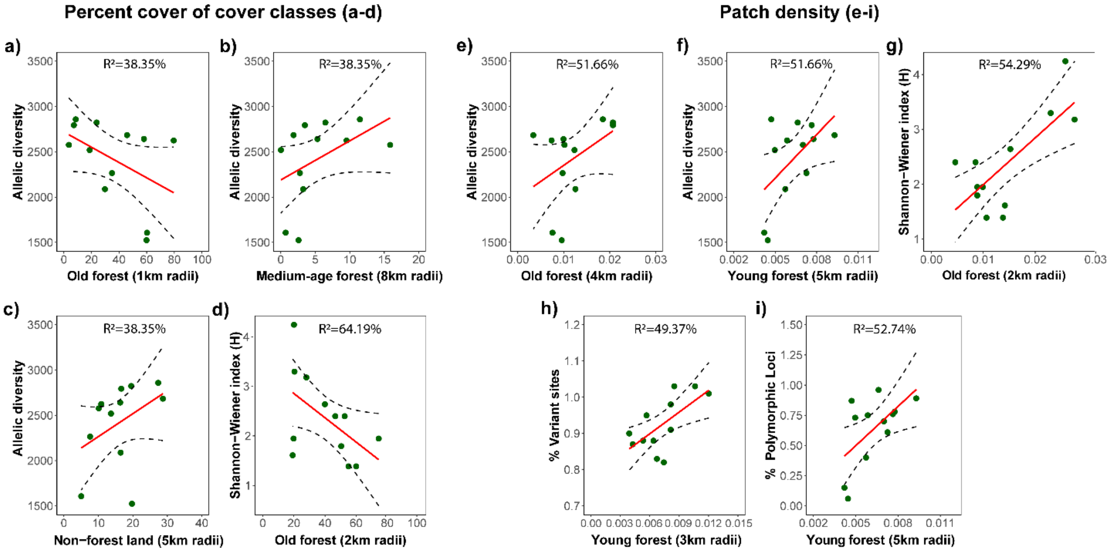


**Figure 10**
**Relationship between the standard measures of genetic diversity in D. flagellare and the significant landscape metrics identified in the GLM models. Panels a to d indicate composition metrics, while panels e to i indicate configuration metrics. Green points represent the D. flagellare populations from the studied forest patches (n = 12). The dashed lines represent the 95%**

**confidence intervals. The X axes have adjusted scales to enhance the visualization of trends.**

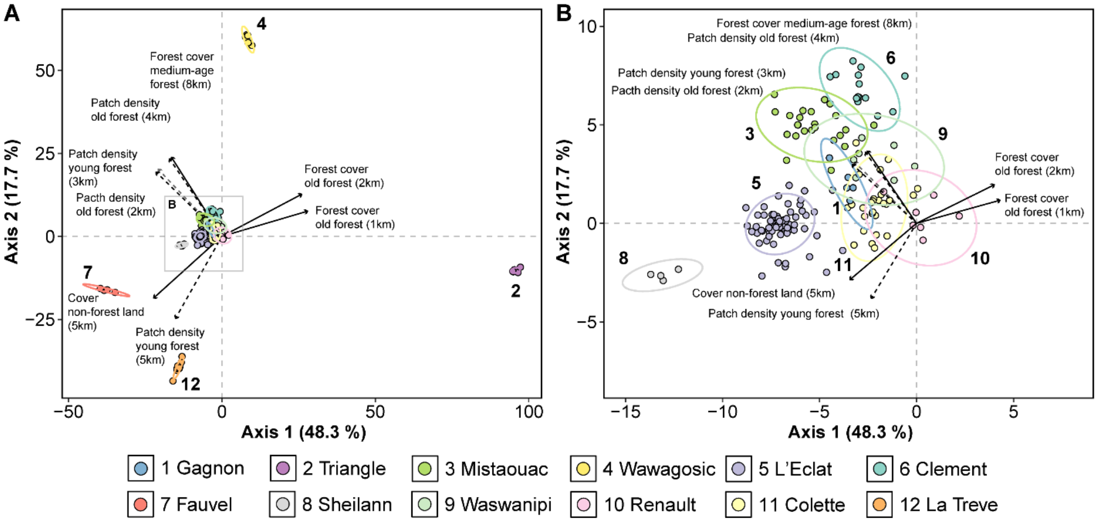
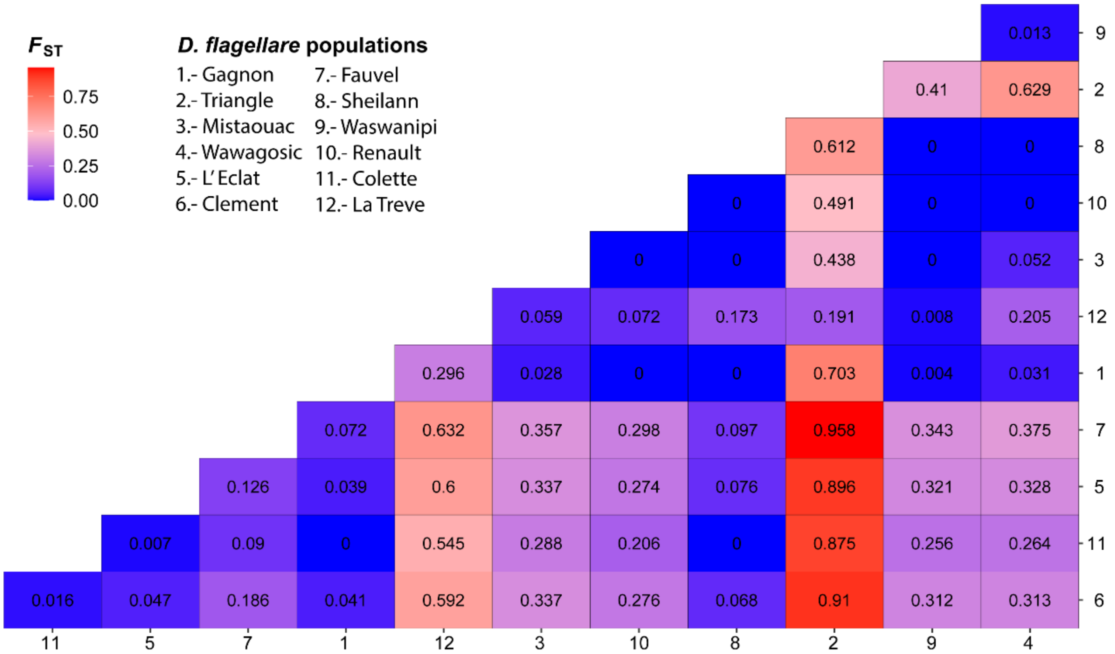


**Figure 11**
**Discriminant Analysis of Principal Components (DAPC) showing the genetic structure of D. flagellare populations in eastern Quebec showed in Figure 8. The proximity of points (individuals) colored by populations suggests genetic similarity. Colors in points and ellipses and numbers indicate the D. flagellare populations. Igen values are shown in parentheses. LCC metrics were added through correlation with the axes using the envfit function. Solid arrows represent forest cover (composition), while dotted arrows indicate patch density (configuration). Panel A shows all D. flagellare populations, while panel B provides a detailed view of the populations in the center of Panel A.**

**Tableau 4**
**Significant landscape metrics from GLMs related to the genetic structure of D. flagellare populations in old forest patches, as presented in the PCoA using envfit. Significant values are marked with asterisks. Kilometers between parenthesis indicate the variable scale effect. r² = variation explained by the multiple regression model, Pr(>r) = significance of the multiple regression calculated using a permutation test.**

| Landscape metric | $r^2$ | Pr(>r) |
|---|---|---|
| Forest cover old forest (1km) | 0.18 | 0.001 *** |
| Forest cover old forest (2km) | 0.05 | 0.008 ** |
| Forest cover medium age forest (8km) | 0.18 | 0.001 *** |
| Cover non-forest land (5km) | 0.45 | 0.001 *** |
| Patch density old forest (2km) | 0.06 | 0.003 ** |
| Patch density old forest (4km) | 0.16 | 0.001 *** |
| Patch density young forest (3km) | 0.03 | 0.053 |

| | | |
|---|---|---|
| Patch density young forest (5km) | 0.14 | 0.001 *** |



| | 11 | 5 | 7 | 1 | 12 | 3 | 10 | 8 | 2 | 9 | 4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | | | | | | | | | | | 0.013 |
| 2 | | | | | | | | | | 0.41 | 0.629 |
| 8 | | | | | | | | | 0.612 | 0 | 0 |
| 10 | | | | | | | | 0 | 0.491 | 0 | 0 |
| 3 | | | | | | | 0 | 0 | 0.438 | 0 | 0.052 |
| 12 | | | | | | 0.059 | 0.072 | 0.173 | 0.191 | 0.008 | 0.205 |
| 1 | | | | | 0.296 | 0.028 | 0 | 0 | 0.703 | 0.004 | 0.031 |
| 7 | | | | 0.072 | 0.632 | 0.357 | 0.298 | 0.097 | 0.958 | 0.343 | 0.375 |
| 5 | | | 0.126 | 0.039 | 0.6 | 0.337 | 0.274 | 0.076 | 0.896 | 0.321 | 0.328 |
| 11 | | 0.007 | 0.09 | 0 | 0.545 | 0.288 | 0.206 | 0 | 0.875 | 0.256 | 0.264 |
| 6 | 0.016 | 0.047 | 0.186 | 0.041 | 0.592 | 0.337 | 0.276 | 0.068 | 0.91 | 0.312 | 0.313 |

**Figure 12**
**Pairwise FST values between D. flagellare populations in Eastern Canada. Axis numbers correspond to population identifiers. FST values range from 0 (indicating no genetic differentiation) to 1 (indicating complete genetic differentiation).**

### *3.4 Discussion*

Our findings demonstrate that both habitat heterogeneity (composition) and its spatial arrangement in the landscape (configuration) influence the genetic diversity and structure of *D. flagellare* in old-growth boreal forest patches. We found that the presence of different forest age classes in the landscape emerged as an informative predictor, contributing positively to the overall explanatory power of the genetic diversity of this species. However, the spatial distribution of these forest classes has positive significant effects on genetic diversity and structure of *D. flagellare*.

### 3.4.1 Effects of LCC on genetic diversity and structure

The LCC effects were not uniform for all genetic diversity variables, suggesting that different aspects of diversity respond differently to landscape patterns at various spatial scales. Our first predictions, which suggested a decline in genetic diversity with the reduction in old-growth forest area, is not supported by the data. We found that allelic diversity and Shannon index of *D. flagellare* decreased when old-growth forest cover increased, at scales between 1 and 2 km. This finding contrasts with the consensus that habitat loss reduces genetic diversity (Pinto et al., 2023; Shaw et al., 2025) and supports the idea that old-growth forest reduction does not always have negative effects on species' genetic diversity (Carvalho et al., 2019). In this case, landscapes dominated by old-growth forests at a 1 km scale may create less favorable conditions for gene flow, possibly due to the predominance by competitive dominance of a few genetic lineages in an environment dominated by clonal reproduction (Cronberg et al., 2006; Lang et al., 2021).

On the other hand, the increase in allelic diversity associated with a higher proportion of mid-aged forests (at 8 km) and non-forest lands (at 5 km) suggests these successional habitats could act as complementary habitats that promote gene flow (Dunning et al., 1992; Pavlacky et al., 2009). Specifically, mid-aged forests adjacent to old-growth patches may provide essential resources for the species, such as decomposing wood and optimal moisture levels. Thus, genetic diversity in old-growth forests adjacent to mid-aged forest may benefit from gene flow with populations in forests of different ages.

The potential positive role of forests of different ages is reinforced by the observed patterns in patch density. Our results indicate that a higher density of old-growth and young forest patches positively influences several genetic diversity metrics. This highlights the importance of landscape configuration and the key role of forest patches beyond old-growth stands. Our findings support the idea that both habitat amount and spatial configuration influence species' population dynamics (Bruggeman et al., 2010). Moreover, they align with the hypothesis proposed by Fahrig et al. (2019) that higher patch density can enhance functional connectivity between populations, facilitating gene flow through suitable habitat corridors. Thus, we support our second and third hypotheses and conclude that fragmentation does not always have negative effects on biodiversity. In some cases, fragmentation can even enhance genetic diversity by increasing microhabitat availability in medium age forest as corridors improving landscape functional connectivity.

According to our ordination analysis, while old forest fragmentation (measured as path density) can positively influence *D. flagellare*'s genetic diversity, it also helps maintain its population genetic structure (Figure 10). This could be due to the presence of sufficient functional connectivity in fragmented old forests, allowing gene flow between populations in different patches (Gómez-Fernández et al., 2016). The maintenance of population structure may also result from the synergy between functionally connected old forests and a high-quality matrix composed of mid-aged forests. Mid-aged forests, being structurally more complex than young forests, may act as a low-resistance habitat for gene flow between populations in old forest patches (Ricketts, 2001). Additionally, the presence of mid-aged forests could favor the presence of dispersal vectors that contribute to *D. flagellare*'s population connectivity. Barbé et al. (2016) identified at least five small mammal species capable of dispersing asexual structures of cryptogams in old forests within the study area. Although the authors did not find *D. flagellare* brood bodies in the captured mammals, this does not rule out zoochory as a potential dispersal mechanism for the species.

While genetic similarity among populations may be explained by the connectivity of complementary habitats, genetic differentiation may result from their absence. Contiguous habitats characterized by non-forest land and a high density of young forest patches, could act as a barrier to *D. flagellare*'s gene flow. Such a barrier may have promoted population differentiation through local colonization-extinction events (McCauley, 1989). Within old forest patches, these dynamics might have been shaped by the local extinction of established populations and their subsequent recolonization by propagules originating from nearby young forests. This scenario is plausible given *D. flagellare*'s rapid and abundant production of brood bodies and their ability to quickly germinate in microhabitats already occupied by other colonies (Kimmerer, 1994) could lead to the dominance of a single genotype. Moreover, the dynamics of microhabitat availability, including the appearance and decomposition of deadwood, may contribute to local extinction (Kimmerer, 1994). However, the arrival of brood bodies from young forests is questionable. In some cases, young forests surrounding old forest patches are in early developmental stages, where suitable microhabitats for the species have not yet formed, leading to the species absence.

If young forests are excluded as sources of propagules, the genetic differentiation driven by an unfavorable landscape matrix may be further shaped by patch-scale effects. As reported by Sierra et al. (2023), the reduction in forest patch size can hinder colonization processes, leading to lower colony densities and increased genotypic differentiation. These patterns contrast with their observations in continuous forests, where such effects were absent. In our study, the genetic differentiation observed in some *D. flagellare* populations may be explained by a combination of patch size effects and isolation by resistance, the latter associated with habitat quality gradients across the landscape (Cushman et al., 2006; Sierra et al., 2023).

### 3.4.2 Implications for forest management and conservation

Our results show that landscape structure influences the genetic diversity of *D. flagellare* at spatial scales of 2–6 km, with some effects extending up to 8 km. This suggests that conservation and management actions should prioritize these scales. Importantly, the spatial scale at which genetic diversity responds to landscape differs from that observed for bryophyte communities as a whole (10 km; Hernández-Rodríguez et al. 2024), underscoring the need for multiscale strategies that integrate both genetic and community-level diversity.

Our study highlights the importance of understanding the relative and significant effects of habitat composition and configuration on genetic diversity. Preserving old-growth forest patches remains essential, particularly for species with predominantly asexual reproduction like *D. flagellare*. However, mid-aged forests also contribute by functioning as a high-quality matrix that facilitates dispersal and helps maintain genetic diversity (Arroyo-Rodríguez et al., 2020). These findings can inform future analyses of connectivity in boreal landscapes. In particular, recognizing the role of mid-aged forests will improve the accuracy of least-cost path models and help identify functional biological corridors (Lee et al., 2021), thereby enhancing conservation planning (Kyaschenko et al., 2024).

Finally, our results should not be interpreted as supporting fragmentation processes with habitat loss. Large, continuous tracts of boreal forest remain vital in the face of rapid deforestation and global ecological risks (Gauthier et al., 2015). Rather, we emphasize the potential of landscape heterogeneity to support restoration and connectivity in already altered forests. Effective conservation planning must go beyond preventing habitat loss, incorporating spatial configuration to sustain ecological functions in boreal ecosystems (Arroyo-Rodríguez et al., 2020).

# CONCLUSION

**Résumé des chapitres principaux**. Cette thèse a été conçue pour identifier les seuils de modification de la forêt boréale à l'échelle du paysage permettant de concilier les activités économiques liées à l'exploitation forestière avec la conservation de la biodiversité dans l'Est du Canada. Dans ce contexte, la recherche contribue également au débat actuel sur les effets de la fragmentation per se et de la perte d'habitat sur la biodiversité. Les bryophytes (mousses, hépatiques et Sphagnum) ont été utilisées comme organismes modèles, en raison de leur richesse, leur dominance dans les forêts boréales et leur sensibilité aux changements environnementaux.

Le chapitre II analyse comment la composition et la configuration du paysage (dans un rayon de 10 km) influencent la diversité des bryophytes, en considérant à la fois la richesse spécifique et la composition des communautés. Les résultats ont montré que la quantité et la distribution spatiale des forêts selon leur âge et leur type de végétation sont des facteurs clés dans la structuration de la diversité des bryophytes à l'échelle de la parcelle. De plus, il a été observé que la réponse à ces variables diffère entre les grands groupes de bryophytes. Fait notable, la diversité des hépatiques chute brusquement lorsque les jeunes forêts sont regroupées et couvrent plus de 40 % de la surface d'un paysage de 10 km de rayon. Tandis que la richesse en mousses diminue de manière progressive avec l'augmentation des surfaces de jeunes forêts, les hépatiques permettent d'établir des seuils concrets suggérant jusqu'à quel point le paysage boréal peut être modifié sans compromettre sa diversité végétale. En outre, la fréquence de plusieurs espèces de bryophytes est influencée par la dominance de différents types de végétation, ce qui a motivé l'étude des patrons de rareté au chapitre III.

Les résultats majeurs du chapitre III indiquent que la majorité des espèces de bryophytes sont rares, du fait de leur dispersion et de leur spécialisation pour les forêts de conifères et les tourbières. Ces patrons de rareté s'expliquent principalement par les traits fonctionnels des espèces et les régimes de perturbation régionaux, qui s'avèrent essentiels pour comprendre cette rareté. Plus précisément, les espèces rares tendent à produire de grandes spores et à adopter une stratégie sexuelle dioïque. En outre, le domaine bioclimatique SPMO abrite une plus grande richesse et un nombre plus élevé d'espèces rares comparativement au BFWB, soulignant l'importance de conserver les forêts de conifères dans le SPMO en tant que réservoirs d'espèces bryophytiques rares.

À la lumière des chapitres II et III, certaines espèces présentes dans les vieilles forêts semblent bénéficier de l'agrégation de forêts de conifères, et maintenir leur fréquence à travers différents types de végétation et domaines bioclimatiques. Cela suggère qu'il existe des espèces résilientes aux configurations paysagères. Ce constat a conduit à se demander si, en analysant la diversité génétique d'une espèce commune, il serait possible de détecter des effets du paysage non visibles à travers l'étude de la seule richesse ou abondance. Pour explorer cette hypothèse, le chapitre IV s'est concentré sur le cas de Dicranum flagellare, une mousse caractéristique des vieilles forêts boréales, afin d'évaluer si la structure du paysage influence sa diversité et sa structure génétique.

Les résultats du chapitre IV ont confirmé que la composition et la configuration du paysage affectent la diversité génétique d'espèces apparemment résilientes. En particulier, il a été montré que D. flagellare est sensible à la structure paysagère jusqu'à une échelle de 8 km, avec un effet plus marqué de la configuration que de la composition. De manière surprenante, la fragmentation des forêts primaires est positivement associée au flux génétique, favorisant la diversité et la préservation de la structure génétique de l'espèce. Les forêts de mi-âge ainsi que les zones non boisées ont également été associées à une plus grande diversité génétique et à une différenciation accrue des populations. Ces résultats révèlent des seuils critiques à partir desquels les changements paysagers peuvent influencer la biodiversité du sous-bois dans un rayon de 8 km.

Ainsi, les chapitres II, III et IV fournissent des éléments clés sur les effets de la composition et de la configuration du paysage sur la diversité des bryophytes boréales :

1. Le type de forêt et sa disposition spatiale, en fonction de l'âge et de la végétation dominante, influencent la richesse et la composition des espèces non vasculaires dans les vieilles forêts boréales.
2. L'augmentation de la surface et de l'agrégation des jeunes forêts réduit la richesse et modifie le turnover des espèces dans les vieux peuplements.
3. La richesse en hépatiques diminue brusquement lorsque les jeunes forêts couvrent plus de 40 % du paysage (dans un rayon de 10 km), ce qui constitue un seuil critique pour la gestion forestière.
4. La diversité bryophytique est déterminée par la présence d'espèces rares spécialistes, dispersées dans les forêts de conifères et les tourbières.
5. Les domaines bioclimatiques SPMO et BFWB présentent un gradient de richesse et de rareté, avec davantage d'espèces rares dans le SPMO.
6. Ce gradient est influencé par un filtre environnemental : plusieurs espèces communes dans le SPMO sont rares dans le BFWB.
7. La rareté des espèces dans le BFWB est liée à un moindre potentiel de dispersion, associé à la production de grandes spores et à la sexualité dioïque.
8. L'analyse génétique révèle des effets paysagers que les mesures classiques de biodiversité peuvent ne pas détecter.
9. La structure du paysage dans un rayon de 8 km influence la diversité et la structure génétique de D. flagellare.
10. Les paysages composés de forêts de mi-âge et de zones non boisées favorisent la diversité génétique et la différenciation des populations.
11. La fragmentation per se des forêts primaires est positivement associée au flux génétique, préservant la diversité génétique.
12. La perte d'habitat (composition) n'est pas directement associée à une réduction de la diversité végétale, et la fragmentation per se peut avoir des effets positifs à plusieurs échelles sur la diversité bryophytique.

Nos résultats répondent aux objectifs de recherche en identifiant les caractéristiques du paysage qui façonnent la diversité des bryophytes à différentes échelles.

**Contributions principales à la recherche**. Parmi les principales contributions de cette thèse, plusieurs éléments se distinguent. Tout d'abord, elle démontre que la composition et la configuration du paysage exercent des effets différenciés sur la richesse spécifique et la composition des communautés bryophytiques, en particulier à l'échelle paysagère d'un rayon de 10 km. Cette distinction permet d'identifier les types de forêts et les structures paysagères les plus favorables à la conservation de la biodiversité bryophytique boréale. En approfondissant cette relation, l'étude révèle également l'existence d'un seuil critique au-delà duquel la richesse en hépatiques chute fortement, en lien avec l'agrégation des jeunes forêts. Ce seuil constitue un repère important pour orienter les stratégies d'aménagement forestier durable.

La recherche a aussi permis une évaluation approfondie de la rareté des espèces à l'échelle régionale, en intégrant à la fois leur fréquence et leur spécialisation écologique. Cette approche souligne le rôle clé que joue la diversité des types de végétation dans le maintien des espèces rares. Dans cette optique, l'étude met en lumière un gradient de richesse et de rareté entre les domaines bioclimatiques du SPMO et du BFWB, en soulignant l'importance des forêts de conifères du SPMO comme refuges potentiels pour ces espèces.

L'exploration des traits fonctionnels associés à la rareté, tels que la taille des spores et la sexualité, permet de mieux comprendre les mécanismes sous-jacents à la dispersion et à la persistance des espèces. Par ailleurs, l'utilisation d'approches de génétique des populations a révélé des effets paysagers subtils, souvent imperceptibles à travers les métriques écologiques classiques, comme le montre le cas de D. flagellare. Cette dimension génétique enrichit notre compréhension de la résilience des espèces communes et éclaire les dynamiques évolutives au sein de paysages anthropisés.

Fait notable, les résultats suggèrent qu'un certain degré de fragmentation du paysage peut exercer un effet positif sur la diversité génétique, remettant en question l'idée selon laquelle la fragmentation aurait systématiquement des conséquences négatives sur la biodiversité — en particulier chez les organismes possédant une forte capacité de dispersion clonale.

Enfin, cette thèse apporte une contribution méthodologique importante à l'analyse intégrée de la biodiversité, en combinant des données écologiques, la distribution des espèces, leurs traits fonctionnels ainsi que la génétique des populations dans une approche centrée sur l'écologie du paysage. Cette intégration multiscalaire et multidimensionnelle ouvre la voie à une compréhension plus fine et nuancée des processus qui structurent la biodiversité boréale.

**Perspectives et implications pour l'aménagement forestier**. Les résultats obtenus dans le cadre de cette thèse ouvrent de nouvelles perspectives pour la gestion durable des forêts boréales, en mettant en lumière l'importance d'intégrer la biodiversité non vasculaire dans les politiques de conservation et d'aménagement du territoire.

L'un des apports clés de cette recherche est la définition de seuils écologiques précis pour le maintien de la diversité des bryophytes. Il est ainsi recommandé de conserver au minimum 60 % de forêts matures dans un paysage d'un rayon de 10 km afin de préserver la richesse spécifique, en particulier les espèces rares qui dépendent de ces habitats. Par ailleurs, la présence de forêts anciennes dans un rayon de 3 km autour d'un site apparaît essentielle pour favoriser la connectivité écologique, condition nécessaire au maintien des populations locales.

Cette thèse met également en évidence des effets potentiellement positifs de la fragmentation per se, en contradiction avec l'idée selon laquelle la fragmentation aurait systématiquement des conséquences négatives sur la biodiversité. Une certaine hétérogénéité paysagère pourrait en effet soutenir la diversité génétique et des espèces. Cela ne constitue pas une justification pour encourager la fragmentation, mais suggère plutôt d'en reconnaître les dynamiques dans les efforts de restauration, en valorisant par exemple les forêts de mi-âge qui jouent un rôle complémentaire entre les îlots de forêts anciennes.

La recherche souligne également la nécessité de prioriser la protection des forêts anciennes et des tourbières, qui fonctionnent comme des refuges cruciaux pour de nombreuses espèces spécialistes et avec de petites populations. Leur conservation devrait être placée au cœur des stratégies de gestion à long terme. En parallèle, une gestion adaptative fondée sur la diversité fonctionnelle des espèces serait bénéfique. L'intégration des traits fonctionnels permettrait d'identifier plus finement les espèces vulnérables aux perturbations du paysage et d'ajuster les efforts de conservation en conséquence.

Enfin, cette étude encourage la valorisation de mosaïques paysagères diversifiées. Plutôt que de viser l'homogénéité, qu'elle soit structurelle ou compositionnelle, une mosaïque équilibrée de forêts matures, de forêts de transition et d'habitats ouverts offrirait un compromis prometteur entre les objectifs de production forestière et ceux de conservation de la biodiversité.

**Recherche future**. Plusieurs axes de recherche émergent de cette thèse et ouvrent la voie à des investigations complémentaires visant à approfondir notre compréhension de l'écologie du paysage boréal à travers sa biodiversité des plantes non vasculaire.

Tout d'abord, l'analyse de la diversité fonctionnelle en relation avec la composition et la configuration du paysage représente une piste prometteuse. En évaluant cette diversité à travers des métriques explicites ou des traits fonctionnels spécifiques, il serait possible d'identifier les caractéristiques écologiques qui rendent certaines espèces plus sensibles aux dynamiques environnementales. Une telle approche permettrait non seulement de mieux comprendre les réponses différentielles des espèces aux modifications du paysage, mais également de prioriser la conservation des fragments forestiers abritant les espèces les plus vulnérables.

Dans la continuité, la question de la connectivité structurelle et fonctionnelle des paysages mérite d'être approfondie. Cette thèse a révélé que l'agrégation des forêts de conifères tend à réduire la richesse en hépatiques et en sphaignes, tandis que celle des forêts de mi-âge semble favoriser la diversité génétique de D. flagellare. Ces résultats, fondés sur une lecture spatiale de la connectivité, gagneraient à être complétés par des outils d'analyse paysagère plus avancés, permettant par exemple de cartographier les corridors écologiques et d'évaluer plus précisément le rôle complémentaire des forêts secondaires dans la connectivité des communautés bryophytiques.

Par ailleurs, une compréhension plus fine de la rareté des espèces à une échelle intermédiaire constituerait un apport significatif. Alors que cette thèse a exploré la rareté à l'échelle bioclimatique, une analyse menée dans un type forestier spécifique ou le long de gradients de perturbation pourrait révéler les facteurs qui conditionnent le déclin ou la persistance des populations locales. Ce niveau de détail offrirait un éclairage essentiel sur les processus par lesquels certaines espèces deviennent rares ou communes à l'échelle locale.

Enfin, l'étude des adaptations locales des populations vivant dans des forêts anciennes constitue un autre axe de recherche pertinent. En identifiant les populations fortement adaptées à leur environnement local, il serait possible de déterminer celles qui sont particulièrement vulnérables aux changements rapides du paysage. Cette information est précieuse pour anticiper les effets du changement climatique ou des pratiques sylvicoles intensives, et mieux évaluer la résilience des communautés non vasculaires face aux perturbations futures.

**Sommaire**. La composition et la configuration du paysage influencent de manière significative la diversité des bryophytes boréales, depuis l'échelle génétique jusqu'à celle des communautés. Ces effets ont été évalués en tenant compte à la fois de l'âge des peuplements forestiers et de leur type de végétation, et leur portée s'étend jusqu'à 8 à 10 km autour des fragments étudiés. Ce rôle structurant du paysage sur la diversité bryophytique a des implications à l'échelle bioclimatique et, en interaction avec les traits fonctionnels des espèces, contribue à expliquer les patrons spécifiques de rareté observés chez ces petites plantes. Ainsi, cette étude, éclairée par les avancées récentes en écologie du paysage, répond à l'objectif d'explorer comment les facteurs paysagers — et non seulement locaux — déterminent la diversité et la distribution des plantes non vasculaires.

# APPENDICE A – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE II

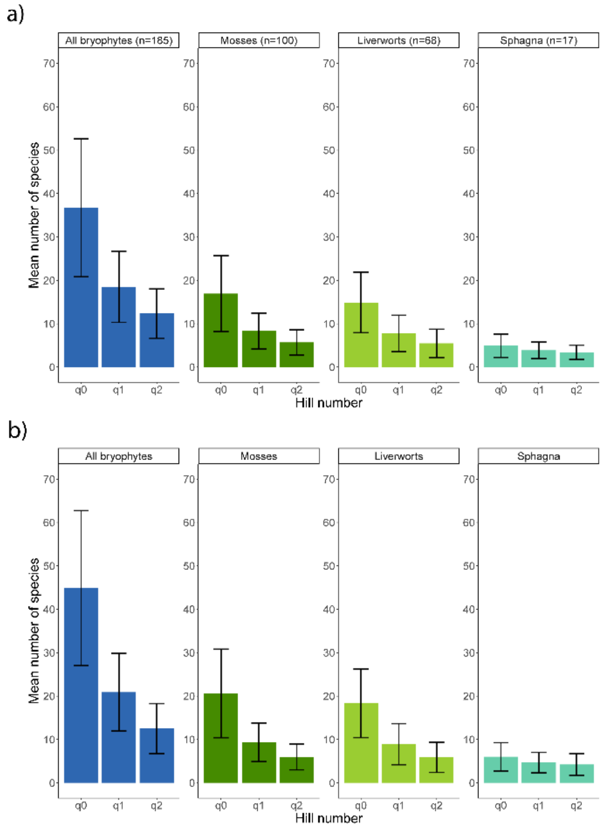


**Figure A 1**
**Diversity values by all bryophytes and by guild recorded in the western boreal forest patches of Quebec with observed (a) and expected data (b). Hill numbers q0 = total species, q1 = common species, q2 = dominant species.**

**Table A 1**
**Correlation and statistical significance for a) observed and b) expected bryophyte diversity. Bryo = all bryophyte guild, Moss = mosses, Live = liverworts, Spha = Sphagna, q0 = species richness, q1 = common species, q2 = dominant species.**

a) Observed data

R = correlation

| | Bryoq0 | Bryo q1 | Bryo q2 | Moss q0 | Moss q1 | Moss q2 | Live q0 | Live q1 | Live q2 | Spha q0 | Spha q1 | Spha q2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bryoq0 | 1 | 0.85 | 0.7 | 0.93 | 0.82 | 0.7 | 0.9 | 0.61 | 0.42 | 0.57 | 0.57 | 0.57 |
| Bryoq1 | 0.85 | 1 | 0.96 | 0.72 | 0.83 | 0.79 | 0.86 | 0.87 | 0.76 | 0.47 | 0.51 | 0.53 |
| Bryoq2 | 0.7 | 0.96 | 1 | 0.57 | 0.78 | 0.79 | 0.75 | 0.89 | 0.84 | 0.34 | 0.4 | 0.41 |
| Mossq0 | 0.93 | 0.72 | 0.57 | 1 | 0.89 | 0.78 | 0.71 | 0.39 | 0.21 | 0.39 | 0.4 | 0.41 |
| Mossq1 | 0.82 | 0.83 | 0.78 | 0.89 | 1 | 0.97 | 0.66 | 0.54 | 0.41 | 0.25 | 0.29 | 0.32 |
| Mossq2 | 0.7 | 0.79 | 0.79 | 0.78 | 0.97 | 1 | 0.57 | 0.53 | 0.44 | 0.13 | 0.17 | 0.2 |
| Liveq0 | 0.9 | 0.86 | 0.75 | 0.71 | 0.66 | 0.57 | 1 | 0.81 | 0.64 | 0.44 | 0.44 | 0.45 |
| Liveq1 | 0.61 | 0.87 | 0.89 | 0.39 | 0.54 | 0.53 | 0.81 | 1 | 0.96 | 0.25 | 0.32 | 0.34 |
| Liveq2 | 0.42 | 0.76 | 0.84 | 0.21 | 0.41 | 0.44 | 0.64 | 0.96 | 1 | 0.14 | 0.22 | 0.25 |
| Spagq0 | 0.57 | 0.47 | 0.34 | 0.39 | 0.25 | 0.13 | 0.44 | 0.25 | 0.14 | 1 | 0.94 | 0.89 |
| Spagq1 | 0.57 | 0.51 | 0.4 | 0.4 | 0.29 | 0.17 | 0.44 | 0.32 | 0.22 | 0.94 | 1 | 0.99 |
| Spagq2 | 0.57 | 0.53 | 0.41 | 0.41 | 0.32 | 0.2 | 0.45 | 0.34 | 0.25 | 0.89 | 0.99 | 1 |

P = significance

| | Bryoq0 | Bryo q1 | Bryo q2 | Moss q0 | Moss q1 | Moss q2 | Live q0 | Live q1 | Live q2 | Spag q0 | Spag q1 | Spag q2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bryoq0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Bryoq1 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Bryoq2 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mossq0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0.05 | 0 | 0 | 0 |
| Mossq1 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0.02 | 0.01 | 0 |
| Mossq2 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0.21 | 0.1 | 0.06 |
| Liveq0 | 0 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 |
| Liveq1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0.02 | 0 | 0 |
| Liveq2 | 0 | 0 | 0 | 0.05 | 0 | 0 | 0 | 0 | #N/D | 0.19 | 0.04 | 0.02 |
| Spagq0 | 0 | 0 | 0 | 0 | 0.02 | 0.21 | 0 | 0.02 | 0.19 | #N/D | 0 | 0 |
| Spagq1 | 0 | 0 | 0 | 0 | 0.01 | 0.1 | 0 | 0 | 0.04 | 0 | #N/D | 0 |
| Spagq2 | 0 | 0 | 0 | 0 | 0 | 0.06 | 0 | 0 | 0.02 | 0 | 0 | #N/D |

**Table A 1**
**Correlation and statistical significance for a) observed and b) expected bryophyte diversity. Bryo = all bryophyte guild, Moss = mosses, Live = liverworts, Spha = Sphagna, q0 = species richness, q1 = common species, q2 = dominant species.**

a) Expected data

R = correlation

| | Bryoq0 | Bryo q1 | Bryo q2 | Moss q0 | Moss q1 | Moss q2 | Live q0 | Live q1 | Live q2 | Spag q0 | Spag q1 | Spag q2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bryoq0 | 1 | 0.81 | 0.67 | 0.91 | 0.8 | 0.67 | 0.88 | 0.56 | 0.37 | 0.51 | 0.5 | 0.46 |
| Bryoq1 | 0.81 | 1 | 0.95 | 0.65 | 0.81 | 0.77 | 0.81 | 0.87 | 0.77 | 0.43 | 0.49 | 0.51 |
| Bryoq2 | 0.67 | 0.95 | 1 | 0.52 | 0.74 | 0.76 | 0.7 | 0.86 | 0.83 | 0.31 | 0.38 | 0.46 |
| Mossq0 | 0.91 | 0.65 | 0.52 | 1 | 0.86 | 0.73 | 0.65 | 0.31 | 0.14 | 0.3 | 0.32 | 0.32 |
| Mossq1 | 0.8 | 0.81 | 0.74 | 0.86 | 1 | 0.96 | 0.6 | 0.5 | 0.39 | 0.21 | 0.28 | 0.34 |
| Mossq2 | 0.67 | 0.77 | 0.76 | 0.73 | 0.96 | 1 | 0.52 | 0.49 | 0.42 | 0.13 | 0.19 | 0.24 |
| Liveq0 | 0.88 | 0.81 | 0.7 | 0.65 | 0.6 | 0.52 | 1 | 0.77 | 0.59 | 0.38 | 0.37 | 0.37 |
| Liveq1 | 0.56 | 0.87 | 0.86 | 0.31 | 0.5 | 0.49 | 0.77 | 1 | 0.95 | 0.25 | 0.33 | 0.4 |
| Liveq2 | 0.37 | 0.77 | 0.83 | 0.14 | 0.39 | 0.42 | 0.59 | 0.95 | 1 | 0.17 | 0.27 | 0.36 |
| Spagq0 | 0.51 | 0.43 | 0.31 | 0.3 | 0.21 | 0.13 | 0.38 | 0.25 | 0.17 | 1 | 0.91 | 0.67 |
| Spagq1 | 0.5 | 0.49 | 0.38 | 0.32 | 0.28 | 0.19 | 0.37 | 0.33 | 0.27 | 0.91 | 1 | 0.87 |
| Spagq2 | 0.46 | 0.51 | 0.46 | 0.32 | 0.34 | 0.24 | 0.37 | 0.4 | 0.36 | 0.67 | 0.87 | 1 |

P = significance

| | Bryoq0 | Bryo q1 | Bryo q2 | Moss q0 | Moss q1 | Moss q2 | Live q0 | Live q1 | Live q2 | Spag q0 | Spag q1 | Spag q2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bryoq0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Bryoq1 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Bryoq2 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mossq0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0.19 | 0 | 0 | 0 |
| Mossq1 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0.04 | 0.01 | 0 |
| Mossq2 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0.22 | 0.07 | 0.02 |
| Liveq0 | 0 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0 | 0 | 0 | 0 |
| Liveq1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | #N/D | 0 | 0.02 | 0 | 0 |
| Liveq2 | 0 | 0 | 0 | 0.19 | 0 | 0 | 0 | 0 | #N/D | 0.12 | 0.01 | 0 |
| Spagq0 | 0 | 0 | 0 | 0 | 0.04 | 0.22 | 0 | 0.02 | 0.12 | #N/D | 0 | 0 |
| Spagq1 | 0 | 0 | 0 | 0 | 0.01 | 0.07 | 0 | 0 | 0.01 | 0 | #N/D | 0 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Spagq2 | 0 | 0 | 0 | 0 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | #N/D |

Methods A1. First, for both observed and expected data, we identified bryophyte diversity outliers by using histograms and boxplots for each variable. We found just one outlier in liverwort values, and it was removed in further analyses. Then, we did scatterplots of each explanatory variable versus response variables to visualize the relationships between landscape metrics and patch size, and bryophyte taxonomic diversity and composition. In the case of q0 (species richness) for observed data, we used a Poisson distribution (Crawley, 2007), while for q1 and q2 and all Hill numbers for expected data, we used a Gaussian distribution.

Second, after diagnosing our model type, we applied a logarithmic transformation to improve model fit. Because we had some sites with 0 values for sphagna data, we added one to each value of the sphagna index to avoid errors in log transformation. Also, we used the restricted maximum likelihood method (REML) (Patterson & Thompson, 1971)to have an optimal smoothing parameter for the curve variation in the models.

Third, we assessed concurvity, a nonlinear measure analogue to collinearity in linear regression (Gu et al., 2010), among landscape metrics using the concurvity function with the mgcv package. We used observed and expected diversity data for the concurvity assessment between landscape metrics. We estimated the concurvity for each explanatory variable, computing three related indices (worst, observed, and estimate) weighted between 0 and 1 (0 = no concurvity problem, and 1 = identifiability lacking). For all models, we removed variables with concurvity with the worst index => 0.8. The worst concurvity indices for explanatory variables in observed data were the same for expected data models (Table S2 and S3). For the models with explanatory variables based on the landscape age classification, we removed the density of old forest patches (concurvity > 0.96) and the target patch size (concurvity > 0.84). For models with explanatory variables based on the landscape forest type classification, mixed and deciduous forest patch density (concurvity > 0.97 and > 0.87 respectively) were removed.

In a fourth step, we ran our models without explanatory variables with concurvity => 0.8. We tested models removing non-significative variables to identify explanatory variables that reduce the AIC values to improve our model fit. After, we chose the model based on the lowest Akaike’s Information Criterion.

**Table A 1**
**Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

a) Observed data

Mosses q0

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.96 | 0.43 | 0.42 | 0.76 | 0.67 | 0.84 |
| OFPD | 0.96 | 1.00 | 0.52 | 0.56 | 0.62 | 0.50 | 0.84 |
| %MAF | 0.43 | 0.52 | 1.00 | 0.77 | 0.61 | 0.48 | 0.44 |
| MAPD | 0.42 | 0.56 | 0.77 | 1.00 | 0.71 | 0.43 | 0.35 |
| %YF | 0.76 | 0.62 | 0.61 | 0.71 | 1.00 | 0.54 | 0.58 |
| YFPD | 0.67 | 0.50 | 0.48 | 0.43 | 0.54 | 1.00 | 0.47 |
| TPS | 0.84 | 0.84 | 0.44 | 0.35 | 0.58 | 0.47 | 1.00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 5E-01 | 1E-01 | 1E-01 | 4E-01 | 2E-01 | 6E-01 |
| OFPD | 4E-01 | 1E+00 | 2E-01 | 3E-01 | 3E-01 | 9E-02 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 6E-01 | 3E-01 | 2E-01 | 9E-02 |
| MAPD | 2E-01 | 5E-01 | 5E-01 | 1E+00 | 3E-01 | 1E-01 | 1E-01 |
| %YF | 3E-01 | 3E-01 | 4E-01 | 6E-01 | 1E+00 | 5E-01 | 4E-01 |
| YFPD | 8E-02 | 2E-01 | 2E-01 | 7E-02 | 1E-01 | 1E+00 | 1E-01 |
| TPS | 2E-01 | 4E-01 | 2E-01 | 2E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 6E-01 | 1E-01 | 1E-01 | 4E-01 | 1E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 3E-01 | 3E-01 | 1E-01 | 3E-01 |
| %MAF | 1E-01 | 2E-01 | 1E+00 | 6E-01 | 3E-01 | 2E-01 | 1E-01 |
| MAPD | 2E-01 | 4E-01 | 6E-01 | 1E+00 | 2E-01 | 1E-01 | 1E-01 |
| %YF | 4E-01 | 3E-01 | 3E-01 | 5E-01 | 1E+00 | 4E-01 | 3E-01 |
| YFPD | 1E-01 | 2E-01 | 1E-01 | 8E-02 | 2E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 4E-01 | 1E-01 | 2E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 2**

**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q0

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 1E+00 | 5E-01 | 4E-01 | 8E-01 | 7E-01 | 1E+00 |
| OFPD | 1E+00 | 1E+00 | 5E-01 | 6E-01 | 6E-01 | 5E-01 | 1E+00 |
| %MAF | 5E-01 | 5E-01 | 1E+00 | 8E-01 | 6E-01 | 5E-01 | 4E-01 |
| MAPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 7E-01 | 4E-01 | 4E-01 |
| %YF | 8E-01 | 6E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 7E-01 |
| YFPD | 7E-01 | 5E-01 | 5E-01 | 4E-01 | 5E-01 | 1E+00 | 5E-01 |
| TPS | 1E+00 | 1E+00 | 4E-01 | 4E-01 | 7E-01 | 5E-01 | 1E+00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 6E-01 | 2E-01 | 5E-02 | 4E-01 | 3E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 6E-02 | 2E-01 | 2E-01 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 2E-01 | 1E-01 | 2E-01 | 2E-01 |
| MAPD | 3E-01 | 5E-01 | 6E-01 | 1E+00 | 2E-01 | 1E-01 | 2E-01 |
| %YF | 4E-01 | 3E-01 | 4E-01 | 1E-01 | 1E+00 | 4E-01 | 3E-01 |
| YFPD | 1E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 5E-01 | 3E-01 | 9E-02 | 3E-02 | 6E-02 | 1E+00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.54 | 0.11 | 0.17 | 0.39 | 0.19 | 0.53 |
| OFPD | 0.61 | 1.00 | 0.16 | 0.35 | 0.25 | 0.13 | 0.36 |
| %MAF | 0.15 | 0.25 | 1.00 | 0.55 | 0.29 | 0.21 | 0.12 |
| MAPD | 0.22 | 0.43 | 0.56 | 1.00 | 0.24 | 0.13 | 0.12 |
| %YF | 0.37 | 0.32 | 0.37 | 0.54 | 1.00 | 0.38 | 0.35 |
| YFPD | 0.16 | 0.18 | 0.16 | 0.09 | 0.18 | 1.00 | 0.11 |
| TPS | 0.54 | 0.45 | 0.14 | 0.20 | 0.13 | 0.18 | 1.00 |

**Table A 3**

**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q1

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 1E+00 | 5E-01 | 4E-01 | 8E-01 | 7E-01 | 1E+00 |
| OFPD | 1E+00 | 1E+00 | 5E-01 | 6E-01 | 6E-01 | 5E-01 | 1E+00 |
| %MAF | 5E-01 | 5E-01 | 1E+00 | 8E-01 | 6E-01 | 5E-01 | 4E-01 |
| MAPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 7E-01 | 4E-01 | 4E-01 |
| %YF | 8E-01 | 6E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 7E-01 |
| YFPD | 7E-01 | 5E-01 | 5E-01 | 4E-01 | 5E-01 | 1E+00 | 5E-01 |
| TPS | 1E+00 | 1E+00 | 4E-01 | 4E-01 | 7E-01 | 5E-01 | 1E+00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 6E-01 | 1E-01 | 1E-01 | 5E-01 | 3E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 2E-01 | 3E-01 | 2E-01 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 3E-01 | 5E-02 | 2E-01 | 2E-01 |
| MAPD | 3E-01 | 5E-01 | 6E-01 | 1E+00 | 1E-01 | 1E-01 | 2E-01 |
| %YF | 4E-01 | 3E-01 | 5E-01 | 2E-01 | 1E+00 | 4E-01 | 3E-01 |
| YFPD | 1E-01 | 2E-01 | 7E-02 | 1E-01 | 3E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 5E-01 | 2E-01 | 1E-01 | 5E-02 | 7E-02 | 1E+00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 5E-01 | 1E-01 | 2E-01 | 4E-01 | 2E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 4E-01 | 2E-01 | 1E-01 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 5E-01 | 3E-01 | 2E-01 | 1E-01 |
| MAPD | 2E-01 | 4E-01 | 6E-01 | 1E+00 | 2E-01 | 1E-01 | 1E-01 |
| %YF | 4E-01 | 3E-01 | 4E-01 | 5E-01 | 1E+00 | 4E-01 | 4E-01 |
| YFPD | 2E-01 | 2E-01 | 2E-01 | 9E-02 | 2E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 5E-01 | 1E-01 | 2E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 4**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

| Sphagna q0 | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Worst* | | | | | | | |
| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
| %OF | 1E+00 | 1E+00 | 4E-01 | 4E-01 | 8E-01 | 7E-01 | 8E-01 |
| OFPD | 1E+00 | 1E+00 | 5E-01 | 6E-01 | 6E-01 | 5E-01 | 8E-01 |
| %MAF | 4E-01 | 5E-01 | 1E+00 | 8E-01 | 6E-01 | 5E-01 | 4E-01 |
| MAPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 7E-01 | 4E-01 | 4E-01 |
| %YF | 8E-01 | 6E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 6E-01 |
| YFPD | 7E-01 | 5E-01 | 5E-01 | 4E-01 | 5E-01 | 1E+00 | 5E-01 |
| TPS | 8E-01 | 8E-01 | 4E-01 | 4E-01 | 6E-01 | 5E-01 | 1E+00 |
| | | | | | | | |
| *Observed* | | | | | | | |
| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
| %OF | 1.00 | 0.59 | 0.12 | 0.17 | 0.41 | 0.16 | 0.56 |
| OFPD | 0.65 | 1.00 | 0.18 | 0.42 | 0.29 | 0.09 | 0.34 |
| %MAF | 0.12 | 0.29 | 1.00 | 0.65 | 0.33 | 0.23 | 0.09 |
| MAPD | 0.28 | 0.37 | 0.59 | 1.00 | 0.26 | 0.13 | 0.10 |
| %YF | 0.42 | 0.34 | 0.44 | 0.46 | 1.00 | 0.45 | 0.37 |
| YFPD | 0.12 | 0.23 | 0.07 | 0.06 | 0.14 | 1.00 | 0.11 |
| TPS | 0.49 | 0.42 | 0.18 | 0.21 | 0.14 | 0.16 | 1.00 |
| | | | | | | | |
| *Estimate* | | | | | | | |
| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
| %OF | 1E+00 | 6E-01 | 1E-01 | 1E-01 | 4E-01 | 1E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 3E-01 | 3E-01 | 1E-01 | 3E-01 |
| %MAF | 1E-01 | 2E-01 | 1E+00 | 6E-01 | 3E-01 | 2E-01 | 1E-01 |
| MAPD | 2E-01 | 4E-01 | 6E-01 | 1E+00 | 2E-01 | 1E-01 | 1E-01 |
| %YF | 4E-01 | 3E-01 | 3E-01 | 5E-01 | 1E+00 | 4E-01 | 3E-01 |
| YFPD | 1E-01 | 2E-01 | 1E-01 | 8E-02 | 2E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 4E-01 | 1E-01 | 2E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 5**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

b) Expected data

Mosses q0

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.96 | 0.43 | 0.42 | 0.76 | 0.67 | 0.84 |
| OFPD | 0.96 | 1.00 | 0.52 | 0.56 | 0.62 | 0.50 | 0.84 |
| %MAF | 0.43 | 0.52 | 1.00 | 0.77 | 0.61 | 0.48 | 0.44 |
| MAPD | 0.42 | 0.56 | 0.77 | 1.00 | 0.71 | 0.43 | 0.35 |
| %YF | 0.76 | 0.62 | 0.61 | 0.71 | 1.00 | 0.54 | 0.58 |
| YFPD | 0.67 | 0.50 | 0.48 | 0.43 | 0.54 | 1.00 | 0.47 |
| TPS | 0.84 | 0.84 | 0.44 | 0.35 | 0.58 | 0.47 | 1.00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 5E-01 | 1E-01 | 1E-01 | 4E-01 | 2E-01 | 6E-01 |
| OFPD | 3E-01 | 1E+00 | 2E-01 | 3E-01 | 3E-01 | 9E-02 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 6E-01 | 3E-01 | 2E-01 | 9E-02 |
| MAPD | 2E-01 | 5E-01 | 5E-01 | 1E+00 | 3E-01 | 1E-01 | 1E-01 |
| %YF | 2E-01 | 3E-01 | 4E-01 | 6E-01 | 1E+00 | 5E-01 | 4E-01 |
| YFPD | 9E-02 | 2E-01 | 2E-01 | 6E-02 | 1E-01 | 1E+00 | 1E-01 |
| TPS | 1E-01 | 4E-01 | 2E-01 | 2E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.57 | 0.10 | 0.12 | 0.40 | 0.15 | 0.51 |
| OFPD | 0.64 | 1.00 | 0.15 | 0.30 | 0.26 | 0.10 | 0.33 |
| %MAF | 0.13 | 0.23 | 1.00 | 0.55 | 0.29 | 0.19 | 0.12 |
| MAPD | 0.23 | 0.38 | 0.56 | 1.00 | 0.24 | 0.13 | 0.12 |
| %YF | 0.38 | 0.30 | 0.35 | 0.55 | 1.00 | 0.39 | 0.34 |
| YFPD | 0.14 | 0.17 | 0.15 | 0.08 | 0.18 | 1.00 | 0.11 |
| TPS | 0.49 | 0.42 | 0.13 | 0.19 | 0.12 | 0.18 | 1.00 |

**Table A 6**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q0

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 1E+00 | 5E-01 | 4E-01 | 8E-01 | 7E-01 | 1E+00 |
| OFPD | 1E+00 | 1E+00 | 5E-01 | 6E-01 | 6E-01 | 5E-01 | 1E+00 |
| %MAF | 5E-01 | 5E-01 | 1E+00 | 8E-01 | 6E-01 | 5E-01 | 4E-01 |
| MAPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 7E-01 | 4E-01 | 4E-01 |
| %YF | 8E-01 | 6E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 7E-01 |
| YFPD | 7E-01 | 5E-01 | 5E-01 | 4E-01 | 5E-01 | 1E+00 | 5E-01 |
| TPS | 1E+00 | 1E+00 | 4E-01 | 4E-01 | 7E-01 | 5E-01 | 1E+00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1E+00 | 5E-01 | 1E-01 | 2E-01 | 4E-01 | 2E-01 | 5E-01 |
| OFPD | 6E-01 | 1E+00 | 2E-01 | 4E-01 | 2E-01 | 2E-01 | 4E-01 |
| %MAF | 1E-01 | 3E-01 | 1E+00 | 6E-01 | 1E-01 | 1E-01 | 2E-01 |
| MAPD | 3E-01 | 5E-01 | 6E-01 | 1E+00 | 2E-01 | 1E-01 | 2E-01 |
| %YF | 4E-01 | 3E-01 | 5E-01 | 6E-01 | 1E+00 | 3E-01 | 3E-01 |
| YFPD | 1E-01 | 2E-01 | 7E-02 | 8E-02 | 2E-01 | 1E+00 | 1E-01 |
| TPS | 5E-01 | 4E-01 | 2E-01 | 2E-01 | 4E-02 | 7E-02 | 1E+00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.54 | 0.11 | 0.17 | 0.39 | 0.19 | 0.53 |
| OFPD | 0.61 | 1.00 | 0.16 | 0.35 | 0.25 | 0.13 | 0.36 |
| %MAF | 0.15 | 0.25 | 1.00 | 0.55 | 0.29 | 0.21 | 0.12 |
| MAPD | 0.22 | 0.43 | 0.56 | 1.00 | 0.24 | 0.13 | 0.12 |
| %YF | 0.37 | 0.32 | 0.37 | 0.54 | 1.00 | 0.38 | 0.35 |
| YFPD | 0.16 | 0.18 | 0.16 | 0.09 | 0.18 | 1.00 | 0.11 |
| TPS | 0.54 | 0.45 | 0.14 | 0.20 | 0.13 | 0.18 | 1.00 |

**Table A 7**

**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q1

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.96 | 0.45 | 0.43 | 0.76 | 0.68 | 0.97 |
| OFPD | 0.96 | 1.00 | 0.52 | 0.60 | 0.64 | 0.50 | 0.98 |
| %MAF | 0.45 | 0.52 | 1.00 | 0.78 | 0.61 | 0.53 | 0.44 |
| MAPD | 0.43 | 0.60 | 0.78 | 1.00 | 0.70 | 0.44 | 0.37 |
| %YF | 0.76 | 0.64 | 0.61 | 0.70 | 1.00 | 0.53 | 0.68 |
| YFPD | 0.68 | 0.50 | 0.53 | 0.44 | 0.53 | 1.00 | 0.47 |
| TPS | 0.97 | 0.98 | 0.44 | 0.37 | 0.68 | 0.47 | 1.00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.51 | 0.14 | 0.15 | 0.47 | 0.31 | 0.47 |
| OFPD | 0.47 | 1.00 | 0.20 | 0.19 | 0.32 | 0.19 | 0.36 |
| %MAF | 0.15 | 0.29 | 1.00 | 0.30 | 0.04 | 0.14 | 0.18 |
| MAPD | 0.27 | 0.52 | 0.59 | 1.00 | 0.14 | 0.12 | 0.16 |
| %YF | 0.48 | 0.34 | 0.45 | 0.20 | 1.00 | 0.34 | 0.31 |
| YFPD | 0.12 | 0.21 | 0.07 | 0.11 | 0.28 | 1.00 | 0.12 |
| TPS | 0.25 | 0.39 | 0.19 | 0.15 | 0.06 | 0.07 | 1.00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.54 | 0.11 | 0.17 | 0.39 | 0.19 | 0.53 |
| OFPD | 0.61 | 1.00 | 0.16 | 0.35 | 0.25 | 0.13 | 0.36 |
| %MAF | 0.15 | 0.25 | 1.00 | 0.55 | 0.29 | 0.21 | 0.12 |
| MAPD | 0.22 | 0.43 | 0.56 | 1.00 | 0.24 | 0.13 | 0.12 |
| %YF | 0.37 | 0.32 | 0.37 | 0.54 | 1.00 | 0.38 | 0.35 |
| YFPD | 0.16 | 0.18 | 0.16 | 0.09 | 0.18 | 1.00 | 0.11 |
| TPS | 0.54 | 0.45 | 0.14 | 0.20 | 0.13 | 0.18 | 1.00 |

**Table A 8**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the age of landscape patches for a) observed and b) expected bryophyte diversity values. %OF = Percentage of old forest; OFDP = Old forest density patches; %MAF = Percentage of medium age forest; MADP = Medium age density patches; %YF = Percentage of young forest; YFPD = Young forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Sphagna q0

*Worst*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.96 | 0.43 | 0.42 | 0.76 | 0.67 | 0.84 |
| OFPD | 0.96 | 1.00 | 0.52 | 0.56 | 0.62 | 0.50 | 0.84 |
| %MAF | 0.43 | 0.52 | 1.00 | 0.77 | 0.61 | 0.48 | 0.44 |
| MAPD | 0.42 | 0.56 | 0.77 | 1.00 | 0.71 | 0.43 | 0.35 |
| %YF | 0.76 | 0.62 | 0.61 | 0.71 | 1.00 | 0.54 | 0.58 |
| YFPD | 0.67 | 0.50 | 0.48 | 0.43 | 0.54 | 1.00 | 0.47 |
| TPS | 0.84 | 0.84 | 0.44 | 0.35 | 0.58 | 0.47 | 1.00 |

*Observed*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.56 | 0.12 | 0.10 | 0.41 | 0.16 | 0.56 |
| OFPD | 0.63 | 1.00 | 0.18 | 0.30 | 0.29 | 0.09 | 0.34 |
| %MAF | 0.13 | 0.30 | 1.00 | 0.60 | 0.33 | 0.23 | 0.08 |
| MAPD | 0.28 | 0.38 | 0.59 | 1.00 | 0.26 | 0.13 | 0.09 |
| %YF | 0.43 | 0.34 | 0.44 | 0.60 | 1.00 | 0.45 | 0.37 |
| YFPD | 0.12 | 0.24 | 0.07 | 0.07 | 0.14 | 1.00 | 0.11 |
| TPS | 0.46 | 0.40 | 0.18 | 0.18 | 0.14 | 0.16 | 1.00 |

*Estimate*

| | %OF | OFPD | %MAF | MAPD | %YF | YFPD | TPS |
|---|---|---|---|---|---|---|---|
| %OF | 1.00 | 0.57 | 0.10 | 0.12 | 0.40 | 0.15 | 0.51 |
| OFPD | 0.64 | 1.00 | 0.15 | 0.30 | 0.26 | 0.10 | 0.33 |
| %MAF | 0.13 | 0.23 | 1.00 | 0.55 | 0.29 | 0.19 | 0.12 |
| MAPD | 0.23 | 0.38 | 0.56 | 1.00 | 0.24 | 0.13 | 0.12 |
| %YF | 0.38 | 0.30 | 0.35 | 0.55 | 1.00 | 0.39 | 0.34 |
| YFPD | 0.14 | 0.17 | 0.15 | 0.08 | 0.18 | 1.00 | 0.11 |
| TPS | 0.49 | 0.42 | 0.13 | 0.19 | 0.12 | 0.18 | 1.00 |

**Table A 3**
**Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

a) Observed data

Mosses q0

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 5E-01 | 6E-01 | 6E-01 | 5E-01 | 5E-01 | 3E-01 |
| CFPD | 5E-01 | 1E+00 | 6E-01 | 7E-01 | 5E-01 | 7E-01 | 4E-01 |
| %MF | 6E-01 | 6E-01 | 1E+00 | 1E+00 | 8E-01 | 7E-01 | 4E-01 |
| MFPD | 6E-01 | 7E-01 | 1E+00 | 1E+00 | 8E-01 | 9E-01 | 5E-01 |
| %DF | 5E-01 | 5E-01 | 8E-01 | 8E-01 | 1E+00 | 1E+00 | 5E-01 |
| DFPD | 5E-01 | 7E-01 | 7E-01 | 9E-01 | 1E+00 | 1E+00 | 6E-01 |
| TPS | 3E-01 | 4E-01 | 4E-01 | 5E-01 | 5E-01 | 6E-01 | 1E+00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 1E-01 | 2E-01 | 3E-01 | 1E-01 | 2E-01 | 2E-01 |
| CFPD | 2E-01 | 1E+00 | 4E-01 | 5E-01 | 3E-01 | 4E-01 | 9E-02 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 9E-01 | 7E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 2E-01 | 8E-01 | 1E+00 | 7E-01 | 8E-01 | 2E-01 |
| %DF | 2E-01 | 2E-01 | 7E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 3E-01 | 2E-01 | 6E-01 | 7E-01 | 9E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

| Liverworts q0 | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Worst* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1E+00 | 6E-01 | 6E-01 | 6E-01 | 5E-01 | 5E-01 | 3E-01 |
| CFPD | 6E-01 | 1E+00 | 5E-01 | 7E-01 | 5E-01 | 7E-01 | 4E-01 |
| %MF | 6E-01 | 5E-01 | 1E+00 | 1E+00 | 8E-01 | 7E-01 | 4E-01 |
| MFPD | 6E-01 | 7E-01 | 1E+00 | 1E+00 | 8E-01 | 9E-01 | 5E-01 |
| %DF | 5E-01 | 5E-01 | 8E-01 | 8E-01 | 1E+00 | 1E+00 | 5E-01 |
| DFPD | 5E-01 | 7E-01 | 7E-01 | 9E-01 | 1E+00 | 1E+00 | 7E-01 |
| TPS | 3E-01 | 4E-01 | 4E-01 | 5E-01 | 5E-01 | 7E-01 | 1E+00 |
| *Observed* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 3E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 4E-01 | 5E-01 | 4E-01 | 5E-01 | 8E-02 |
| %MF | 3E-01 | 4E-01 | 1E+00 | 9E-01 | 2E-01 | 4E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 8E-01 | 1E+00 | 1E-01 | 5E-01 | 2E-01 |
| %DF | 2E-01 | 4E-01 | 7E-01 | 6E-01 | 1E+00 | 6E-01 | 3E-01 |
| DFPD | 3E-01 | 6E-01 | 6E-01 | 6E-01 | 4E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 5E-02 | 1E-01 | 1E+00 |
| *Estimate* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1.00 | 0.49 | 0.24 | 0.32 | 0.17 | 0.24 | 0.14 |
| CFPD | 0.26 | 1.00 | 0.32 | 0.51 | 0.33 | 0.39 | 0.10 |
| %MF | 0.39 | 0.32 | 1.00 | 0.81 | 0.54 | 0.59 | 0.16 |
| MFPD | 0.41 | 0.55 | 0.75 | 1.00 | 0.53 | 0.76 | 0.22 |
| %DF | 0.14 | 0.40 | 0.53 | 0.56 | 1.00 | 0.86 | 0.30 |
| DFPD | 0.20 | 0.56 | 0.46 | 0.59 | 0.77 | 1.00 | 0.31 |
| TPS | 0.20 | 0.17 | 0.17 | 0.14 | 0.11 | 0.20 | 1.00 |

**Table A 3**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q1

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 6E-01 | 6E-01 | 6E-01 | 5E-01 | 5E-01 | 3E-01 |
| CFPD | 6E-01 | 1E+00 | 5E-01 | 7E-01 | 5E-01 | 7E-01 | 4E-01 |
| %MF | 6E-01 | 5E-01 | 1E+00 | 1E+00 | 8E-01 | 7E-01 | 4E-01 |
| MFPD | 6E-01 | 7E-01 | 1E+00 | 1E+00 | 8E-01 | 9E-01 | 5E-01 |
| %DF | 5E-01 | 5E-01 | 8E-01 | 8E-01 | 1E+00 | 1E+00 | 5E-01 |
| DFPD | 5E-01 | 7E-01 | 7E-01 | 9E-01 | 1E+00 | 1E+00 | 7E-01 |
| TPS | 3E-01 | 4E-01 | 4E-01 | 5E-01 | 5E-01 | 7E-01 | 1E+00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1.00 | 0.50 | 0.21 | 0.30 | 0.17 | 0.34 | 0.15 |
| CFPD | 0.31 | 1.00 | 0.36 | 0.54 | 0.39 | 0.58 | 0.16 |
| %MF | 0.34 | 0.35 | 1.00 | 0.88 | 0.38 | 0.35 | 0.20 |
| MFPD | 0.34 | 0.58 | 0.82 | 1.00 | 0.34 | 0.53 | 0.13 |
| %DF | 0.19 | 0.40 | 0.65 | 0.63 | 1.00 | 0.65 | 0.16 |
| DFPD | 0.28 | 0.57 | 0.56 | 0.64 | 0.64 | 1.00 | 0.06 |
| TPS | 0.22 | 0.15 | 0.17 | 0.13 | 0.03 | 0.10 | 1.00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**

**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Sphagna q0

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1.00 | 0.54 | 0.64 | 0.61 | 0.49 | 0.53 | 0.34 |
| CFPD | 0.54 | 1.00 | 0.56 | 0.68 | 0.52 | 0.74 | 0.44 |
| %MF | 0.64 | 0.56 | 1.00 | 0.97 | 0.78 | 0.70 | 0.41 |
| MFPD | 0.61 | 0.68 | 0.97 | 1.00 | 0.76 | 0.87 | 0.54 |
| %DF | 0.49 | 0.52 | 0.78 | 0.76 | 1.00 | 0.99 | 0.51 |
| DFPD | 0.53 | 0.74 | 0.70 | 0.87 | 0.99 | 1.00 | 0.60 |
| TPS | 0.34 | 0.44 | 0.41 | 0.54 | 0.51 | 0.60 | 1.00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 3E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 2E-01 | 1E+00 | 4E-01 | 5E-01 | 4E-01 | 4E-01 | 8E-02 |
| %MF | 3E-01 | 4E-01 | 1E+00 | 9E-01 | 2E-01 | 6E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 9E-01 | 1E+00 | 1E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 6E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 6E-01 | 7E-01 | 4E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

a) Expected data

Mosses q0

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1.00 | 0.54 | 0.64 | 0.61 | 0.49 | 0.53 | 0.34 |
| CFPD | 0.54 | 1.00 | 0.56 | 0.68 | 0.52 | 0.74 | 0.44 |
| %MF | 0.64 | 0.56 | 1.00 | 0.97 | 0.78 | 0.70 | 0.41 |
| MFPD | 0.61 | 0.68 | 0.97 | 1.00 | 0.76 | 0.87 | 0.54 |
| %DF | 0.49 | 0.52 | 0.78 | 0.76 | 1.00 | 0.99 | 0.51 |
| DFPD | 0.53 | 0.74 | 0.70 | 0.87 | 0.99 | 1.00 | 0.60 |
| TPS | 0.34 | 0.44 | 0.41 | 0.54 | 0.51 | 0.60 | 1.00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 1E-01 | 3E-01 | 1E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 2E-01 | 5E-01 | 3E-01 | 4E-01 | 9E-02 |
| %MF | 4E-01 | 4E-01 | 1E+00 | 9E-01 | 7E-01 | 6E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 2E-01 | 1E+00 | 7E-01 | 8E-01 | 2E-01 |
| %DF | 2E-01 | 4E-01 | 2E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 3E-01 | 6E-01 | 2E-01 | 7E-01 | 9E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 8E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Liverworts q1

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 6E-01 | 6E-01 | 6E-01 | 5E-01 | 5E-01 | 3E-01 |
| CFPD | 6E-01 | 1E+00 | 5E-01 | 7E-01 | 5E-01 | 7E-01 | 4E-01 |
| %MF | 6E-01 | 5E-01 | 1E+00 | 1E+00 | 8E-01 | 7E-01 | 4E-01 |
| MFPD | 6E-01 | 7E-01 | 1E+00 | 1E+00 | 8E-01 | 9E-01 | 5E-01 |
| %DF | 5E-01 | 5E-01 | 8E-01 | 8E-01 | 1E+00 | 1E+00 | 5E-01 |
| DFPD | 5E-01 | 7E-01 | 7E-01 | 9E-01 | 1E+00 | 1E+00 | 7E-01 |
| TPS | 3E-01 | 4E-01 | 4E-01 | 5E-01 | 5E-01 | 7E-01 | 1E+00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 3E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 4E-01 | 5E-01 | 4E-01 | 5E-01 | 8E-02 |
| %MF | 3E-01 | 4E-01 | 1E+00 | 9E-01 | 1E-01 | 3E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 8E-01 | 1E+00 | 8E-02 | 4E-01 | 2E-01 |
| %DF | 2E-01 | 4E-01 | 7E-01 | 6E-01 | 1E+00 | 5E-01 | 3E-01 |
| DFPD | 3E-01 | 6E-01 | 6E-01 | 6E-01 | 3E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 9E-02 | 1E-01 | 1E+00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**
**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

| Liverworts q1 | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Worst* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1E+00 | 6E-01 | 6E-01 | 6E-01 | 5E-01 | 5E-01 | 3E-01 |
| CFPD | 6E-01 | 1E+00 | 5E-01 | 7E-01 | 5E-01 | 7E-01 | 4E-01 |
| %MF | 6E-01 | 5E-01 | 1E+00 | 1E+00 | 8E-01 | 7E-01 | 4E-01 |
| MFPD | 6E-01 | 7E-01 | 1E+00 | 1E+00 | 8E-01 | 9E-01 | 5E-01 |
| %DF | 5E-01 | 5E-01 | 8E-01 | 8E-01 | 1E+00 | 1E+00 | 5E-01 |
| DFPD | 5E-01 | 7E-01 | 7E-01 | 9E-01 | 1E+00 | 1E+00 | 7E-01 |
| TPS | 3E-01 | 4E-01 | 4E-01 | 5E-01 | 5E-01 | 7E-01 | 1E+00 |
| *Observed* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 4E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 4E-01 | 5E-01 | 4E-01 | 6E-01 | 8E-02 |
| %MF | 3E-01 | 4E-01 | 1E+00 | 9E-01 | 3E-01 | 3E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 | 5E-01 | 2E-01 |
| %DF | 2E-01 | 4E-01 | 7E-01 | 6E-01 | 1E+00 | 6E-01 | 3E-01 |
| DFPD | 3E-01 | 6E-01 | 6E-01 | 6E-01 | 6E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 3E-02 | 9E-02 | 1E+00 |
| *Estimate* | | | | | | | |
| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
| %CF | 1E+00 | 5E-01 | 2E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 3E-01 | 1E+00 | 3E-01 | 5E-01 | 3E-01 | 4E-01 | 1E-01 |
| %MF | 4E-01 | 3E-01 | 1E+00 | 8E-01 | 5E-01 | 6E-01 | 2E-01 |
| MFPD | 4E-01 | 6E-01 | 7E-01 | 1E+00 | 5E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 5E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 5E-01 | 6E-01 | 8E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 2E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

**Table A 3**

**(Continued) Concurvity indices (worst, observed and estimated) for explanatory variables based on the forest type of landscape patches for a) observed and b) expected bryophyte diversity values. %CF = Percentage of coniferous forest; CFPD = Coniferous patch density; %MF = Percentage of mixed forest; MFPD = Mixed forest patch density; %DF = Percentage of deciduous forest; DFPD = Deciduous forest patch density; TPS = Target patch size (ha). Values => 0.8 suggest high concurvity.**

Sphagna Q0

*Worst*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1.00 | 0.54 | 0.64 | 0.61 | 0.49 | 0.53 | 0.34 |
| CFPD | 0.54 | 1.00 | 0.56 | 0.68 | 0.52 | 0.74 | 0.44 |
| %MF | 0.64 | 0.56 | 1.00 | 0.97 | 0.78 | 0.70 | 0.41 |
| MFPD | 0.61 | 0.68 | 0.97 | 1.00 | 0.76 | 0.87 | 0.54 |
| %DF | 0.49 | 0.52 | 0.78 | 0.76 | 1.00 | 0.99 | 0.51 |
| DFPD | 0.53 | 0.74 | 0.70 | 0.87 | 0.99 | 1.00 | 0.60 |
| TPS | 0.34 | 0.44 | 0.41 | 0.54 | 0.51 | 0.60 | 1.00 |

*Observed*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1E+00 | 4E-01 | 3E-01 | 3E-01 | 2E-01 | 2E-01 | 1E-01 |
| CFPD | 2E-01 | 1E+00 | 4E-01 | 5E-01 | 4E-01 | 4E-01 | 8E-02 |
| %MF | 3E-01 | 4E-01 | 1E+00 | 9E-01 | 2E-01 | 6E-01 | 2E-01 |
| MFPD | 3E-01 | 6E-01 | 9E-01 | 1E+00 | 1E-01 | 8E-01 | 2E-01 |
| %DF | 1E-01 | 4E-01 | 6E-01 | 6E-01 | 1E+00 | 9E-01 | 3E-01 |
| DFPD | 2E-01 | 6E-01 | 6E-01 | 7E-01 | 4E-01 | 1E+00 | 3E-01 |
| TPS | 2E-01 | 1E-01 | 2E-01 | 1E-01 | 1E-01 | 2E-01 | 1E+00 |

*Estimate*

| | %CF | CFPD | %MF | MFPD | %DF | DFPD | TPS |
|---|---|---|---|---|---|---|---|
| %CF | 1.00 | 0.44 | 0.22 | 0.29 | 0.16 | 0.21 | 0.15 |
| CFPD | 0.26 | 1.00 | 0.33 | 0.51 | 0.32 | 0.40 | 0.10 |
| %MF | 0.40 | 0.32 | 1.00 | 0.81 | 0.54 | 0.59 | 0.16 |
| MFPD | 0.40 | 0.55 | 0.75 | 1.00 | 0.54 | 0.77 | 0.21 |
| %DF | 0.14 | 0.40 | 0.54 | 0.57 | 1.00 | 0.87 | 0.27 |
| DFPD | 0.20 | 0.56 | 0.48 | 0.61 | 0.78 | 1.00 | 0.28 |
| TPS | 0.19 | 0.17 | 0.18 | 0.14 | 0.11 | 0.20 | 1.00 |

**Table A 4**
**Species studied. Nomenclature is based on accepted names of the Quebec-Labrador bryophyte database (Société québécoise de bryologie, 2023).**

| Guilds and species | Acronym |
|---|---|
| Mosses | |
| *Amblystegium serpens* (Hedw.) Schimp. | Ambser |
| *Atrichum altecristatum* (Renauld & Cardot) B.B. Smyth & L.C.D. Smyth | Atralt |
| *Atrichum crispulum* Schimp. ex Besch. | Atrcri |
| *Atrichum tenellum* (Röhl.) Bruch & Schimp. | Atrten |
| *Aulacomnium palustre* (Hedw.) Schwägr. | Aulpal |
| *Blindia acuta* (Hedw.) Bruch & Schimp. | Bliacu |
| *Brachythecium acuminatum* (Hedw.) Austin | Braacu |
| *Brachythecium campestre* (Müll. Hal.) Schimp. | Bracam |
| *Brachythecium curtum* (Lindb.) Limpr. | Bracur |
| *Brachythecium erythrorrhizon* Schimp. | Braery |
| *Brachythecium populeum* (Hedw.) Schimp. | Brapop |
| *Brachythecium reflexum* (Starke) Schimp. | Braref |
| *Brachythecium rivulare* Schimp. | Brariv |
| *Brachythecium rutabulum* (Hedw.) Schimp. | Brarut |
| *Brachythecium starkii* (Brid.) Schimp. | Brasta |
| *Brachythecium velutinum* (Hedw.) Schimp. | Bravel |
| *Breidleria pratensis* (Koch ex Spruce) Loeske | Brepra |
| *Brotherella recurvans* (Michx.) M. Fleisch. | Brorec |
| *Calliergon cordifolium* (Hedw.) Kindb. | Calcor |
| *Calliergon giganteum* (Schimp.) Kindb. | Calgig |
| *Callicladium haldanianum* (Grev.) H.A. Crum | Calhal |
| *Calliergon richardsonii* (Mitt.) Kindb. | Calric |
| *Campyliadelphus chrysophyllus* (Brid.) Kanda | Camchr |
| *Campylophyllum hispidulum* (Brid.) Hedenäs | Camhis |
| *Campylium protensum* (Brid.) Kindb. | Camste |
| *Ceratodon purpureus* (Hedw.) Brid. | Cerpur |
| *Dicranum flagellare* Hedw. | Dicfla |
| *Dicranum fulvum* Hook. | Dicful |
| *Dicranum fuscescens* Turner | Dicfus |
| *Dicranella heteromalla* (Hedw.) Schimp. | Dichet |
| *Dicranum leioneuron* Kindb. | Diclei |
| *Dicranum montanum* Hedw. | Dicmon |
| *Dicranum ontariense* W.L. Peterson | Dicont |
| *Dicranum polysetum* Sw. | Dicpol |
| *Dicranum scoparium* Hedw. | Dicsco |
| *Dicranum undulatum* Schrad. ex Brid. | Dicund |

**Table A 4**
**(Continued) Species studied. Nomenclature is based on accepted names of the Quebec-Labrador bryophyte database (Société québécoise de bryologie, 2023).**

| | |
|---|---|
| *Ditrichum pusillum* (Hedw.) Hampe | Ditpus |
| *Drepanocladus aduncus* (Hedw.) Warnst. | Dreadu |
| *Eurhynchiastrum pulchellum* (Hedw.) Ignatov & Huttunen | Eurpul |
| *Fissidens bryoides* Hedw. | Fisbry |
| *Fissidens osmundoides* Hedw. | Fisosm |
| *Hamatocaulis vernicosus* (Mitt.) Hedenäs | Hamver |
| *Herzogiella striatella* (Brid.) Z. Iwats. | Herstr |
| *Herzogiella turfacea* (Lindb.) Z. Iwats. | Hertur |
| *Hygroamblystegium varium* (Hedw.) Mönk. | Hygvar |
| *Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel | Hyltri |
| *Hylocomium splendens* (Hedw.) Schimp. | Hylspl |
| *Hypnum curvifolium* Hedw. | Hypcur |
| *Hypnum fauriei* Cardot | Hypfau |
| *Hypnum imponens* Hedw. | Hypimp |
| *Hypnum pallescens* (Hedw.) P. Beauv. | Hyppal |
| *Hypnum recurvatum* (Lindb. & Arnell) Kindb. | Hyprec |
| *Isopterygiopsis muelleriana* (Schimp.) Z. Iwats. | Isomue |
| *Isopterygiopsis pulchella* (Hedw.) Z. Iwats. | Isopul |
| *Kindbergia praelonga* (Hedw.) Ochyra | Kinpra |
| *Koponeniella graminicolor* (Brid.) Huttunen, Ignatov, Min Li & Y.F. Wang | Kopgra |
| *Leptodictyum riparium* (Hedw.) Warnst. | Leprip |
| *Meesia triquetra* (L. ex Jolycl.) Ångström | Meetri |
| *Mnium spinulosum* Bruch & Schimp. | Mnispi |
| *Oncophorus wahlenbergii* Brid. | Oncwah |
| *Plagiothecium cavifolium* (Brid.) Z. Iwats. | Placav |
| *Plagiomnium cuspidatum* (Hedw.) T.J. Kop. | Placus |
| *Plagiothecium denticulatum* (Hedw.) Schimp. | Pladen |
| *Plagiomnium drummondii* (Bruch & Schimp.) T.J. Kop. | Pladru |
| *Plagiomnium ellipticum* (Brid.) T.J. Kop. | Plaell |
| *Plagiothecium laetum* Schimp. | Plalae |
| *Plagiomnium medium* (Bruch & Schimp.) T.J. Kop. | Plamed |
| *Platygyrium repens* (Brid.) Schimp. | Plarep |
| *Pleurozium schreberi* (Willd. ex Brid.) Mitt. | Plesch |
| *Pohlia cruda* (Hedw.) Lindb. | Pohcruda |
| *Pohlia elongate* Hedw. | Pohelo |
| *Pohlia nutans* (Hedw.) Lindb. | Pohnut |
| *Pohlia sphagnicola* (Bruch & Schimp.) Broth. | Pohsph |

**Table A 4**
**(Continued) Species studied. Nomenclature is based on accepted names of the Quebec-Labrador bryophyte database (Société québécoise de bryologie, 2023).**

| | |
|---|---|
| *Polytrichum commune* Hedw. | Polcom |
| *Polytrichum commune perigoniale* Hedw. | Polcom_per |
| *Polytrichum juniperinum Hedw.* | Poljun |
| *Polytrichastrum pallidisetum* (Funck) G.L. Sm. | Polpal |
| *Polytrichum strictum* Menzies ex Brid. | Polstr |
| *Ptilium crista-castrensis* (Hedw.) De Not. | Pticricas |
| *Pylaisia intricata* (Hedw.) Schimp. | Pylint |
| *Rhizomnium pseudopunctatum* (Bruch & Schimp.) T.J. Kop. | Rhipse |
| *Rhizomnium punctatum* (Hedw.) T.J. Kop. | Rhipun |
| *Rhodobryum ontariense* (Kindb.) Kindb. | Rhoont |
| *Rhynchostegium serrulatum* (Hedw.) A. Jaeger | Rhyser |
| *Rhytidiadelphus subpinnatus* (Lindb.) T.J. Kop. | Rhysub |
| *Sanionia uncinata* (Hedw.) Loeske | Sanunc |
| *Sarmentypnum exannulatum* (Schimp.) Hedenäs | Sarexa |
| *Schistostega pennata* (Hedw.) F. Weber & D. Mohr | Schpen |
| *Serpoleskea subtilis* (Hedw.) Loeske | Sersub |
| *Splachnum ampullaceum* Hedw. | Splamp |
| *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs | Strstr |
| *Tetraplodon angustatus* (Hedw.) Bruch & Schimp. | Tetang |
| *Tetraphis pellucida* Hedw. | Tetpel |
| *Thuidium recognitum* (Hedw.) Lindb. | Thurec |
| *Tomentypnum falcifolium* (Renauld ex Nichols) Tuom. | Tomfal |
| *Tomentypnum nitens* (Hedw.) Loeske | Tomnit |
| *Ulota coarctata* (P. Beauv.) Hammar | Ulocoa |
| *Ulota crispula* Bruch | Ulocri |
| *Warnstorfia fluitans* (Hedw.) Loeske | Warflu |
| Liverworts | |
| *Anastrophyllum michauxii* (F. Weber) H. Buch | Anamic |
| *Barbilophozia barbata* (Schmidel ex Schreb.) Loeske | Barbar |
| *Barbilophozia hatcheri* (A. Evans) Loeske | Barhat |
| *Bazzania tricrenata* (Wahlenb.) Lindb. | Baztric |
| *Bazzania trilobata* (L.) Gray | Baztril |
| *Blepharostoma trichophyllum* (L.) Dumort. | Bletri |
| *Calypogeia integristipula* Steph. | Calint |
| *Calypogeia muelleriana* (Schiffn.) Müll. Frib. | Calmue |
| *Calypogeia neesiana* (C. Massal. & Carestia) Müll. Frib. | Calnee |
| *Calypogeia sphagnicola* (Arnell & J. Perss.) Warnst. & Loeske | Calsph |

**Table A 4**
**(Continued) Species studied. Nomenclature is based on accepted names of the Quebec-Labrador bryophyte database (Société québécoise de bryologie, 2023).**

| | |
|---|---|
| *Calypogeia suecica* (Arnell & J. Perss.) Müll. Frib. | Calsue |
| *Cephalozia bicuspidate* (L.) Dumort. | Cepbic |
| *Cephaloziella divaricate* (Sm.) Schiffn. | Cepdiv |
| *Cephaloziella elachista* (J.B. Jack ex Gottsche & Rabenh.) Schiffn. | Cepela |
| *Cephaloziella hampeana* (Nees) Schiffn. ex Loeske | Cepham |
| *Cephaloziella rubella* (Nees) Warnst | Ceprub |
| *Cephaloziella spinigera* (Lindb.) Warnst. | Cepspi |
| *Crossocalyx hellerianus* (Nees ex Lindenb.) Meyl. | Croshel |
| *Chiloscyphus pallescens* (Ehrh.) Dumort. | Chipal |
| *Chiloscyphus polyanthos* (L.) Corda | Chipol |
| *Frullania eboracensis* Lehm. | Fruebo |
| *Frullania oakesiana* Austin | Fruoak |
| *Fuscocephaloziopsis catenulata* (Huebener) Váňa & L. Söderstr. | Fuscat |
| *Fuscocephaloziopsis connivens* (Dicks.) Váňa & L. Söderstr. | Fuscon |
| *Fuscocephaloziopsis loitlesbergeri* (Schiffn.) Váňa & L. Söderstr. | Fusloi |
| *Fuscocephaloziopsis lunulifolia* (Dumort.) Váňa & L. Söderstr. | Fuslun |
| *Fuscocephaloziopsis macrostachya* (Kaal.) Váňa & L. Söderstr. | Fusmac |
| *Fuscocephaloziopsis pleniceps* (Austin) Váňa & L. Söderstr. | Fusple |
| *Geocalyx graveolens* (Schrad.) Nees | Geogra |
| *Gymnocolea inflata* (Huds.) Dumort. | Gyminf |
| *Lepidozia reptans* (L.) Dumort. | Leprep |
| *Liochlaena lanceolata* Nees | Liolan |
| *Lophocolea bidentata* (L.) Dumort. | Lopcoa |
| *Lophocolea heterophylla* (Schrad.) Dumort. | Lophet |
| *Lophozia ascendens* (Warnst.) R.M. Schust. | Lopasc |
| *Lophozia guttulata* (Lindb. & Arnell) A. Evans | Lopgut |
| *Lophozia guttulata* (Lindb. & Arnell) A. Evans | Lopgut |
| *Lophozia silvicola* H. Buch | Lopsil |
| *Lophozia ventricosa* (Dicks.) Dumort. | Lopven |
| *Mesoptychia heterocolpos* (Thed. ex Hartm.) L. Söderstr. & Váňa | Meshet |
| *Mesoptychia rutheana* (Limpr.) L. Söderstr. & Váňa | Mesrut |
| *Mylia anomala* (Hook.) Gray | Mylano |
| *Mylia taylorii* (Hook.) Gray | Myltay |
| *Neoorthocaulis attenuatus* (Mart.) L. Söderstr., De Roo & Hedd. | Neoatt |
| *Neoorthocaulis floerkei* (F. Weber & D. Mohr) L. Söderstr., De Roo & Hedd. | Neoflo |
| *Nowellia curvifolia* (Dicks.) Mitt. | Nowcur |
| *Obtusifolium obtusum* (Lindb.) S.W. Arnell | Obtobt |

**Table A 4**
**(Continued) Species studied. Nomenclature is based on accepted names of the Quebec-Labrador bryophyte database (Société québécoise de bryologie, 2023).**

| | |
|---|---|
| *Odontoschisma denudatum* (Mart.) Dumort. | Ododen |
| *Odontoschisma fluitans* (Nees) L. Söderstr. & Váňa | Odoflu |
| *Pellia epiphylla* (L.) Corda | Pelepi |
| *Plagiochila porelloides* (Torr. ex Nees) Lindenb. | Plapor |
| *Ptilidium ciliare* (L.) Hampe | Pticil |
| *Ptilidium pulcherrimum* (Weber) Vain. | Ptipul |
| *Radula complanate* (L.) Dumort. | Radcom |
| *Riccardia latifrons* (Lindb.) Lindb. | Riclat |
| *Riccardia palmata* (Hedw.) Carruth. | Ricpal |
| *Scapania apiculate* Spruce | Scaapi |
| *Scapania irrigua* (Nees) | Scairr |
| *Scapania nemorea* (L.) Grolle | Scanem |
| *Scapania paludicola* Loeske & Müll. Frib. | Scapal |
| *Schljakovia kunzeana* (Huebener) Konstant. & Vilnet | Schkun |
| *Schistochilopsis incisa* (Schrad.) Konstant. | Schinc |
| *Sphenolobus hellerianus* (Nees ex Lindenb.) Steph. | Sphhel |
| *Sphenolobus minutus* (Schreb. ex D. Crantz) Berggr. | Sphmin |
| *Syzygiella autumnalis* (DC.) K. Feldberg, Váňa, Hentschel & Heinrichs | Syzaut |
| *Tritomaria laxa* (Lindb.) Stotler & Crand.-Stotl. | Trilax |
| *Tritomaria exsectiformis* (Breidl.) Schiffn. ex Loeske | Triexs |
| *Tritomaria quinquedentata* (Huds.) H. Buch | Triqui |
| Sphagna | |
| *Sphagnum angustifolium* (Warnst.) C.E.O. Jensen | Sphang |
| *Sphagnum capillifolium* (Ehrh.) Hedw. | Sphcap |
| *Sphagnum cuspidatum* Ehrh. ex Hoffm. | Sphcus |
| *Sphagnum fallax* H. Klinggr. | Sphfal |
| *Sphagnum flexuosum* Dozy & Molk. | Sphfle |
| *Sphagnum fuscum* (Schimp.) H. Klinggr. | Sphfus |
| *Sphagnum girgensohnii* Russow | Sphgir |
| *Sphagnum magellanicum* Brid. | Sphmag |
| *Sphagnum pulchrum* (Lindb.) Warnst. | Sphpul |
| *Sphagnum quinquefarium* (Lindb.) Warnst. | Sphqui |
| *Sphagnum rubellum* Wilson | Sphrub |
| *Sphagnum russowii* Warnst. | Sphrus |
| *Sphagnum squarrosum* Crome | Sphsqu |
| *Sphagnum subtile (Russow)* Warnst. | Sphsubtile |
| *Sphagnum tenerum* Sull. & Lesq. ex Sull. | Sphtenerum |

| | |
|---|---|
| *Sphagnum warnstorfii* Russow | Sphwar |
| *Sphagnum wulfianum* Girg. | Sphwul |

**Table A 5**
**(Generalized additive models assessing the effects of landscape composition and configuration based on the a) age and b) forest type using observed bryophyte diversity. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.**

a) Age landscape classification

| Response variables | Explanatory variable | edf | p-value |
|---|---|---|---|
| Mosses *q0* | Percentage of young forest area | 1.356 | 0.03322 * |
| | Percentage of medium forest area | 4.422 | 0.00139 ** |
| | Percentage old forest area | 1 | 0.02672 * |
| | Density of young forest patches | 1 | 0.41321 |
| Liverworts *q0* | Percentage of young forest area | 5.929 | 0.000861 *** |
| | Percentage of medium forest area | 3.102 | 0.180779 |
| | Percentage old forest area | 1 | 0.033274 * |
| | Density of young forest patches | 2.794 | 0.046337 * |
| Liverworts *q1* | Percentage of young forest area | 6.354 | 0.001158 ** |
| | Percentage of medium forest area | 1 | 0.640231 |
| | Percentage old forest area | 2.66 | 0.225984 |
| | Density of young forest patches | 4.137 | 0.000111 *** |
| Sphagna *q0* | Percentage of young forest area | 1 | 0.1967 |
| | Percentage of medium forest area | 4.173 | 0.0729 |
| | Percentage old forest area | 1 | 0.261 |
| | Density of young forest patches | 1 | 0.6701 |

b) Forest type landscape classification

| Response variables | Explanatory variable | edf | p-value |
|---|---|---|---|
| Mosses *q0* | Percentage of conifers area | 2.557 | 0.030483 * |
| | Density of conifer forest patches | 3.167 | 0.11037 |
| | Percentage of mixed forest area | 1 | 0.105355 |
| | Percentage of deciduous forest area | 1 | 0.853753 |
| | Target stand size | 1.903 | 0.000431 *** |
| Liverworts *q0* | Percentage of conifers area | 2.005 | 0.03419 * |
| | Density of conifer forest patches | 1.703 | 0.00132 ** |
| | Percentage of mixed forest area | 1 | 0.73242 |
| | Percentage of deciduous forest area | 3.263 | 0.00831 ** |
| | Target stand size | 1 | 3.13E-01 |
| Liverworts *q1* | Percentage of conifers area | 2.081 | 0.0224 * |
| | Density of conifer forest patches | 2.143 | 0.0000206 *** |
| | Percentage of mixed forest area | 1 | 0.0194 * |
| | Percentage of deciduous forest area | 1.733 | 0.0261 * |
| | Target stand size | 1.66 | 4.91E-01 |

**Table A 5**
**(Continued) Generalized additive models assessing the effects of landscape composition and configuration based on the a) age and b) forest type using observed bryophyte diversity. Significant relationships are shown in bold, and the significance level is marked with asterisks: *** = p <0.0001, ** = p <0.001, * = p <0.05, (.) = marginal effects.**

| | | | |
|---|---|---|---|
| Sphagna *q0* | Percentage of conifers area | 1.766 | 0.03274 * |
| | Density of conifer forest patches | 1 | 0.00489 ** |
| | Percentage of mixed forest area | 1 | 0.12048 |
| | Percentage of deciduous forest area | 2.744 | 0.14364 |
| | Target stand size | 1 | 0.0354 * |

# APPENDICE B – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE III

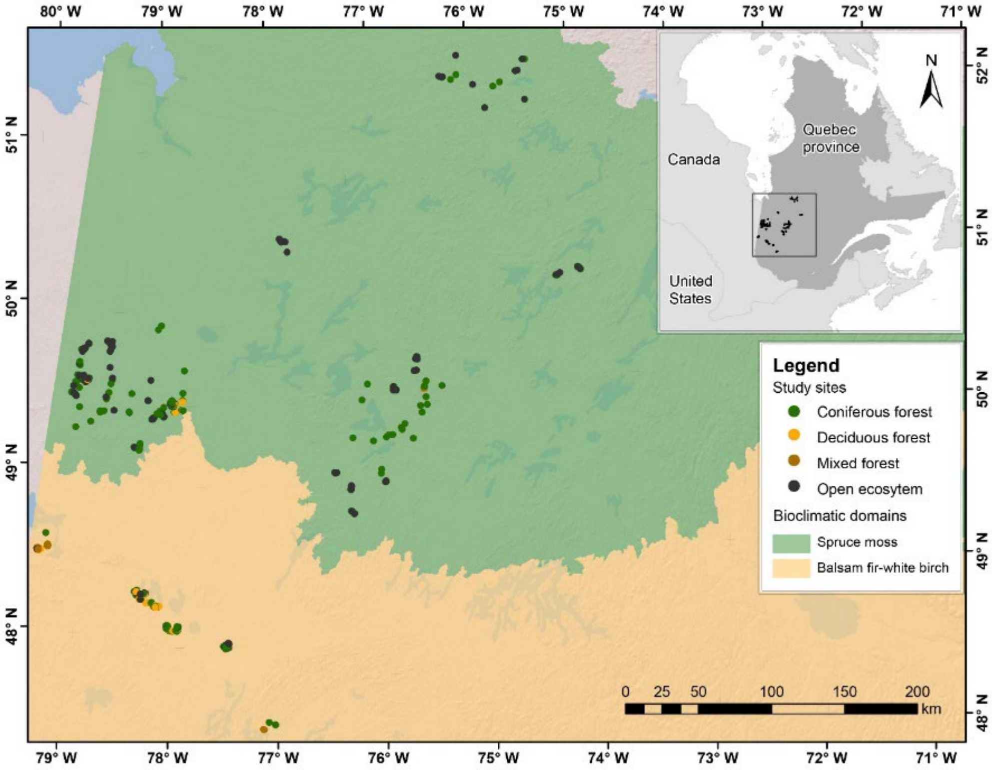


**Figure B1**
**Study area showing our sampling sites in two bioclimatic domains across boreal Quebec, a province in Eastern Canada. The area on the map represents 310, 000 km$^2$. The different colors of the dots indicate the forest types sampled.**

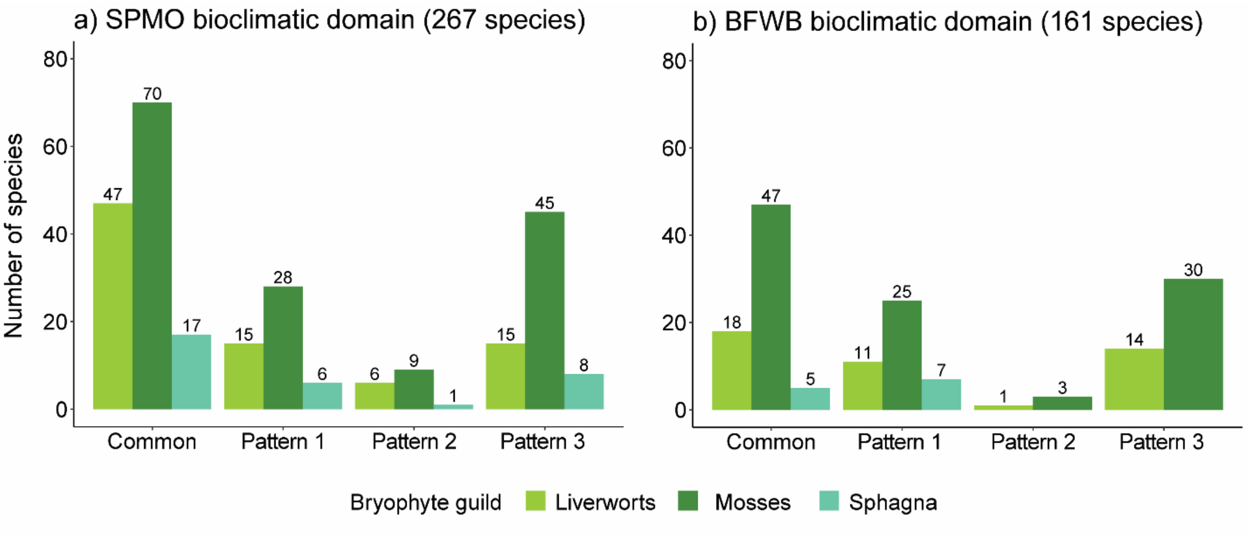


**Figure B2**
**Number of common and rare species by rarity form (Pattern 1= sparse population generalists, Pattern 2 = abundant specialists, and Pattern 3 = sparse population specialists) by bryophyte lineage in the a) spruce moss (SPMO) and b) balsam fir-white birch (BFWB) bioclimatic domains. Definitions of the rarity patterns are found in Table 4. The total of species by bioclimatic domain is indicated in the panel titles.**

### Methods B1

### Works consulted for the literature review about bryophyte functional traits related to dispersal and life-history.

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- Schuster, R.M. (1992). The Hepaticae and Anthocerotae of North America, Vol. 5. Field Museum of Natural History, Chicago, USA.
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**Table B1**
**Number of forests stands sampled by forest type in western Quebec.**

| Forest type | Number of stands sampled by forest type |
|---|---|
| Coniferous forests | 418 |
| Deciduous forest | 106 |
| Mixed forest | 76 |
| Open ecosystem | 330 |

**Table B2**
**Richness (q0), frequent (q1), and dominant (q2) species of bryophytes by lineage recorded in four forest stand types in two bioclimatic domains in Eastern Canada. The highest possible sample coverage is 1.0. Hill's numbers are represented by q0 (richness), q1 (exponential of Shannon to quantify frequent species), and q2 (Simpson Inverse to quantify dominant species) (Hill 1973; Jost 2006). The analyses included rarefaction/extrapolation to evaluate the possibility of finding more species in each taxonomic diversity dimension (Chao and Jost 2012). We used occurrence number, as an abundance measure for the analysis following Hsieh et al. (2016) and Chao et al. (2014), with 95% confidence intervals and 50 permutations.**

| Bioclimatic domain | Bryophyte lineage | Forest stand type (*N* of records) | Richness (q0) | Frequent species (q1) | Dominant species (q2) | Sample coverage (SC) |
|---|---|---|---|---|---|---|

**Table B2**

**(Continued) Richness (q0), frequent (q1), and dominant (q2) species of bryophytes by lineage recorded in four forest stand types in two bioclimatic domains in Eastern Canada. The highest possible sample coverage is 1.0. Hill's numbers are represented by q0 (richness), q1 (exponential of Shannon to quantify frequent species), and q2 (Simpson Inverse to quantify dominant species) (Hill 1973; Jost 2006). The analyses included rarefaction/extrapolation to evaluate the possibility of finding more species in each taxonomic diversity dimension (Chao and Jost 2012). We used occurrence number, as an abundance measure for the analysis following Hsieh et al. (2016) and Chao et al. (2014), with 95% confidence intervals and 50 permutations.**

| | | | | | | |
|---|---|---|---|---|---|---|
| Spruce moss | Liverworts | Coniferous (9 111) | 72 | 16 | 8 | 1.00 |
| | | Deciduous (197) | 18 | 9 | 6 | 0.99 |
| | | Mixed forest (303) | 22 | 9 | 6 | 0.98 |
| | | Open ecosystems (3 618) | 68 | 23 | 14 | 1.00 |
| | Mosses | Coniferous (13 512) | 120 | 18 | 8 | 1.00 |
| | | Deciduous (597) | 56 | 25 | 15 | 0.98 |
| | | Mixed forest (815) | 42 | 23 | 18 | 0.99 |
| | | Open ecosystems (8 532) | 113 | 22 | 12 | 1.00 |
| | Sphagnum | Coniferous (3 130) | 23 | 9 | 7 | 1.00 |
| | | Deciduous (6) | 4 | 4 | 4 | 0.76 |
| | | Mixed forest (1) | 1 | 1 | 1 | 1.00 |
| | | Open ecosystems (2 585) | 32 | 9 | 7 | 1.00 |

**Table B2**

**(Continued) Richness (q0), frequent (q1), and dominant (q2) species of bryophytes by lineage recorded in four forest stand types in two bioclimatic domains in Eastern Canada. The highest possible sample coverage is 1.0. Hill's numbers are represented by q0 (richness), q1 (exponential of Shannon to quantify frequent species), and q2 (Simpson Inverse to quantify dominant species) (Hill 1973; Jost 2006). The analyses included rarefaction/extrapolation to evaluate the possibility of finding more species in each taxonomic diversity dimension (Chao and Jost 2012). We used occurrence number, as an abundance measure for the analysis following Hsieh et al. (2016) and Chao et al. (2014), with 95% confidence intervals and 50 permutations.**

| | | | | | | |
|---|---|---|---|---|---|---|
| Balsam fir-white birch | Liverworts | Coniferous (1 902) | 33 | 6 | 3 | 1.00 |
| | | Deciduous (966) | 23 | 8 | 6 | 0.99 |
| | | Mixed forest (1 120) | 25 | 7 | 5 | 0.99 |
| | | Open ecosystems (597) | 25 | 7 | 5 | 0.99 |
| | Mosses | Coniferous (4 241) | 78 | 20 | 13 | 1.00 |
| | | Deciduous (3 464) | 73 | 23 | 14 | 1.00 |
| | | Mixed forest (3 117) | 59 | 23 | 15 | 1.00 |
| | | Open ecosystems (2 223) | 66 | 22 | 13 | 0.99 |
| | Sphagnum | Coniferous (209) | 12 | 7 | 5 | 1.00 |
| | | Deciduous (22) | 7 | 4 | 3 | 0.78 |
| | | Mixed forest (5) | 2 | 2 | 2 | 1.00 |
| | | Open ecosystems (113) | 9 | 6 | 5 | 0.97 |

Hill, M. O. (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology, 54, 427-432.

Jost, L. (2006) Entropy and diversity. Entropy and diversity, 113, 363-375.

**Table B3**
**Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| Species | Acronym | SPMO | BFWB | Sexual condition | Asexual propagules | Spore size |
|---|---|---|---|---|---|---|
| *Amblystegium serpens* (Hedw.) Schimp. | mAmbser | C | C | M | A | S |
| *Anastrophyllum michauxii* (F. Weber) H. Buch | hAnamic | P3 | | D | P | S |
| *Aneura pinguis* (L.) Dumort. | hAnepin | P1 | P1 | D | A | S |
| *Atrichum altecristatum* (Renauld & Cardot) B.B. Smyth & L.C.D. Smyth | mAtralt | P1 | P1 | B | A | S |
| *Atrichum crispum* (James) Sull. | mAtrcrispum | P1 | | D | A | S |
| *Atrichum tenellum* (Röhl.) Bruch & Schimp. | mAtrten | P1 | | D | A | S |
| *Aulacomnium palustre* (Hedw.) Schwägr. | mAulpal | C | C | D | P | S |
| *Barbilophozia barbata* (Schreb.) Loeske | hBarbar | C | P1 | D | A | S |
| *Barbilophozia hatcheri* (A. Evans) Loeske | hBarhat | P3 | | D | P | S |
| *Barbilophozia sudetica* (Nees ex Huebener) L. Söderstr., De Roo & Hedd. | hBarsude | P1 | | D | P | S |
| *Bazzania tricrenata* (Wahlenb.) Lindb. | hBaztric | P2 | P1 | D | A | S |
| *Bazzania trilobata* (L.) Gray | hBaztril | P3 | C | D | P | S |
| *Blepharostoma trichophyllum* (L.) Dumort. | hBletri | C | C | B | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Blindia acuta* (Hedw.) Bruch & Schimp. | mBliacu | P3 | | D | A | S |
| *Brachythecium acuminatum* (Hedw.) Austin | mBraacum | P1 | C | D | A | S |
| *Brachythecium acutum* (Mitt.) Sull. | mBraact | P3 | C | M | A | S |
| *Brachythecium campestre* (Müll. Hal.) Schimp. | mBracam | C | C | M | A | S |
| *Brachythecium curtum* (Lindb.) Limpr. | mBracur | C | C | M | A | S |
| *Brachythecium erythrorrhizon* Schimp. | mBraery | C | P3 | D | A | S |
| *Brachythecium falcatum* (Grout) H.A. Crum | mBrafal | P3 | P1 | M | A | S |
| *Brachythecium laetum* (Brid.) Schimp. | mBralae | P3 | | D | A | S |
| *Brachythecium novae-angliae* (Sull. & Lesq.) Jaeg. | mBrynova | | P3 | D | A | S |
| *Brachythecium plumosum* (Hedw.) Schimp. | mBraplu | P3 | | M | A | S |
| *Brachythecium populeum* (Hedw.) Schimp. | mBrapop | P1 | P1 | M | A | S |
| *Brachythecium reflexum* (Starke) Schimp. | mBraref | C | C | M | A | S |
| *Brachythecium rivulare* Schimp. | mBrariv | P1 | | D | A | S |
| *Brachythecium rutabulum* (Hedw.) Schimp. | mBrarut | C | P1 | M | A | S |
| *Brachythecium starkei* (Brid.) Schimp. | mBrasta | C | C | M | A | S |
| *Brachythecium velutinum* (Hedw.) Schimp. | mBravel | C | P1 | M | A | S |
| *Breidleria pratensis* (Koch ex Spruce) Loeske | mBrepra | C | P3 | D | A | S |
| *Brotherella recurvans* (Michx.) M. Fleisch. | mBrorec | C | C | D | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Bryoerythrophyllum recurvirostrum* (Hedw.) P.C. Chen | mBryrecu | | P3 | M | A | S |
| *Bryum caespiticium* Hedw. | mBrycae | P3 | | D | P | S |
| *Bryum capillare* Hedw. | mBrycap | P3 | | D | P | S |
| *Bryum creberrimum* Taylor | mBrycreb | | P1 | M | A | S |
| *Bryum pallescens* Schleich. ex Schwägr. | mBrypallescens | P3 | | M | A | S |
| *Bryum pseudotriquetrum* (Hedw.) G. Gaertn., B. Mey. & Scherb. | mBrypse | P1 | P3 | D | P | S |
| *Callicladium haldanianum* (Grev.) H.A. Crum | mCalhal | C | C | M | A | S |
| *Calliergon cordifolium* (Hedw.) Kindb. | mCalcor | P1 | P1 | M | A | S |
| *Calliergon richardsonii* (Mitt.) Kindb. | mCalric | P1 | P3 | M | A | L |
| *Calypogeia integristipula* Stephani | hCalint | C | P3 | M | P | S |
| *Calypogeia muelleriana* (Schiffn.) Müll. Frib. | hCalmue | C | C | M | P | S |
| *Calypogeia neesiana* (C. Massal. & Carestia) Müll. Frib. | hCalnee | C | C | M | P | S |
| *Calypogeia neogaea* (R.M. Schust.) Bakalin | hCalneo | C | P3 | M | A | S |
| *Calypogeia sphagnicola* (Arnell & J. Perss.) Warnst. & Loeske | hCalsph | C | P3 | M | P | S |
| *Calypogeia suecica* (Arnell & J. Perss.) Müll. Frib. | hCalsue | P1 | | D | P | S |
| *Campyliadelphus chrysophyllus* (Brid.) Kanda | mCamchr | C | C | D | A | S |
| *Campylium protensum* (Brid.) Kindb. | mCampro | C | | D | A | S |
| *Campylium stellatum* (Hedw.) C.E.O. Jensen | mCamste | C | | D | A | S |

**Table B3 (Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Campylophyllum halleri* (Hedw.) M. Fleisch. | mCamhall | | P3 | M | A | S |
| *Campylophyllum hispidulum* (Brid.) Hedenäs | mCamhis | C | C | M | A | S |
| *Cephalozia ambigua* C. Massal. | hCepamb | P3 | | M | P | S |
| *Cephalozia bicuspidata* (L.) Dumort. | hCepbic | C | P3 | M | P | S |
| *Cephaloziella divaricata* (Sm.) Schiffn. | hCepdiv | P1 | | D | P | NP |
| *Cephaloziella elachista* (J.B. Jack ex Gottsche & Rabenh.) Schiffn. | hCepela | C | P3 | M | P | S |
| *Cephaloziella hampeana* (Nees) Schiffn. ex Loeske | hCepham | C | | M | P | S |
| *Cephaloziella rubella* (Nees) Warnst. | hCeprub | C | P1 | M | P | S |
| *Cephaloziella spinigera* (Lindb.) Warnst. | hCepspi | C | | M | P | S |
| *Ceratodon purpureus* (Hedw.) Brid. | mCerpur | C | P1 | D | A | S |
| *Chiloscyphus pallescens* (Ehrh.) Dumort. | hChipal | P3 | | M | A | S |
| *Cinclidium stygium* Sw. | mCinsty | P2 | | M | A | L |
| *Climacium dendroides* (Hedw.) F. Weber & D. Mohr | mClidend | C | P3 | D | A | S |
| *Conocephalum salebrosum* Szweyk., Buczkowska & Odrzykoski | hConsal | | P3 | D | A | L |
| *Crossocalyx hellerianus* (Nees ex Lindenb.) Meyl. | hSphhel | C | | D | P | S |
| *Ctenidium subrectifolium* (Brid.) G. Pedano ex W.R. Buck & B.H. Allen | mCtesub | P3 | | D | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Dichodontium pellucidum* (Hedw.) Schimp. | mDicpell | P3 | | D | P | S |
| *Dicranella heteromalla* (Hedw.) Schimp. | mDichet | C | C | D | A | S |
| *Dicranum acutifolium* (Lindb. & Arnell) C.E.O. Jensen | mDicacu | C | | B | A | S |
| *Dicranum flagellare* Hedw. | mDicfla | C | C | D | A | S |
| *Dicranum fragilifolium* Lindb. | mDicfra | P3 | | D | A | S |
| *Dicranum fulvum* Hook. | mDicful | P1 | P1 | D | A | S |
| *Dicranum fuscescens* Turner | mDicfus | C | C | D | A | S |
| *Dicranum groenlandicum* Brid. | mDicgro | P3 | | D | A | S |
| *Dicranum leioneuron* Kindb. | mDiclei | P3 | P3 | M | A | S |
| *Dicranum majus* Turner | mDicmaj | P1 | P1 | M | A | S |
| *Dicranum montanum* Hedw. | mDicmon | C | C | D | A | S |
| *Dicranum ontariense* W.L. Peterson | mDicont | C | P1 | M | A | S |
| *Dicranum polysetum* Sw. | mDicpol | C | C | M | A | S |
| *Dicranum scoparium* Hedw. | mDicsco | C | C | B | A | S |
| *Dicranum spurium* Hedw. | mDicspu | P1 | | M | A | S |
| *Dicranum undulatum* Schrad. ex Brid. | mDicund | C | P1 | M | A | S |
| *Dicranum viride* (Sull. & Lesq.) Lindb. | mDicvir | | P3 | D | A | S |

**Table B3**
**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Ditrichum lineare* (Sm.) Lindb. | mDitlin | P3 | | D | P | S |
| *Ditrichum pusillum* (Hedw.) Hampe | mDitpus | P3 | | D | A | S |
| *Drepanocladus aduncus* (Hedw.) Warnst. | mDreadu | C | P3 | D | A | L |
| *Drepanocladus polygamus* (Schimp.) Hedenäs | mDreppol | P3 | | M | A | L |
| *Eurhynchiastrum pulchellum* (Hedw.) Ignatov & Huttunen | mEurpul | P3 | C | B | A | S |
| *Fissidens bryoides* Hedw. | mFisbry | P3 | | B | A | S |
| *Fissidens osmundoides* Hedw. | mFisosm | P1 | | D | A | S |
| *Frullania eboracensis* Lehm. | hFruebo | C | | D | P | NP |
| *Frullania inflata* Gottsche | hFruinf | | P3 | M | A | S |
| *Frullania oakesiana* Austin | hFruoak | C | C | M | A | L |
| *Fuscocephaloziopsis catenulata* (Huebener) Váňa & L. Söderstr. | hCepcat | P1 | P1 | D | P | S |
| *Fuscocephaloziopsis connivens* (Dicks.) Váňa & L. Söderstr. | hCepcon | C | C | M | P | S |
| *Fuscocephaloziopsis leucantha* (Spruce) Váňa & L. Söderstr. | hCepleu | P3 | | D | P | S |
| *Fuscocephaloziopsis loitlesbergeri* (Schiffn.) Váňa & L. Söderstr. | hCeploi | C | | M | A | S |
| *Fuscocephaloziopsis lunulifolia* (Dumort.) Váňa & L. Söderstr. | hCeplun | C | C | B | P | S |
| *Fuscocephaloziopsis macrostachya* (Kaal.) Váňa & L. Söderstr. | hCepmac | P3 | | D | P | NP |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Fuscocephaloziopsis pleniceps* (Austin) Váňa & L. Söderstr. | hCepple | C | | M | P | S |
| *Geocalyx graveolens* (Schrad.) Nees | hGeogra | C | C | M | A | S |
| *Gymnocolea inflata* (Huds.) Dumort. | hGyminf | C | P3 | D | A | S |
| *Hamatocaulis vernicosus* (Mitt.) Hedenäs | mHamver | P3 | | D | A | S |
| *Hedwigia ciliata* (Hedw.) P. Beauv. | mHedcil | | P3 | M | A | S |
| *Helodium blandowii* (F. Weber & D. Mohr) Warnst. | mHelbla | P3 | | M | A | S |
| *Herzogiella striatella* (Brid.) Z. Iwats. | mHerstr | P3 | P3 | M | A | S |
| *Herzogiella turfacea* (Lindb.) Z. Iwats. | mHertur | C | C | M | A | S |
| *Homalia trichomanoides* (Hedw.) Schimp. | mHomtri | P3 | P3 | B | A | S |
| *Hygroamblystegium varium* (Hedw.) Mönk. | mHygvar | C | C | M | A | S |
| *Hygrohypnum eugyrium* (Schimp.) Loeske | mHygeug | P3 | P3 | M | A | S |
| *Hylocomiadelphus triquetrus* (Hedw.) Ochyra & Stebel | mRhytri | C | C | D | A | S |
| *Hylocomiastrum umbratum* (Hedw.) M. Fleisch. ex Broth. | mHylumb | P2 | P3 | D | A | S |
| *Hylocomium splendens* (Hedw.) Schimp. | mHylspl | C | C | D | A | S |
| *Hypnum cupressiforme* Hedw. | mHypcup | C | C | D | A | S |
| *Hypnum curvifolium* Hedw. | mHypcur | P1 | | D | A | S |
| *Hypnum fauriei* Cardot | mHypfau | P1 | C | M | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Hypnum imponens* Hedw. | mHypimp | C | C | D | A | S |
| *Hypnum lindbergii* Mitt. | mCallind | P2 | C | D | A | S |
| *Hypnum pallescens* (Hedw.) P. Beauv. | mHyppal | C | C | M | A | S |
| *Hypnum recurvatum* (Lindb. & Arnell) Kindb. | mHyprec | P3 | | M | A | S |
| *Hypnum vaucheri* Lesq. | mHypvau | P3 | | D | A | S |
| *Isopaches bicrenatus* (Schmidel ex Hoffm.) H. Buch | hLopbic | P2 | | M | P | S |
| *Isopterygiopsis muelleriana* (Schimp.) Z. Iwats. | mIsomue | P1 | | D | P | S |
| *Isopterygiopsis pulchella* (Hedw.) Z. Iwats. | mIsopul | P1 | | M | P | S |
| *Kindbergia praelonga* (Hedw.) Ochyra | mKinpra | P1 | P3 | D | A | S |
| *Koponeniella graminicolor* (Brid.) Huttunen, Ignatov, Min Li & Y.F. Wang | mBrygra | P3 | | D | A | S |
| *Kurzia pauciflora* (Dicks.) Grolle | hKurpau | P1 | | D | A | S |
| *Lepidozia reptans* (L.) Dumort. | hLeprep | C | C | M | A | S |
| *Leptobryum pyriforme* (Hedw.) Wilson | mLeppyr | P3 | | M | P | S |
| *Leptodictyum riparium* (Hedw.) Warnst. | mLeprip | P1 | | M | A | S |
| *Lewinskya speciosa* (Nees) F. Lara, Garilleti & Goffinet | mOrtspe | P1 | P1 | M | A | S |
| *Liochlaena lanceolata* Nees | hJunlei | C | P1 | M | A | S |

**Table B3**
**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lophocolea bidentata* (L.) Dumort. | hChicoa | C | C | M | A | S |
| *Lophocolea heterophylla* (Schrad.) Dumort. | hChipro | C | C | M | P | S |
| *Lophozia ascendens* (Warnst.) R.M. Schust. | hLopasc | C | | D | P | S |
| *Lophozia guttulata* (Lindb. & Arnell) A. Evans | hLopgut | C | P1 | D | P | S |
| *Lophozia longiflora* (Nees) Schiffn. | hLoplongid | C | | D | P | S |
| *Lophozia silvicola* H. Buch | hLopsil | C | | D | P | S |
| *Lophozia ventricosa* (Dicks.) Dumort. | hLopven | C | C | D | P | S |
| *Marchantia polymorpha* L. | hMarpol | P1 | | D | A | S |
| *Meesia triquetra* (L. ex Jolycl.) Ångström | mMeetri | P3 | | D | A | L |
| *Mesoptychia heterocolpos* (Thed. ex Hartm.) L. Söderstr. & Váňa | hMeshet | P1 | | D | P | S |
| *Mesoptychia rutheana* (Limpr.) L. Söderstr. & Váňa | hLeirut | P3 | | M | A | S |
| *Mnium marginatum* (Dicks. ex With.) P. Beauv. | mMnimarg | C | P3 | M | A | L |
| *Mnium spinulosum* Bruch & Schimp. | mMnispi | C | C | M | A | S |
| *Mylia anomala* (Hook.) Gray | hMylano | C | | D | A | S |
| *Mylia taylorii* (Hook.) Gray | hMyltay | P1 | P3 | D | A | S |
| *Neoorthocaulis attenuatus* (Mart.) L. Söderstr., De Roo, Hedd. | hBaratt | C | C | D | P | S |
| *Nowellia curvifolia* (Dicks.) Mitt. | hNowcur | C | C | B | P | S |
| *Nyholmiella obtusifolia* (Schrad. ex Brid.) Holmen & E. Warncke | mNyhobt | P3 | P1 | D | P | S |

**Table B3**
**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Obtusifolium obtusum* (Lindb.) S.W. Arnell | hLopobt | P1 | | D | P | S |
| *Odontoschisma denudatum* (Mart.) Dumort. | hOdoden | C | | D | P | S |
| *Odontoschisma fluitans* (Nees) L. Söderstr. & Váňa | hClaflu | C | P2 | D | P | S |
| *Odontoschisma francisci* (Hook.) L. Söderstr. & Váňa | hClafra | C | | D | P | S |
| *Oncophorus virens* (Hedw.) Brid. | hOncvir | | P1 | M | A | S |
| *Oncophorus wahlenbergii* Brid. | mOncwah | C | P1 | M | A | S |
| *Orthotrichum anomalum* Hedw. | mOrtanom | P3 | | M | A | S |
| *Orthotrichum ohioense* Sull. & Lesq. | mOrtohi | | P3 | M | A | S |
| *Oxyrrhynchium hians* (Hedw.) Loeske | mOxyhia | P2 | | D | A | S |
| *Pallavicinia lyellii* (Hook.) Gray | hPallye | P2 | | D | A | S |
| *Paludella squarrosa* (Hedw.) Brid. | mPalsqu | P3 | | D | A | S |
| *Palustriella falcata* (Brid.) Hedenäs | mCrafalc | P1 | | D | A | S |
| *Paraleucobryum longifolium* (Ehrh. ex Hedw.) Loeske | mParlon | P2 | | D | A | L |
| *Pellia epiphylla* (L.) Corda | hPeleph | P3 | P1 | M | A | L |
| *Pellia neesiana* (Gottsche) Limpr. | hPelnee | P2 | | D | A | L |
| *Plagiochila porelloides* (Torr. ex Nees) Lindenb. | hPlapor | C | | D | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Plagiomnium cuspidatum* (Hedw.) T.J. Kop. | mPlacus | C | C | M | A | S |
| *Plagiomnium drummondii* (Bruch & Schimp.) T.J. Kop. | mPladru | C | C | M | A | S |
| *Plagiomnium ellipticum* (Brid.) T.J. Kop. | mPlaell | C | C | D | A | L |
| *Plagiomnium medium* (Bruch & Schimp.) T.J. Kop. | mPlamed | C | P3 | M | A | L |
| *Plagiomnium rostratum* (Schrad.) T.J. Kop. | mPlaros | P3 | | M | A | L |
| *Plagiothecium cavifolium* (Brid.) Z. Iwats. | mPlacav | C | C | D | P | S |
| *Plagiothecium denticulatum* (Hedw.) Schimp. | mPladen | C | C | B | P | S |
| *Plagiothecium laetum* Schimp. | mPlalae | C | C | M | A | S |
| *Plagiothecium latebricola* Schimp. | mPlalat | C | C | D | A | S |
| *Platygyrium repens* (Brid.) Schimp. | mPlarep | C | C | D | P | S |
| *Pleurozium schreberi* (Willd. ex Brid.) Mitt. | mPlesch | C | C | D | A | S |
| *Pogonatum dentatum* (Menzies ex Brid.) Brid. | mPogden | C | | D | A | S |
| *Pohlia cruda* (Hedw.) Lindb. | mPohcruda | C | | B | A | L |
| *Pohlia elongata* Hedw. | mPohelo | P3 | | B | A | S |
| *Pohlia filum* (Schimp.) Mårtensson | mPohfil | P3 | | D | P | S |
| *Pohlia nutans* (Hedw.) Lindb. | mPohnut | C | C | B | A | S |
| *Pohlia sphagnicola* (Bruch & Schimp.) Broth. | mPohsph | C | | D | A | S |
| *Pohlia wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews | mPohwahl | P3 | | D | A | S |
| *Polytrichastrum alpinum* (Hedw.) G.L. Sm. | mPolalpi | P3 | | B | A | S |

**Table B3**
**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Polytrichum commune* Hedw. | mPolcom | C | C | D | A | S |
| *Polytrichum densifolium* Wilson ex Mitt. | mPolfor | P3 | P3 | B | A | S |
| *Polytrichum juniperinum* Hedw. | mPoljun | C | P1 | D | A | S |
| *Polytrichum longisetum* Sw. ex Brid. | mPollon | P1 | P1 | B | A | S |
| *Polytrichum pallidisetum* Funck | mPolpal | C | P1 | B | A | S |
| *Polytrichum piliferum* Hedw. | mPolpil | P2 | P1 | D | A | S |
| *Polytrichum strictum* Menzies ex Brid. | mPolstr | C | P1 | D | A | S |
| *Pseudobryum cinclidioides* (Huebener) T.J. Kop. | mPsecin | P2 | | D | A | L |
| *Pseudocampylium radicale* (P. Beauv.) Vanderp. & Hedenäs | mPserad | P1 | P3 | M | A | S |
| *Pseudoleskeella nervosa* (Brid.) Nyholm | mPsenerv | | P3 | D | P | S |
| *Pseudotaxiphyllum distichaceum* (Mitt.) Z. Iwats. | mPsedis | | P2 | M | P | NP |
| *Pseudotaxiphyllum elegans* (Brid.) Z. Iwats. | mPseeleg | P3 | | D | P | S |
| *Ptilidium ciliare* (L.) Hampe | hPticil | C | C | D | A | L |
| *Ptilidium pulcherrimum* (Weber) Vain. | hPtipul | C | C | D | A | L |
| *Ptilium crista-castrensis* (Hedw.) De Not. | mPticricas | C | C | D | A | S |
| *Pylaisia intricata* (Hedw.) Schimp. | mPylint | C | C | M | A | L |
| *Pylaisia polyantha* (Hedw.) Schimp. | mPylpol | P1 | C | M | A | S |

**Table B3**
**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Pylaisia selwynii* Kindb. | mPylselw | P1 | C | M | A | S |
| *Racomitrium microcarpum* (Hedw.) Brid. | mRacmicr | P3 | P3 | D | A | S |
| *Radula complanata* (L.) Dumort. | hRadcom | P1 | P1 | M | A | L |
| *Rhizomnium gracile* T.J. Kop. | mRhigra | P3 | | D | A | L |
| *Rhizomnium pseudopunctatum* (Bruch & Schimp.) T.J. Kop. | mRhipse | C | P1 | M | A | L |
| *Rhizomnium punctatum* (Hedw.) T.J. Kop. | mRhipun | C | P1 | D | P | L |
| *Rhodobryum ontariense* (Kindb.) Kindb. | mRhoont | P3 | | D | A | S |
| *Rhynchostegium serrulatum* (Hedw.) A. Jaeger | mRhyser | P1 | P1 | M | A | S |
| *Rhytidiadelphus subpinnatus* (Lindb.) T.J. Kop. | mRhysub | P2 | P2 | D | A | S |
| *Riccardia latifrons* (Lindb.) Lindb. | hRiclat | C | P1 | M | A | S |
| *Riccardia multifida* (L.) Gray subsp. multifida | hRicmult | P3 | | M | A | S |
| *Riccardia palmata* (Hedw.) Carruth. | hRicpal | P2 | | D | P | S |
| *Riccardia vitrea* Furuki | hRicvitr | P1 | | D | A | S |
| *Sanionia uncinata* (Hedw.) Loeske | mSanunc | C | C | M | A | S |
| *Sarmentypnum exannulatum* (Schimp.) Hedenäs | mSarexa | C | | D | A | S |
| *Scapania apiculata* Spruce | hScaapi | P1 | C | D | P | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Scapania irrigua* (Nees) Nees | hScairr | C | P3 | D | P | S |
| *Scapania mucronata* H. Buch | hScamuc | P3 | P3 | D | P | S |
| *Scapania nemorea* (L.) Grolle | hScanem | P3 | | D | P | S |
| *Scapania paludicola* Loeske & Müll. Frib. | hScapalc | C | | D | P | NP |
| *Scapania uliginosa* (Lindenb.) Dumort. | hScauli | P3 | | D | A | S |
| *Schistidium agassizii* Sull. & Lesq. | mSchagas | | P3 | M | A | S |
| *Schistochilopsis grandiretis* (Lindb. ex Kaal.) Konstant. | hSchgra | P1 | | D | P | S |
| *Schistochilopsis incisa* (Schrad.) Konstant. | hSchinc | P1 | | D | P | S |
| *Schistostega pennata* (Hedw.) F. Weber & D. Mohr | mSchpen | P3 | | D | P | S |
| *Schljakovia kunzeana* (Huebener) Konstant. & Vilnet | hBarkun | C | | D | P | S |
| *Scorpidium revolvens* (Sw.) Rubers | mScorev | C | | M | A | S |
| *Scorpidium scorpioides* (Hedw.) Limpr. | mScosco | P3 | | D | A | S |
| *Serpoleskea subtilis* (Hedw.) Loeske | mPlasub | P1 | | M | A | S |
| *Solenostoma gracillimum* (Sm.) R.M. Schust. | hJungra | P2 | | D | A | S |
| *Sphagnum angustifolium* (Warnst.) C.E.O. Jensen | sSphang | C | C | D | A | S |
| *Sphagnum annulatum* Warnst. | sSphann | P3 | | D | A | L |

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**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Sphagnum balticum* (Russow) C.E.O. Jensen | sSphbal | P3 | | D | A | L |
| *Sphagnum capillifolium* (Ehrh.) Hedw. | sSphcap | C | C | D | A | S |
| *Sphagnum centrale* C.E.O. Jensen | sSphcen | P1 | C | D | A | L |
| *Sphagnum contortum* Schultz | sSphcon | P3 | | D | A | S |
| *Sphagnum cuspidatum* Ehrh. ex Hoffm. | sSphcus | C | | D | A | L |
| *Sphagnum fallax* H. Klinggr. | sSphfal | C | | D | A | L |
| *Sphagnum flexuosum* Dozy & Molk. | sSphfle | P1 | P1 | D | A | S |
| *Sphagnum fuscum* (Schimp.) H. Klinggr. | sSphfus | C | P1 | D | A | L |
| *Sphagnum girgensohnii* Russow | sSphgir | C | C | D | A | S |
| *Sphagnum isoviitae* Flatberg | sSphiso | P3 | | D | A | L |
| *Sphagnum lindbergii* Schimp. | sSphlin | P1 | | B | A | L |
| *Sphagnum magellanicum* Brid. | sSphmag | C | P1 | D | A | L |
| *Sphagnum majus* (Russow) C.E.O. Jensen | sSphmaj | C | | D | A | L |
| *Sphagnum palustre* L. | sSphpal | P3 | | D | A | L |
| *Sphagnum papillosum* Lindb. | sSphpap | P1 | | D | A | L |
| *Sphagnum platyphyllum* (Lindb.) Warnst. | sSphpla | P3 | | D | A | L |
| *Sphagnum pulchrum* (Lindb.) Warnst. | sSphpul | C | | D | A | L |
| *Sphagnum quinquefarium* (Lindb.) Warnst. | sSphqui | C | P1 | B | A | S |
| *Sphagnum riparium Ångström* | sSphrip | P1 | | D | A | S |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Sphagnum rubellum Wilson* | sSphrub | C | P1 | D | A | L |
| *Sphagnum russowii Warnst.* | sSphrus | C | P1 | D | A | L |
| *Sphagnum squarrosum Crome* | sSphsqu | P1 | C | M | A | L |
| *Sphagnum subfulvum Sjörs* | sSphsubf | P3 | | M | A | L |
| *Sphagnum subsecundum Nees* | sSphsubs | P2 | | D | A | L |
| *Sphagnum subtile (Russow) Warnst.* | sSphsubtile | C | | D | A | L |
| *Sphagnum tenellum (Brid.) Brid.* | sSphtenellum | P3 | | M | A | L |
| *Sphagnum wulfianum Girg.* | sSphwul | C | P1 | B | A | S |
| *Sphenolobus minutus (Schreb.) Berggr.* | hAnamin | C | P3 | D | P | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Splachnum ampullaceum* Hedw. | mSplamp | P3 | P3 | D | A | S |
| *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs | mStrstr | C | | D | A | S |
| *Syzygiella autumnalis* (DC.) K. Feldberg, Váňa, Hentschel & J. Heinrichs | hJamaut | C | C | D | A | S |
| *Tetraphis pellucida* Hedw. | mTetpel | C | C | M | P | S |
| *Tetraplodon angustatus* (Hedw.) Bruch & Schimp. | mTetang | P3 | | B | A | S |
| *Thuidium delicatulum* (Hedw.) Schimp. | mThudeli | | P3 | D | A | S |
| *Thuidium recognitum* (Hedw.) Lindb. | mThurec | C | C | D | A | S |
| *Tomentypnum falcifolium* (Renauld ex Nichols) Tuom. | mTomfal | C | | D | A | S |
| *Tomentypnum nitens* (Hedw.) Loeske | mTomnit | C | P2 | D | A | S |
| *Tortella humilis* (Hedw.) Jenn. | mTorhumi | | P3 | M | A | S |
| *Trematodon ambiguus* (Hedw.) Hornsch. | mTreamb | P2 | P3 | M | A | L |
| *Tritomaria exsecta* (Schmidel) Schiffn. ex Loeske | hTriexsecta | P3 | | D | P | S |
| *Tritomaria exsectiformis* (Breidl.) Schiffn. ex Loeske | hTriexsecti | C | P3 | D | P | S |
| *Tritomaria laxa* (Lindb.) Stotler & Crand.-Stotl. | hSchlax | C | P3 | D | P | S |
| *Tritomaria quinquedentata* (Huds.) H. Buch | hTriqui | P3 | | D | A | S |
| *Ulota coarctata* (P. Beauv.) Hammar | mUlocoa | P1 | P1 | M | A | S |

**Table B3**

**(Continued) Boreal bryophyte species in spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains in boreal western Quebec, Canada. The species acronym used in the analysis is presented. The letter at the beginning of the acronym represents the bryophyte linage (m=moss, h=liverworts, s=sphagnum). The species present in each bioclimatic domain is indicated by its rarity pattern (C= Common, P1= sparse population generalists, P2 = abundant specialists, and P3 = sparse population specialists). Information about the sexual condition (D= Dioicous, M= Monoicous, B= Both), production of asexual propagules (P= present, A=Absent), and spore size (Small= S, Large=L, NP = not reported, U=uncertain) of each specie is provided.**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Ulota crispa* (Hedw.) Brid. | mUlocri | C | P3 | M | A | L |
| *Warnstorfia fluitans* (Hedw.) Loeske | mWarflu | C | P1 | M | A | S |

**Table B4**

**Differences in a) rarity patterns and b) functional traits and rarity variables related to bryophyte metacommunities between bioclimatic domains presented in the NMDS by *envfit*. $r^2$ = variation explained by the multiple regression model; P = significance calculated by permutation test. Significant variables are presented in bold.**

a) Rarity patterns

| Bryophyte lineage | Rarity pattern | $r^2$ | P |
|---|---|---|---|
| Total of species | Common | 0.24 | 0.00 |
| | Pattern 1 | 0.04 | 0.00 |
| | Pattern 2 | 0.01 | 0.00 |
| | Pattern 3 | 0.02 | 0.00 |
| Liverworts | Common | 0.23 | 0.00 |
| | Pattern 1 | 0.01 | 0.04 |
| | Pattern 2 | 0.01 | 0.01 |
| | Pattern 3 | 0.02 | 0.00 |
| Mosses | Common | 0.08 | 0.00 |
| | Pattern 1 | 0.04 | 0.00 |
| | Pattern 2 | 0.01 | 0.00 |
| | Pattern 3 | 0.01 | 0.01 |
| Sphagna | Common | 0.23 | 0.00 |
| | Pattern 1 | 0.00 | 0.74 |
| | Pattern 2 | 0.00 | 0.62 |
| | Pattern 3 | 0.00 | 0.52 |

**Table B4**

**(Continued) Differences in a) rarity patterns and b) functional traits and rarity variables related to bryophyte metacommunities between bioclimatic domains presented in the NMDS by *envfit*. $r^2$ = variation explained by the multiple regression model; P = significance calculated by permutation test. Significant variables are presented in bold.**

| b) Functional traits and rarity variables | | | |
|---|---|---|---|
| Life-history traits | Dioicous species | 0.57 | 0.00 |
| | Monoicous species | 0.67 | 0.00 |
| | Both sexual conditions | 0.06 | 0.00 |
| | Asexual reproduction | 0.32 | 0.00 |
| Dispersal trait | Large spores | 0.22 | 0.00 |
| Rarity variables | Exclusive species | 0.35 | 0.00 |
| | Species with rarity pattern change | 0.43 | 0.00 |

**Table B5**

**The PERMANOVA analysis with *adonis* function revealed significant differences in community composition between the spruce moss (SPMO) and balsam fir-white birch (BFWB) bioclimatic domains.**

| Source | Df | Sum of Squares | R² | F | p-value |
|---|---|---|---|---|---|
| Bioclimatic domains | 1 | 22.46 | 0.067 | 69.016 | 0.001 *** |
| Residual | 962 | 313.09 | 0.933 | - | - |
| Total | 963 | 335.56 | 1.000 | - | - |

# APPENDICE C – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE IV

Methods C1.
Loci constructions and SNPs calling: Mapping to a reference

We mapped our cleaned reads from process-radtaqs to an available transcriptome of the species *Dicranum scoparium* Hedw. (1KP, Lang et al., 2021) using the software bwa v0.7 (Li, 2013). With the Samtools suite (Danecek et al., 2021), we converted the outputs of bwa (SAM format) to the equivalent compressed BAM format as suggested by Rochette and Catchen (2017). To build the loci, the gstacks module from Stacks v. 2.5 (Rochette et al., 2019) was run considering each individual a single population . We then estimated missing-data with adegenet v.2.0.2. (Jombart, 2008) package in R, transforming vcf file into a genind and genlight formats, and re-run gstacks excluding samples with less than 900 loci and more than 60% of missing-data (Hodel et al., 2017) to create a high-quality dataset consisting of 191 samples. The single nucleotide polymorphisms (SNPs) were filtered using the population module from Stacks v. 2.5. First, we considered each individual as a single population, we selected loci present in at least 75% (-R 0.75) of the individuals and we called linked and unlinked (--write-single-snp) SNPs.

**Table C1**
**Scale effect analysis of genetic diversity variables using glms and the multi-fit function for uncorrelated landscape variables. The lowest AIC (Akaike Information Criterion) values, showing the best model, are highlighted in grey. The acronyms are formed by forest cover (CF) or patch density (PD) for each forest class: young forest (YF), medium-age forest (MF), old forest (OF), or non-forest land (NF).**

Shannon-Wiener Index (H)

| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
|---|---|---|---|---|---|---|
| 1km | 31.72 | 33.83 | 35.24 | 30.82 | 34.80 | 34.85 |
| 2km | 31.66 | 33.15 | 35.15 | 30.53 | 29.91 | 35.62 |
| 3km | 32.48 | 33.37 | 35.19 | 31.06 | 26.51 | 35.19 |
| 4km | 33.14 | 34.16 | 35.19 | 31.54 | 28.31 | 35.54 |
| 5km | 33.35 | 34.62 | 35.33 | 32.69 | 29.75 | 35.58 |
| 6km | 33.81 | 35.06 | 35.41 | 33.63 | 30.23 | 35.33 |
| 7km | 34.18 | 35.10 | 35.43 | 34.08 | 31.91 | 35.53 |
| 8km | 34.85 | 34.78 | 35.30 | 34.63 | 34.10 | 35.32 |
| 9km | 35.38 | 34.90 | 35.11 | 34.90 | 35.10 | 35.17 |
| 10km | 35.61 | 34.89 | 34.85 | 35.05 | 35.39 | 35.04 |

Expected number of Multi-Locus Genotypes (eMLG)

| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
|---|---|---|---|---|---|---|
| 1km | 58.98 | 59.87 | 59.91 | 58.96 | 59.91 | 59.92 |
| 2km | 58.89 | 59.81 | 59.92 | 58.93 | 58.88 | 59.77 |
| 3km | 58.66 | 59.78 | 59.93 | 58.97 | 58.74 | 59.86 |
| 4km | 58.75 | 59.79 | 59.93 | 59.16 | 58.95 | 59.93 |
| 5km | 58.56 | 59.87 | 59.91 | 59.28 | 59.08 | 59.85 |
| 6km | 58.41 | 59.92 | 59.82 | 59.59 | 58.69 | 59.93 |
| 7km | 58.10 | 59.92 | 59.75 | 59.77 | 58.09 | 59.90 |
| 8km | 58.21 | 59.90 | 59.79 | 59.86 | 59.30 | 59.93 |
| 9km | 58.64 | 59.92 | 59.84 | 59.89 | 59.76 | 59.92 |
| 10km | 59.23 | 59.92 | 59.89 | 59.92 | 59.91 | 59.90 |

Allelic Diversity

| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
|---|---|---|---|---|---|---|
| 1km | 941.31 | 1066.91 | 1141.52 | 1057.10 | 1133.10 | 1141.55 |
| 2km | 994.07 | 1080.63 | 1127.59 | 1028.52 | 1126.24 | 1100.77 |
| 3km | 1012.54 | 1047.21 | 1130.91 | 1014.03 | 1006.64 | 1032.80 |
| 4km | 1061.06 | 994.12 | 1116.23 | 1015.02 | 972.71 | 940.05 |
| 5km | 1056.42 | 966.50 | 1108.76 | 990.28 | 982.38 | 856.95 |

**Table C1**

**(Continued) Scale effect analysis of genetic diversity variables using glms and the multi-fit function for uncorrelated landscape variables. The lowest AIC (Akaike Information Criterion) values, showing the best model, are highlighted in grey. The acronyms are formed by forest cover (CF) or patch density (PD) for each forest class: young forest (YF), medium-age forest (MF), old forest (OF), or non-forest land (NF).**

| | | | | | | |
|---|---|---|---|---|---|---|
| 6km | 1092.33 | 953.96 | 1091.66 | 1031.64 | 977.33 | 906.63 |
| 7km | 1102.83 | 962.09 | 1091.05 | 1036.56 | 1040.04 | 963.03 |
| 8km | 1110.68 | 953.00 | 1089.68 | 1040.77 | 1109.60 | 1015.27 |
| 9km | 1129.47 | 985.58 | 1068.27 | 1028.70 | 1130.14 | 1000.46 |
| 10km | 1140.80 | 1019.96 | 1038.99 | 1008.24 | 1107.28 | 1017.03 |

| Percentage of variant sites | | | | | | |
|---|---|---|---|---|---|---|
| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
| 1km | -23.93 | -23.64 | -25.69 | -25.05 | -23.76 | -28.57 |
| 2km | -24.18 | -23.35 | -25.25 | -24.62 | -23.80 | -27.87 |
| 3km | -24.23 | -23.58 | -24.07 | -24.61 | -23.51 | -29.94 |
| 4km | -24.43 | -23.83 | -23.61 | -24.24 | -23.73 | -26.84 |
| 5km | -24.59 | -24.30 | -23.51 | -24.32 | -24.37 | -25.68 |
| 6km | -24.51 | -24.40 | -23.40 | -23.82 | -24.19 | -23.85 |
| 7km | -24.18 | -24.46 | -23.35 | -23.51 | -23.92 | -23.43 |
| 8km | -23.86 | -24.43 | -23.35 | -23.45 | -23.63 | -23.38 |
| 9km | -23.78 | -24.63 | -23.35 | -23.43 | -23.49 | -23.41 |
| 10km | -23.67 | -24.82 | -23.35 | -23.41 | -23.43 | -23.36 |

| Percentage of polymorphic loci | | | | | | |
|---|---|---|---|---|---|---|
| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
| 1km | 7.06 | 8.17 | 9.10 | 7.72 | 9.03 | 8.85 |
| 2km | 7.70 | 8.46 | 8.84 | 7.37 | 9.07 | 7.99 |
| 3km | 7.89 | 8.19 | 8.96 | 7.13 | 7.92 | 6.59 |
| 4km | 8.46 | 7.54 | 8.82 | 7.29 | 7.67 | 5.42 |
| 5km | 8.43 | 7.31 | 8.76 | 6.97 | 7.96 | 3.97 |
| 6km | 8.75 | 7.18 | 8.61 | 7.77 | 7.84 | 5.53 |
| 7km | 8.81 | 7.31 | 8.64 | 8.01 | 8.41 | 6.83 |
| 8km | 8.85 | 7.24 | 8.66 | 8.13 | 8.99 | 7.65 |
| 9km | 9.03 | 7.71 | 8.43 | 8.03 | 9.10 | 7.42 |
| 10km | 9.11 | 8.17 | 8.10 | 7.83 | 8.95 | 7.77 |

**Table C1**

**(Continued) Scale effect analysis of genetic diversity variables using glms and the multi-fit function for uncorrelated landscape variables. The lowest AIC (Akaike Information Criterion) values, showing the best model, are highlighted in grey. The acronyms are formed by forest cover (CF) or patch density (PD) for each forest class: young forest (YF), medium-age forest (MF), old forest (OF), or non-forest land (NF).**

| Nucleotide diversity: Pi (π) | | | | | | |
|---|---|---|---|---|---|---|
| Scale | FC OF | FC MF | FC YF | FC NF | PD OF | PD YF |
| 1km | -5.55 | -5.48 | -5.51 | -5.52 | -5.81 | -9.48 |
| 2km | -5.66 | -5.55 | -5.49 | -5.53 | -8.19 | -7.39 |
| 3km | -5.58 | -5.49 | -5.55 | -5.52 | -6.67 | -11.22 |
| 4km | -5.73 | -6.19 | -5.49 | -5.60 | -6.32 | -9.89 |
| 5km | -5.59 | -6.58 | -5.48 | -5.53 | -6.39 | -10.95 |
| 6km | -5.58 | -7.10 | -5.48 | -5.65 | -5.91 | -10.63 |
| 7km | -5.48 | -7.04 | -5.48 | -5.67 | -5.88 | -7.85 |
| 8km | -5.49 | -6.65 | -5.48 | -5.60 | -6.39 | -7.71 |
| 9km | -5.50 | -6.33 | -5.49 | -5.51 | -6.24 | -8.57 |
| 10km | -5.50 | -5.90 | -5.50 | -5.48 | -5.67 | -8.34 |

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