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UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

IMPACT DE LA PROPORTION DE MÉLÈZE LARICIN EN CANOPÉE SUR LA
COMPOSITION, LA DIVERSITÉ ET LES TRAITS FONCTIONNELS DES
PLANTES VASCULAIRES ET DES BRYOPHYTES EN SOUS-BOIS

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

À LA MAITRISE EN ÉCOLOGIE

PAR

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RÉSUMÉ

Le mélèze est le seul conifère à feuille caduque en Amérique du Nord. Cette caractéristique distingue la fonction écosystémique du mélèze des autres conifères et des feuillus. Afin de mieux connaître sa fonction écosystémique en forêt boréale, nous avons étudié son impact sur la composition, la diversité et les traits fonctionnels des communautés de plantes vasculaires et de bryophytes. Nous avons donc déterminé les caractéristiques hydrogéochimiques du sol, la fermeture et la densité de la canopée, ainsi que la composition et les traits fonctionnels des communautés de plantes vasculaires et de bryophytes de sous-bois dans 15 sites sélectionnés pour couvrir un gradient de proportion de mélèzes dans des forêts d'épinettes noires du nord du Québec. Dix quadrats d'inventaire et d'échantillonnage ont été placés dans chaque site. De plus, nous avons installé des quadrats de suivi de l'impact de l'ajout d'aiguilles de mélèze sur les communautés de sous-bois dans un site d'épinettes noires dépourvu de mélèze. Nos résultats montrent qu'avec une augmentation de la proportion de mélèze en canopée, il y a une augmentation de la diversité de plantes vasculaires, de la surface spécifique des feuilles, de la concentration en azote, et une diminution de la concentration en carbone foliaire, ainsi qu'une transition des espèces associées aux peuplements pauvres de conifères vers des espèces de milieux plus riches de forêts comportant du mélèze. Pour les bryophytes, nous avons noté une diminution du nombre d'espèces et une mortalité causée par la chute de la litière de mélèze, mais aussi une augmentation de la concentration en azote dans les bryophytes persistantes. En conclusion, ces connaissances montrent que le mélèze en forte proportion aurait comme fonction écosystémique de fertiliser et de structurer le sol, permettant ainsi de rendre des sols organiques improductifs plus productifs. Des études devraient être entreprises pour évaluer la densité optimale de plantation et le temps nécessaire à la création d'un sol productif.

Mots clés : Mélèze Laricin, *Larix laricina* (du Roi) K. Koch, Forêt boréale, Traits fonctionnels, Mousses, Herbacées, Arbustes, Sol organique, Paludification

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Mise en contexte et problématique

La forêt boréale est constamment perturbée, à différentes fréquences et intensités, par divers types de perturbations dont les plus importantes sont les coupes forestières, les feux, les chablis, les épidémies et les inondations. Ces perturbations affectent la flore, la faune, ainsi que les services écosystémiques rendus à l'humain. Ainsi, afin d'assurer les ressources nécessaires à la survie et au bien être futur des humains, il est donc d'intérêt de prédire l'impact des différentes perturbations sur la composition et la structure de la flore, de la faune et du sol. Cependant, pour faire des modèles de prédiction précis, nous avons besoin de meilleures connaissances sur la dynamique forestière.

La dynamique forestière est le processus de changement de la composition et de la structure des communautés végétales en fonction du temps et des perturbations (MRN, 2013). L'évolution de ce processus dépend de la fréquence, de l'intensité et de l'ampleur des perturbations, ainsi que du climat, du milieu et des caractéristiques du peuplement, notamment, la composition forestière et le degré de paludification (MRN, 2013). Dans le nord-ouest du Québec, la dynamique forestière est principalement influencée par l'interaction entre la fréquence et la sévérité des feux, ainsi que l'effet de cette interaction sur le processus de paludification (Simard et al., 2007). La

paludification engendre une augmentation de la profondeur de la couche organique du sol, un rehaussement de la nappe phréatique et une diminution de la productivité des arbres. En plus des feux, la coupe avec rétention de la régénération et des sols peut augmenter le risque de paludification et la perte de productivité (Lafleur et al., 2010). La paludification est donc un enjeu important pour l'aménagement forestier dans la région.

Le sous-bois forestier est une composante importante de l'écosystème parce qu'il représente une diversité floristique, un habitat et des ressources pour la faune et exerce différentes fonctions, notamment dans la régénération de la strate arborescente, le cyclage des nutriments, ainsi que l'activité biologique du sol (Nilsson & Wardle, 2005). Le sous-bois varie entre les types de forêts, par exemple on retrouve des espèces de milieux plus riches et une plus grande diversité de plantes vasculaires sous une canopée de feuillus en comparaison à une canopée de conifères (Légaré et al., 2001). Comme la canopée et le sous-bois sont en interaction continue et qu'elles ont un impact sur la composition et la structure de chacun (Légaré et al., 2002; Mestre et al., 2017; Nilsson & Wardle, 2005), il est important d'avoir des connaissances sur la composition et la fonction de ces deux strates végétales pour mieux comprendre la dynamique forestière.

Le mélèze laricin (*Larix laricina* (Du Roi) K. Koch) est un des conifères les plus répandus en Amérique du Nord (Johnston, 1990). Au Québec, on le retrouve sur tout le territoire forestier, mais plus particulièrement en tourbière boréale (Cauboue, 2007). Cette grande distribution de l'espèce est due à sa capacité d'adaptation à une grande variabilité de conditions environnementales, telles que des températures et des précipitations extrêmes, ainsi que sa capacité à croître sur différents types de sol (Cauboue, 2007; Johnston, 1990).

Plusieurs études se sont intéressées aux facteurs de stress et de perturbation (Burnside et al., 2013; Islam & Macdonald, 2004), à la répartition (Dufour-Tremblay et al., 2012; C. Evans et al., 2016) et au cycle de vie du mélèze (Brown et al., 1988; Chakravarty & Chatarpaul, 1990; Clausen & Kozlowski, 1970). Cependant, très peu d'études, à notre connaissance, se sont intéressées à l'impact du mélèze sur les communautés de sous-bois (Fowells, 1965). Pourtant, l'apport de ces connaissances pourrait permettre une meilleure compréhension de la dynamique forestière et ainsi faire de meilleures prévisions de la succession forestière. Ces prévisions sont utiles pour parfaire les plans d'aménagement forestier.

1.2 État des connaissances

1.2.1 Caractéristiques des mélézins

On retrouve des mélézins dans une grande variété de milieux, mais davantage dans les forêts tourbeuses et les tourbières. Le sol est soit, organique fibreux, organique mésique, organique humique ou tourbeux humique (Taylor et al., 2000). Ces milieux sont très humides, souvent mal drainés et paludifiés (matière organique de plus de 20 cm d'épaisseur).

La paludification est le phénomène d'accumulation graduelle de matière organique (Payette & Rochefort, 2001). Pour qu'il y ait paludification, il y a d'abord une modification des conditions environnementales du milieu, favorisant un excès hydrique ou la fluctuation de la nappe phréatique (Vitt & Wieder, 2008). L'excès hydrique survient lorsqu'il y a plus de précipitations que d'évapotranspiration dans un milieu ayant une nappe phréatique superficielle (Payette & Rochefort, 2001). Dû à l'excès hydrique, il y a une diminution de la température du sol et le développement d'une zone anoxique, ce qui permet la colonisation du milieu par certaines espèces végétales, bactériennes et fongiques spécialisées. Mis à part certaines espèces, la majorité des

espèces de plantes vasculaires ont une productivité réduite, voir impossible dans ce type de milieu. Ainsi, ce milieu est caractérisé par un faible taux de décomposition, un degré d'acidité plus élevé qu'en pessière noire, ainsi qu'une accumulation de matière organique.

En plus de favoriser la paludification du milieu, lorsque la nappe phréatique est superficielle, les sols sont mal aérés (Campbell, 1980), les nutriments sont peu disponibles pour la croissance des plantes (Ponnamperuma, 1984) et la température de la matière organique est basse (Lee, 1980). Pour les plantes ligneuses, une mauvaise aération du sol entraîne une diminution de la transpiration, de la conductance stomatique, du taux net d'assimilation, de l'efficacité de l'utilisation de l'eau et de la photosynthèse (Islam et al., 2003). La faible disponibilité des nutriments et la faible température de la matière organique sont des facteurs limitants pour l'établissement et la croissance des plantes terrestres. De plus, les plantes qui sont soumises à un excès hydrique et qui n'y sont pas adaptées accumulent de l'éthylène, un composé qui inhibe, entre autres, le taux net d'assimilation de CO₂, la transpiration et la conductance stomatique (Blake & Reid, 1981). Une nappe phréatique superficielle augmente la mortalité racinaire, le taux de décomposition des racines et diminue le ratio racine/tige de l'arbre (Kozlowski, 1986).

Les adaptations morphologiques et physiologiques aux conditions d'excès hydrique sont nombreuses chez le mélèze laricin. Entre autres, il y a le développement de racines adventives (Calvo-Polanco et al., 2012), l'hypertrophie des lenticelles à la base de la tige (Islam & Macdonald, 2004), ainsi que le maintien de la capacité de transporter l'oxygène aux racines pour assurer une respiration minimale (Conlin & Lieffers, 1993). Malgré ces différentes adaptations, on observe une diminution de la productivité du mélèze lorsqu'il pousse en conditions de sursaturation en eau (Islam et al., 2003).

1.2.2 Caractéristiques du mélèze

Le mélèze laricin est le seul conifère à aiguilles caduques au Québec (Cauboue, 2007). La hauteur moyenne d'un individu mature est de 15 à 23 m avec un diamètre à hauteur de poitrine (DHP) moyen entre 36 et 51 cm (Johnston, 1990). La longévité du mélèze est généralement de 150 ans (Johnston, 1990).

Les aiguilles du mélèze peuvent atteindre une longueur de 10 à 25 mm et sont regroupées en faisceau (Marie-Victorin et al., 2002). Les éléments azote (N), phosphore (P), calcium (Ca), magnésium (Mg), potassium (K), zinc (Zn), aluminium (Al), fer (Fe), manganèse (Mn) et bore (B) se retrouvent dans les aiguilles et leur concentration dépend des conditions environnementales du milieu (Tilton, 1977). En comparaison avec l'épinette noire (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), avec qui le mélèze partage des habitats, la concentration d'azote contenue dans les aiguilles du mélèze serait plus du double (Lieffers & Macdonald, 1990). Avant la chute des aiguilles, la concentration en N et en K diminue dans les aiguilles, tandis que la concentration des autres éléments demeure inchangée (Tilton, 1977). Pour ce qui est de la transpiration journalière estivale, elle serait deux fois plus élevée que celle de l'épinette noire dans les mêmes conditions (Kimmins, 2004).

Le réseau racinaire du mélèze se trouve à la surface du sol (entre 30 et 60 cm de profondeur) et peut être assez étendu dans de bonnes conditions de croissance (Fowells, 1965). Sous une couverture de sphaignes favorisant la saturation en eau du sol, le mélèze remplace continuellement ses racines par des racines au-dessus des anciennes afin d'assurer sa respiration et son apport en éléments nutritifs dans des conditions de paludification. De plus, un réseau de racines adventives est produit par le mélèze lorsqu'il est soumis à une période prolongée d'inondations ou d'épidémie d'insectes (Fowells, 1965).

Le mélèze est une espèce pionnière, dont les semis tolèrent mal l'ombre, limitant ainsi la colonisation du sous-bois par l'espèce. L'épinette noire, qui est une espèce de fin de succession, est généralement l'espèce qui remplacera progressivement le mélèze dans la strate arborescente (Cauboue, 2007; Fowells, 1965). Pour avoir une germination optimale, la graine de mélèze a besoin de certaines conditions, soit une humidité constante sur de l'humus ou sur des mousses à croissance lente telles que *Mnium* spp., *Drepanocladus* spp. et *Helodium* spp. (Fowells, 1965). Dans des conditions environnementales similaires, le mélèze a un taux de croissance plus élevé que l'épinette noire (Jutras et al., 2006).

1.2.3 Rôle des communautés de plantes vasculaires de sous-bois dans l'écosystème forestier

Les communautés de plantes vasculaires, incluant les arbustes et les plantes herbacées, jouent un rôle important dans l'écosystème forestier (Nilsson & Wardle, 2005). En effet, elles influencent la succession de la strate supérieure (Messier et al., 1998), le cycle des nutriments (Weber & Van Cleve, 1981), ainsi que l'habitat et les ressources pour la faune (Gunnarsson et al., 2004). Ces communautés de sous-bois sont dynamiques (Chipman & Johnson, 2002) et varient en fonction de la structure et la composition de la canopée et du sol (Chen et al., 2004). Plus précisément, elles sont influencées par le degré de la pente (Reich et al., 2001), la quantité de lumière (Légaré et al., 2002), de nutriments (Wardle & Zackrisson, 2005), le type d'humus (Qian et al., 2003) et le pH du sol (Wardle & Zackrisson, 2005).

1.2.4 Rôle des bryophytes dans l'écosystème forestier

Les bryophytes sont des plantes dépourvues de vaisseaux, ce qui les distingue des plantes vasculaires. Ils absorbent donc l'eau et les nutriments par la surface de leur corps, le rendant du même coup sensible aux changements d'humidité environnants et

aux polluants atmosphériques (Glime, 2017; Hoodaji et al., 2012; Streeter, 1970). En forêt boréale, les bryophytes constituent une grande proportion de la biomasse végétale et de la diversité végétale (Barbier et al., 2008). Ils ont un impact sur la température du sol (Gornall et al., 2007), le cycle des nutriments (Turetsky et al., 2012), la décomposition de la matière organique (Turetsky et al., 2010), l'humidité (Turetsky et al., 2012) et la diversité de microhabitats fauniques (Belyea & Baird, 2006; Nungesser, 2003). De plus, les bryophytes ont des effets positifs ou négatifs sur la germination et la croissance de plantes vasculaires dépendamment des espèces et des conditions abiotiques (Gornall et al., 2011). Ainsi, un changement dans l'abondance et la composition des communautés de bryophytes influencera le fonctionnement de l'écosystème. Les principaux facteurs abiotiques limitant la composition et la répartition des bryophytes sont la quantité de précipitations (Busby et al., 1978) et la quantité de lumière (Raabe et al., 2010). Les principaux facteurs biotiques sont la stratégie de dispersion des propagules (Caners et al., 2009), la composition et la structure de la canopée (McGee & Kimmerer, 2002), l'accumulation de la litière de feuillus (Jean et al., 2020), les interactions interspécifiques (Caners et al., 2010), ainsi que la disponibilité de microhabitats de croissance (Diamond et al., 2020; Frego & Carleton, 1995).

1.2.5 La diversité du sous-bois en forêt boréale

La diversité totale (plantes vasculaires et bryophytes) en sous-bois est sensiblement la même entre les différents couverts forestiers de la forêt boréale (Fenton & Bergeron, 2011). Un couvert forestier composé de feuillus est favorable aux communautés de plantes vasculaires et défavorable aux bryophytes, puisqu'il est généralement plus fertile (Légaré et al., 2002; Nieppola & Carleton, 1991). À l'inverse, un couvert forestier composé de conifères est favorable aux bryophytes et défavorable aux plantes herbacées, puisqu'il est généralement plus pauvre et acide (Barbier et al., 2008;

Chipman & Johnson, 2002). Ainsi, l'augmentation de la diversité des bryophytes compense la diminution de celle des plantes vasculaires et vice-versa.

1.2.6 L'approche scientifique par traits fonctionnels

Les traits fonctionnels des plantes ont un impact sur la productivité primaire nette de l'écosystème, le taux de décomposition et le carbone et l'azote total du sol (Garnier et al., 2004). Il est donc possible de comprendre une partie du fonctionnement de l'écosystème en étudiant les traits fonctionnels des plantes. L'approche par traits fonctionnels est simple dans le sens qu'elle ne demande ni analyses génétiques complexes ni compétences taxonomiques (Violle et al., 2007). En effet, plutôt que d'identifier les espèces, les traits sont mesurés en considérant qu'il s'agit d'espèces différentes dans les modèles. De plus, il est possible de comparer ces mesures de traits à travers diverses communautés végétales dans le monde. Ainsi, pour étudier l'écologie végétale à une échelle plus grande, la méthode par traits fonctionnels est avantageuse comparativement à l'approche par espèce. Les traits fonctionnels utilisés sont sélectionnés de manière à être faciles à mesurer (Cornelissen et al., 2003), ainsi qu'à répondre à plusieurs processus physiques et physiologiques pour minimiser le nombre de traits mesurés, puisque certains peuvent être corrélés entre eux, ce qui augmente le bruit dans les résultats (Weiher et al., 1999). En effet, on peut avoir le même résultat avec 3 traits fonctionnels bien choisis qu'avec 14 traits (Pierce et al., 2017).

1.2.7 Les traits fonctionnels utilisés pour étudier les plantes vasculaires

La surface spécifique des feuilles (SLA), la densité de tissus (LDMC) et la concentration en azote foliaire (LNC) ont été proposées comme marqueurs fonctionnels par Garnier et al., (2004), puisqu'ils peuvent être utilisés pour noter l'impact des changements des communautés sur le fonctionnement de l'écosystème et qu'ils sont faciles à interpréter. De plus, l'établissement de marqueurs permet une

homogénéité dans le choix de traits pour différentes études. La SLA correspond à la surface d'interception de la lumière d'une feuille par unité de masse sèche. Il s'agit d'une approximation du taux d'assimilation et de la croissance relative de la plante (Shipley, 2002). Le LDMC est une approximation de la densité de tissus, permettant d'approximer la rétention de nutriments par la plante (Smart et al., 2017). La LNC est une approximation de la concentration d'azote dans les feuilles et permet l'approximation du niveau de photosynthèse de la plante (Evans, 1989).

1.2.8 Les traits fonctionnels utilisés pour étudier les bryophytes

L'approche par traits fonctionnels a été peu utilisée chez les bryophytes comparativement aux plantes vasculaires. Les traits fonctionnels les plus couramment utilisés sont les suivants : la capacité de rétention de l'eau (Rice et al., 2008), la quantité de chlorophylle a et b, la surface spécifique de la tige, la quantité d'azote (Chen et al., 2016), la densité de tiges, le volume de la tige, la hauteur moyenne de la colonie (Michel et al., 2012) et le pH (Cornelissen et al., 2006).

1.3 Objectifs de l'étude et hypothèses de travail

1.3.1 Objectifs de l'étude

L'objectif général de l'étude est de déterminer l'impact du mélèze laricin sur la composition, la diversité et les traits fonctionnels des bryophytes et des plantes vasculaires en forêt boréale. Afin de répondre à cet objectif, nous avons défini les 3 objectifs spécifiques suivants :

1. Déterminer l'impact de la proportion de mélèze en canopée sur la composition et la diversité des plantes vasculaires et des bryophytes

2. Déterminer l'impact de la proportion de mélèze en canopée sur les traits fonctionnels des communautés de plantes vasculaires et de bryophytes
3. Déterminer l'impact de la chute des aiguilles de mélèze sur la composition et l'abondance des communautés de plantes vasculaires et de bryophytes

1.3.2 Hypothèses de travail

Nous nous attendons à un changement significatif de la composition, de la richesse en espèces et des traits fonctionnels des plantes vasculaires et bryophytes de sous-bois en fonction de la proportion de mélèzes dans la canopée, car la perte des aiguilles de mélèze pourrait apporter plus de lumière et de nutriments au sous-étage, comparativement à l'épinette noire (Messier et al., 1998; Paré & Cleve, 1993; Prescott et al., 2000). Cependant, nous nous attendons à ce que la diversité totale (addition de la richesse des bryophytes et des plantes vasculaires) soit similaire entre les différentes proportions de mélèzes, puisqu'il a été démontré que la diversité totale est similaire entre les différents couverts forestiers de la forêt boréale (Fenton & Bergeron, 2011). De plus, nous supposons que la chute des aiguilles sur les bryophytes entrainera la mortalité des bryophytes, tel qu'observée avec les feuilles des bouleaux (Jean et al., 2020).

CHAPITRE II

IMPACT OF LARCH ON COMPOSITION, DIVERSITY AND FUNCTIONAL TRAITS OF VASCULAR PLANT AND BRYOPHYTE COMMUNITIES IN THE BOREAL UNDERGROWTH

2.1 Abstract

The larch is the only deciduous conifer in North America. This characteristic distinguishes it from other conifers and hardwoods in terms of its potential function in ecosystems. In order to better understand the ecosystemic function of larch in the boreal forest, we studied its impact on the composition, diversity and functional traits of vascular plant and bryophyte communities. We therefore determined soil hydrogeochemical characteristics, canopy openness and density, and the composition and functional traits of understory vascular and bryophyte communities at 15 sites selected to cover a larch proportion gradient in black spruce stands of northern Quebec. Ten inventory quadrats were sampled at each site. In addition, we installed quadrats to monitor the impact of larch needles on understory communities in a black spruce site without larch. Our results illustrate that with an increase in the proportion of larch in the canopy, there is an increase in vascular plant diversity, leaf size, foliar nitrogen and a decrease in foliar carbon concentration, as well as a transition from species associated with poor coniferous stands to species of richer forest environments associated with

an increase in larch proportion . For bryophytes, we noted a decrease in the number of species and mortality caused by larch litterfall, but also an increase in nitrogen concentration in persistent bryophytes. In conclusion, this knowledge suggests that larch could have the capacity to create a layer of productive soil for vascular plants over an low-productive organic soil, such as peat. Studies should be undertaken to evaluate the optimal planting density and the time required to create a productive soil.

2.2 Introduction

Forests are one of the world's largest ecosystems, covering 1/3 of the Earth's surface (FAO, 2020). The boreal forest represents 1/3 of the global forest area (Brandt et al., 2013) and is found mostly in Canada, Russia and Alaska (Potapov et al., 2008). The boreal forest is a forest biome among which the larch is present in abundance (Mamet et al., 2019). There are 13 globally distributed *Larix* species, of which the only species found in the Canadian boreal forest is *Larix laricina* (Du Roi) K. Koch (Cauboue, 2007; Mamet et al., 2019). Larch is one of the most widespread conifers in North America and is the only deciduous conifer (Johnston, 1990). This wide distribution of the species is due to its ability to adapt to a wide range of environmental conditions, such as extreme temperatures and precipitation, as well as its ability to grow on different soil types (Cauboue, 2007; Johnston, 1990). In the Canadian boreal forest, larch is found throughout the forest, but particularly in peatlands (Cauboue, 2007). In this environment, larch grows faster than any other conifer (Johnston, 1990; Jutras et al., 2006). Larch is a pioneer species, whose seedlings are intolerant to shade, but tolerant to flooding, which limits their colonization of the understory and favours their establishment in peatlands. For larch needles, they are richer in nitrogen than those of the black spruce, the dominant species in the boreal forest. Canopy trees have an effect on understory conditions, including litter production, respiration, biotic interactions,

understory light transmission, etc., which impacts vascular plant and cryptogam composition and diversity (Chávez & Macdonald, 2010; Macdonald & Fenniak, 2007).

In return, the understory has an essential role in maintaining the structure and function of the forest ecosystem (Gilliam, 2007; Nilsson & Wardle, 2005), upper stratum succession (Hart & Chen, 2006; Messier et al., 1998), nutrient cycling (Weber & Cleve, 1981), and fauna habitat and resources (De Grandpré et al., 2003; Gunnarsson et al., 2004; Nilsson & Wardle, 2005). Understory communities are dynamic (Chipman & Johnson, 2002) and vary with canopy and soil structure and composition (Chen et al., 2004). Thus, knowing the interaction between trees and the understory is important to better understand natural dynamics and ecosystem function (Gilliam & Roberts, 2003). To date, very little is known about the interaction between larch and understory communities.

This study aimed to assess the effect of the proportion of larch in the canopy of black spruce stands on the composition of shrubs, herbaceous plants, and bryophytes in the understory. Our specific objectives were to understand the impact of larch proportion in the canopy on (1) composition and diversity of understory vegetation communities, (2) on functional trait variation of the understory communities and (3) to understand the impact of larch needle drop on understory communities. We expected a significant change in composition, species richness and functional traits with changes in larch proportion in the canopy because needle loss could bring more light and nutrients to the understory (Messier et al., 1998; Paré & Cleve, 1993; Prescott et al., 2000). Furthermore, we assume that needle drop on bryophytes will result in bryophyte mortality, as observed with birch and aspen leaves (Jean et al., 2020; Startsev et al., 2008).

2.3 Methods

2.3.1 Study area

The boreal forest is dominated by black spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) in association with white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lambert), white pine (*Pinus strobus* Linnaeus), larch (*Larix laricina* (Du Roi) K. Koch), balsam fir (*Abies balsamea* (Linnaeus) Miller), trembling aspen (*Populus tremuloides* Michaux), balsam poplar (*Populus balsamifera* Linnaeus), and paper birch (*Betula papyrifera* Marshall) (MFFP, 2020). This region has an abundance of wetlands (18.2 to 58.0 % of the area; Pellerin & Poulin, 2013), due to the poor drainage of the clay soil, generated by glacial Lake Ojibway from 8200 BP, cold temperatures, and relatively abundant precipitation (average annual temperature of 0°C, 643.8 mm of rain and 265.3 cm of snow) (Environnement Canada, 2013). These climatic and forest conditions are conducive to forest fires, flooding, insect outbreaks and windthrow disturbances that are part of the natural forest dynamics of the region (Bergeron et al., 2002). In addition to these natural disturbances, silviculture and mining play a role in the composition of the forest stand mosaic.

2.3.2 Selection of sites and inventory quadrats

Based on the Quebec ecoforestry maps (MFFP, 2020), 15 sites were selected that had the following characteristics: larch-spruce composition, 50-70 years post stand replacing disturbance, accessible by road or trail and within a 40 km radius of the nearest village “Villebois”. Thus, sites are close to each others, share similar climatic history, site conditions and have a similar commercial value in terms of comparable basal area (Appendix 1). Finally, site selection ensured a balanced number of stands in

different larch canopy proportions (4 sites of 0 %, 4 sites of 0-25 %, 4 sites of 25-50 %, 4 sites of 50-75 % and 3 sites of 75-100 %) defined by the mean of 5 visual assignment of larch proportion coverage within a 10m radius of random points in the site. A more precise measure of larch proportion was made later in the process. Despite our search, a 4th site was not found for the 75-100 % category in the vicinity. In each of the 15 sites, 10 quadrats of 4 m² were randomly localized, taking care not to have any other tree species than black spruce and larch within 5m radius of their center. A five m radius quadrat (78.5 m²) was overlaid to determine local influence of trees on 4 m² quadrat. This radius was established based on Okland et al. (1999) study that showed that single tree have an influence on the understory within one meter from the stem.

2.3.3 Sampling

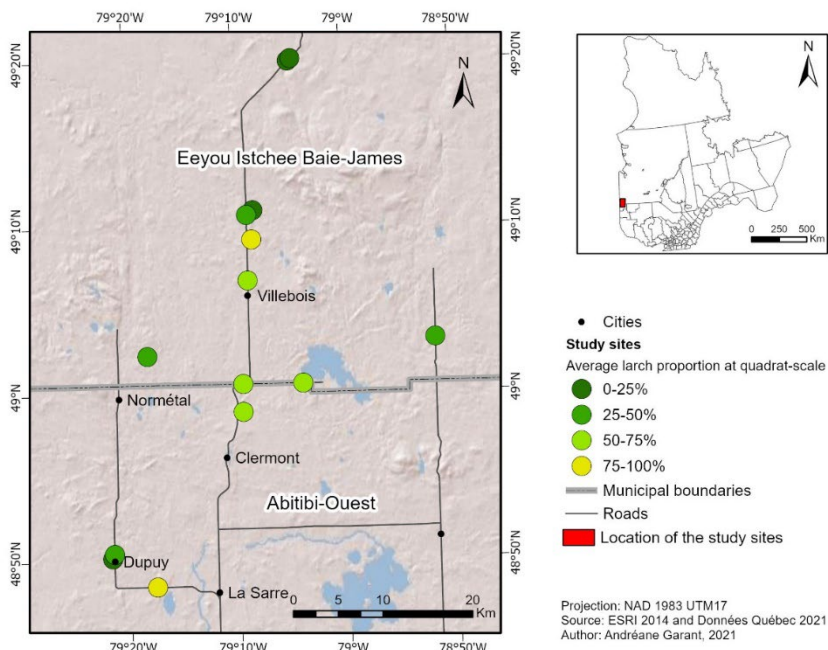


Figure 2.1 Location of the study sites in the regions of Abitibi-West and Eeyou Istchee James Bay. The proportion of larch is illustrated by the color of the circle for each site.

Field inventory was conducted from 2019 to 2021 in Northwestern Quebec, Canada (Figure 2.1). Our first objective was to understand how the proportion of larch in the canopy changes the ecological function of the ecosystem by looking at its effect on the composition and diversity of understory vegetation communities. Thus, for each of the 10 quadrats of 4 m² in the 15 sites, we conducted floristic inventories, abundance measurements on bryophytes, herbaceous plants, and shrubs and environmental condition measurements.

In order to know the abundance of each understory species related to the proportion of larch in the canopy, at each 4 m² quadrat, we made visual estimates of percent cover (1–100 %) for each vascular plant and bryophyte species. We brought back unknown vascular plants specimens in a press and bryophytes specimen in paper bags for laboratory identification.

To define the proportion of larch around quadrats, we recorded the species and diameter at breast height (DBH) of all trees within a 5m radius of each quadrat. This DBH correspond to a high average of 1.35 m. Then, we calculated the basal area of each tree with DBH data to assess a proportion of larch in the quadrat based on total basal area within 5m radius. To get a proxy for understory moisture and its effect on herbaceous, shrub and bryophyte composition, tree density (number of stems of any tree species) within 5 m of the center of the quadrat was calculated from the species and diameter data.

To see if the proportion of larch in the canopy correlates with the average summer water table depth, 1.52 m long metal rods were driven into each quadrat center to a depth of one meter in the forest floor in early June 2020 and were removed in late September 2020. The difference between the height of the rod at the soil surface and

the height of the oxidation is used to determine the average depth of the water table for the season. This method, which has been previously proven (Fenton et al., 2006), was chosen for its simplicity and because high precision was not required for this point.

To understand the effect of soil nutrient concentration on the composition of vascular plants and bryophyte communities, a composite soil sample per quadrat was formed from five subsamples of humus decomposed to an H5-H6 (Von Post chart), i.e., when the origin of the organic matter could no longer be defined. This stage was reached when the first layer of organic matter below the fibrous layer was attained. The name of this organic layer is mesisol. The depth at which this stage of decomposition was reached was noted to serve as a proxy for the inverse of the litter decomposition rate. These composite samples were then sieved to 2 mm and analyzed in the laboratory to determine the average composition of nitrogen, phosphorus, potassium, calcium, magnesium (Mehlich 3 method and ICP-OES analysis with Agilent 5110 DV) and pH (1:1 method with water). In addition, in order to know the effect of the depth of organic matter on the composition of these communities, a direct measurement of the thickness of the organic matter was carried out for each quadrat using a 1.20m long soil corer. When the depth exceeded 1.20 m, the value >1.20 m was noted.

Finally, to understand the effect of the amount of understory light on the communities, a measurement of canopy openness in each quadrat center was made in the direction of the four cardinal points with the spherical crown densiometer (Forestry Suppliers, Convex Model A). Another measurement of canopy openness was made prior to larch needle bud burst in the spring for two sites with spruce only and two sites with 75-100 % larch. This will allow to determine if the absence of larch needles in the canopy in the spring had a more significant effect on the composition of understory communities in comparison with close spruce forest.

2.3.4 Needle transfert

To experimentally test the effect of larch needle drop on vascular plants and bryophyte communities, we set 18 permanent 1m² quadrats at a site with no larch and a majority of black spruce. Nine permanent quadrats were placed on existing colonies of feather mosses (FM) including *Pleurozium schreberi* (Willd. ex Brid.) Mitt, *Ptilium crista-castrensis* (Hedw.) and *Hylocomium splendens* (Hedwig) and nine permanent quadrats on existing colonies of Sphagnum (S) including *Sphagnum capillifolium* (Ehrhart) Hedwig., *Sphagnum russowii* Warnst., *Sphagnum wulfianum* Girg. and *Sphagnum angustifolium* (Warnst.). A photo and inventory of the herbaceous, shrub, and bryophyte species present were taken for each quadrat as a reference of the initial situation before the needles were transferred. Once a year after the needles were deposited, a new photo was taken and an inventory and percent cover of species were taken on these quadrats.

In the falls of 2019, 2020, and 2021, larch needles were collected on bedsheets laid on the forest floor in a stand with a larch dominated canopy (75-100 %), to minimize contamination by needles of other species. For each bedsheet, the mass of needles collected was divided by the bedsheet area to obtain a representative mass of needles that fell on 1 m². On six permanent quadrats, consisting of three S colonies and three FM colonies, 50 % of the equivalent mass of 1 m² was deposited. On the six other quadrats, 100 % of this same mass of needles was deposited. The six additional quadrats, three of each species, served as controls.

To assess the contribution of larch and spruce to the total mass of needles harvested, several random subsamples of needles were sorted and then weighed by species. Thus,

larch needles deposited on the permanent quadrats could be considered to contain less than 5 % spruce needles.

2.3.5 Functional traits

To understand the functional trait variation of the understory communities across a gradient of larch proportion in the canopy (objective 2) we made functional trait measurements of herbaceous, shrub and bryophyte species. For herbaceous and shrub species (vascular plants), the average cover percentage of the species that represent the most biomass of the site were added together until at least 80 % was obtained (“most abundant species”) (Garnier et al., 2004). Then, at least 4g of dry leaf mass from each of these species was harvested in all sites (not necessarily in inventory quadrats) following the standardized protocol of Garnier et al., (2001) for nutritional and leaf pH analyses. The 10 largest intact leaves of each species were scanned with a scanner (Epson Expression 12000XL) and weighed fresh, then oven dried to calculate the specific leaf area (SLA) and the leaf dry matter content (LDMC). For species with very small leaves, such as *Gaultheria hispidula*, we scanned a shoot and removed the stem with GIMP software for analysis and weighted all leaves together. The remaining leaves of each species were oven dried for 24 hours at 80°C and then ground (Thomas Scientific model 18Y51) for carbon (C) and nitrogen (N) analysis (Dumas method on Vario Max Cube company Elementar and analyzed by TCD) in laboratory. In addition to analyzing the community traits, we looked in more detail at the traits of *Alnus incana* subsp. *Rugosa* which was present along the larch gradient.

To characterize the function of bryophyte communities in our quadrats, we selected the following five functional traits: ratio of water volume absorbed to bryophyte volume (ml/cm^3), time for 50 % water loss (h), drying rate ($\log(\text{g}/\text{h})$), C (%) and N (%) content,

and the LDMC (g/g). These traits were measured on five 5 g dry weight subsamples from five randomly selected bryophyte samples from inventory quadrats per site. These subsamples are an amalgam of stems of different bryophyte species without conservation of colony structure and preserving species proportion. Most of debris and non-photosynthetic parts were removed from the samples. To make the measurements, the bryophyte subsamples were placed in yogurt-type pots into which 500 ml of water was added. After one night of soaking, the excess water that was not absorbed by the bryophytes was collected in a 500 ml (+/- 2.5 ml) graduated cylinder. The subsample was then placed in a mesh bag to preserve it and then turned 20 times in a salad spinner. The weight was recorded, and the experiment was repeated until a stable weight (+/- 0.1 g) was reached. Once a stable weight was reached, the subsample was weighed, to obtain its weight at field capacity and the water at the bottom of the spinner was added to the 500 ml graduated cylinder. By subtracting this new volume from the initial 500 ml, we obtain the water absorption capacity of the subsample. Then, to know the volume at field capacity of the sub-sample, it was placed in an overflow vase filled with water. The water having been expelled from the vase during this maneuver was collected in a graduated cylinder of 100ml (+/- 0.5 ml). The volume obtained in the cylinder corresponds to the volume of the bryophyte subsample in cm³. Finally, in order to know the drying rate and the time to lose 50% of the water content of each subsample, these subsamples, at field capacity, were placed uniformly in weighing cups and a mass measurement was taken after 30 minutes, 1h, 1h30, 2h, 4h, 6h, 21h, 30h, 45h and 54h. To measure the C and N concentration, bryophyte samples were oven dried for 24 hours at 80 °C and then ground (Thomas Scientific model 18Y51) for analysis (Dumas method on Vario Max Cube company Elementar and analyzed by TCD) in laboratory.

2.3.6 Statistical analysis

All analyses were performed using the R 4.1.0 software (R Core Team, 2020). We removed site #12 because there were marks on the trees that suggested that the stand had been thinned, making it incomparable with the other sites.

Firstly, we used a linear mixed model approach to examine the relationship between each environmental variable and continuous data of the larch proportion in canopy measured at the quadrat level with site as random variable. Sites were set as a random variable in this and subsequent analyses to account for the site effect. We presented these results in larch canopy categories (LCC) to facilitate visualization. LCC include quadrats in four equidistant categories according to the larch proportion within 5m radius of plot center (A: 0-25 %, B: 25-50 %, C: 50-75 %, D: 75-100 %). Secondly, we analyze the impact of larch proportion on species diversity and composition of bryophyte and vascular plant communities (Objective 1). We examined the effect of larch proportion in canopy on species richness at the quadrat level (alpha α diversity), and at the site level (gamma γ diversity). We analysed species richness (α and γ) of vascular and bryophyte communities with a linear mixed model between the number of species (quadrat level for alpha and site level for gamma) and larch proportion in the canopy with site as random variable. Dissimilarity measures (beta β diversity) between quadrats sharing the same larch canopy category (LCC), was also analysed. Total beta diversity and the proportion explained by β_{repl} and β_{rich} was calculated with beta.multi function (R package “BAT”; Cardoso et al., 2021) and represented by a bar plot (Microsoft® Excel® for Microsoft 365 MSO (16.0.14131.20278)). β_{repl} indicates species replacement, that is the degree to which species are replaced within quadrats of the same LCC. β_{rich} indicates differences in richness, in other words, differences in the number of species within quadrats of the same LCC. All diversity models (α , β and

γ) were performed using species abundance data. Then, we calculated the mean cover and the frequency of each species belonging to a similar LCC. We consider a frequency over 50 % as a common species in this LCC. Also, when a species was found in two or less LCC, we consider it as a specific species for this or these LCC.

Quadrat-scale community composition was then represented in two separate graphs for vascular plants and bryophytes with a Principal coordinates analysis (PCoA) ordination performed on all abundance data using the Bray-Curtis distance and the Lingoes correction (package *ape*; Paradis & Schliep, 2019). To show how environmental conditions in the understory impact quadrat scale community composition, we added environmental variables (tree density, phosphorus, pH, water table depth, canopy openness, mesisol depth, C:N ratio and organic matter depth) to the ordination as a vector using the “*env.fit*” function (package *vegan*; Oksanen et al., 2020). To test the relative importance of larch proportion in explaining understory species composition patterns in each quadrat, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) on 9999 permutations with the function *adonis2* (package *vegan*; Oksanen et al., 2020). Then, species were plotted according to their weighted average coordinates.

We compared bryophyte functional traits along the larch proportion (continuous data) and vascular plant along a LCC at site level (categorical data) instead of quadrat level like for β diversity, to determine the impact of larch proportion on ecosystem functioning (objective 2). To determine if there is a significant variation in trait values along the larch proportion gradient, we used a linear mixed model for each trait measured as a community mean as dependent variable, the proportion of larch as independent variable and site as random variable. We also examined trait value

variation at the species level (*Alnus incana* subsp. *Rugosa*), using a linear mixed model with site as random variable.

The impact of the addition of larch needles on bryophyte and vascular plant composition and abundance was analysed using PERMANOVAs with the *adonis2* function (package *vegan*; Oksanen et al., 2020) on 9999 permutations on all species abundance data for three years (fixed variables). We did it first only on 50 % needles data and then on 100 % data. An ANOVA was also performed to assess if there existed a significant annual difference in abundance of *P. schreberi*, *H. splendens* and *P. cristata-castrensis* that visually seemed more affected by the needle treatment (personal observations).

2.4 Results

2.4.1 Environmental variables

Comparing quadrats with different amounts of larch in the canopy showed that quadrats with higher LCCs had lower tree density and higher average DBH (Table 1). Despite this result, we obtain a similar or slightly higher basal area with more than 25 % of larch, with maximum basal areas in mixed stand (Table 1). However, we obtain a canopy opening that is greater in pure stands than in mixed stands (B and C). The lower basal area in black spruce stands (category A) is correlated (p value = 1.9×10^{-6}) with a lower amount of light in the understory. There were no significant differences for the other categories. We also found a greater amount of light in the undergrowth in the spring in quadrats with high larch cover compared to closed spruce forest without larch ($t = -18.717$, p -value = 1×10^{-13}). The other environmental variables did not vary along the

larch gradient in part due to the important amount of variation at the site level (results not shown).

Table 2.1 Mean values \pm standard deviation of environmental variables among the four LCC (A = 0-25 %, B = 25-50 %, C = 50-75 %, D = 75-100 %). Results of linear mixed models with the site as a random factor on continuous LCC data are shown. To facilitate the visualization of results, we presented them in categories (LCC). Significant variables are in bold ($p < 0.05$).

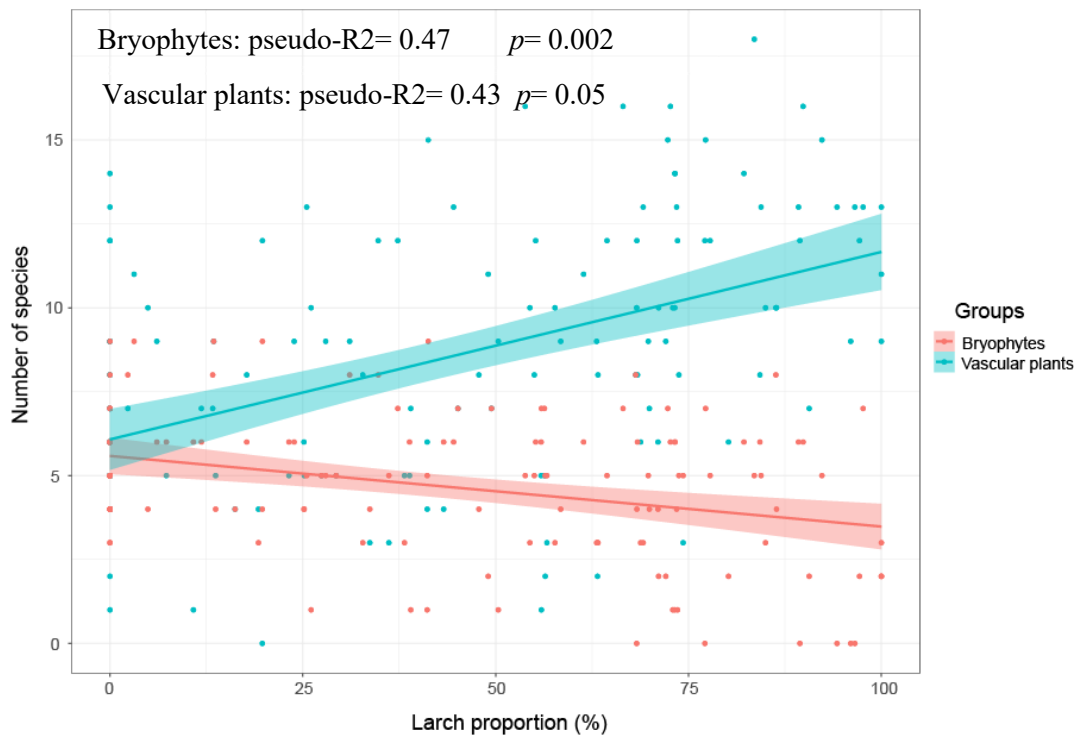
LCC	A (>0-25%)	B (>25-50%)	C (>50-75%)	D (>75%)	T-value	p value
Basal area (m²/ha)	11.62 \pm 5.15	15.45 \pm 4.59	17.77 \pm 6.52	15.16 \pm 6.35	3.66	4x10⁻⁴
Canopy opening (%)	30.77 \pm 14.13	22.72 \pm 8.12	22.24 \pm 7.29	28.21 \pm 8.08	-2.10	0.04
Mean DBH (cm)	10.28 \pm 1.90	12.42 \pm 2.62	14.75 \pm 3.12	15.68 \pm 2.82	5.38305	0.00
Mesisol depth (cm)	25.41 \pm 11.76	20.05 \pm 12.05	18.95 \pm 14.83	13.27 \pm 4.48	-0.23	0.81
Organic matter depth (cm)	77.37 \pm 48.20	95.15 \pm 40.10	102.08 \pm 33.22	110.08 \pm 24.16	1.30	0.20
Soil C:N *	25.98 \pm 5.23	23.64 \pm 4.91	23.30 \pm 3.60	20.23 \pm 1.90	-0.17	0.87
Soil calcium (mg g ⁻¹ dry soil) *	4.00 \pm 2.72	3.30 \pm 2.44	5.73 \pm 2.89	6.18 \pm 2.84	-0.38	0.70
Soil carbon (%) *	39.38 \pm 5.83	40.16 \pm 7.27	40.44 \pm 5.36	36.91 \pm 3.93	0.01	0.99
Soil magnesium (mg g ⁻¹ dry soil) *	0.72 \pm 0.38	0.59 \pm 0.39	1.01 \pm 0.47	0.99 \pm 0.39	-0.46	0.64
Soil nitrogen (%) *	1.56 \pm 0.32	1.76 \pm 0.44	1.76 \pm 0.29	1.84 \pm 0.28	-0.15	0.88
Soil pH (unit) *	4.37 \pm 0.72	4.26 \pm 0.63	4.74 \pm 0.70	4.87 \pm 0.58	0.30	0.76
Soil phosphorus (mg g ⁻¹ dry soil) *	0.018 \pm 0.010	0.015 \pm 0.006	0.015 \pm 0.009	0.017 \pm 0.008	0.04	0.96
Soil potassium (mg g ⁻¹ dry soil) *	0.19 \pm 0.10	0.18 \pm 0.07	0.18 \pm 0.11	0.18 \pm 0.05	0.28	0.78
Tree density (Number of tree within 5m radius of quadrat center)	23.69 \pm 8.70	22.73 \pm 10.53	18.74 \pm 9.60	12.92 \pm 5.10	-1.87	0.06
Water table depth (cm)	24.38 \pm 10.72	22.95 \pm 6.17	20.52 \pm 12.88	28.58 \pm 12.86	0.10	0.92

* Five samples per site were taken for soil variables instead of 10 as for other variables

2.4.2 Understory diversity

Along the larch gradient, the average number of bryophyte species per quadrat (alpha diversity) decreased slightly (6 to 4), while the average number of vascular plant species doubled (6 to 12; Figure 2a). At the site level, the number of species per site (gamma diversity) shows a similar pattern as that found at the quadrat level, except that the bryophyte gamma diversity remains constant along the larch gradient (Figure 2b). For bryophytes, there is a mean of 10 species per site regardless of the proportion of larch in the canopy (Figure 2b). For vascular plants, there is a mean of 10 species with less than 25 % larch in the canopy and a mean of 25 species with more than 50 % (Figure 2b).

a)



b)

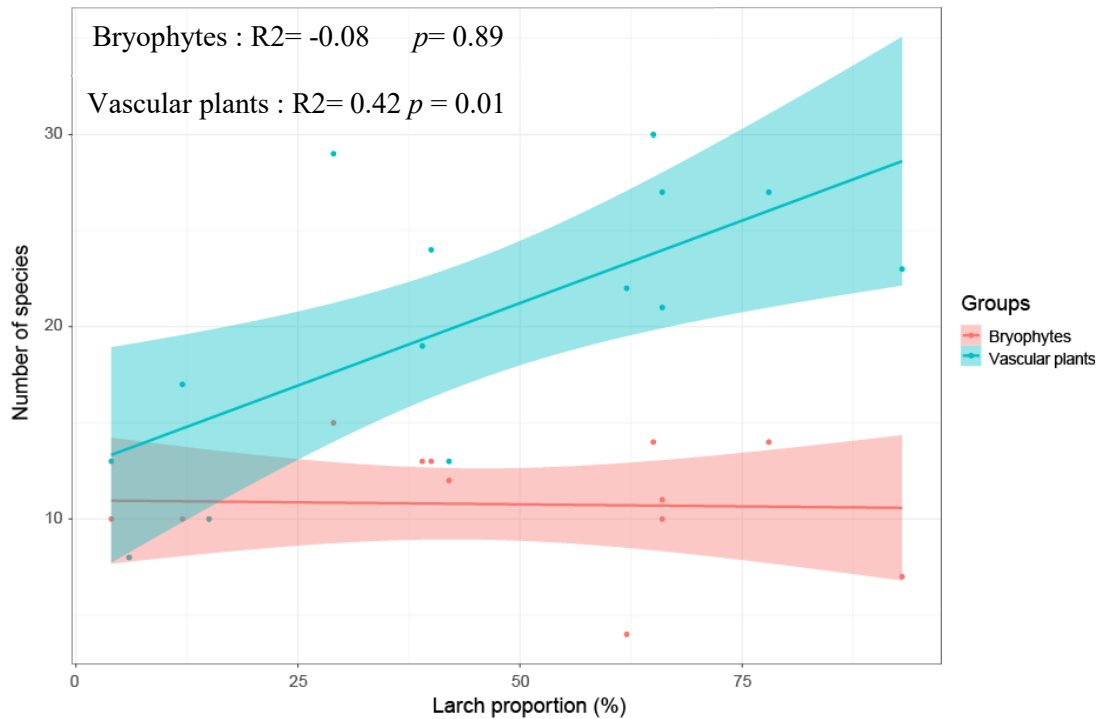


Figure 2.2 Variation in the number of vascular plant and bryophyte species as a function of larch proportion at (a) 4 m² quadrat level and (b) at site level. Colored area represents the standard error. Linear mixed models were used in (a) and simple linear models were used in (b). Regardless of the model used for the analyses, a linear model with standard error was used to illustrate the relation on both graphs.

Bryophyte communities had a higher dissimilarity among the quadrats under a higher proportion of larch (β_{Total}) (Figure 3). Moreover, dissimilarity, which is explained primarily by β_{repl} in quadrats of category A, is replaced by β_{rich} with increasing LCC. This means that between category A quadrats, there is a similar number of species, but different species among quadrats. For category B and C, there is about the same proportion of dissimilarity explained by both β_{repl} and β_{rich} . Finally, among category

D quadrats, there is variation in the number of species present, but the species are mostly the same. The maximum percentage of dissimilarity is 80 % found for D quadrats and the minimum percentage is 60 % found for A quadrats.

There was a different pattern of β diversity for vascular plants. Indeed, they were more similar across quadrats in stands that were pure spruce or larch (A and D), than in mixed stands (B and C) (β Total). Moreover, the dissimilarity, which is first explained equally by β repl and β rich gives way to β repl with increasing proportion of larch. The maximum percentage of dissimilarity is 81 % for B quadrats and the minimum percentage is 69 % for A quadrats.

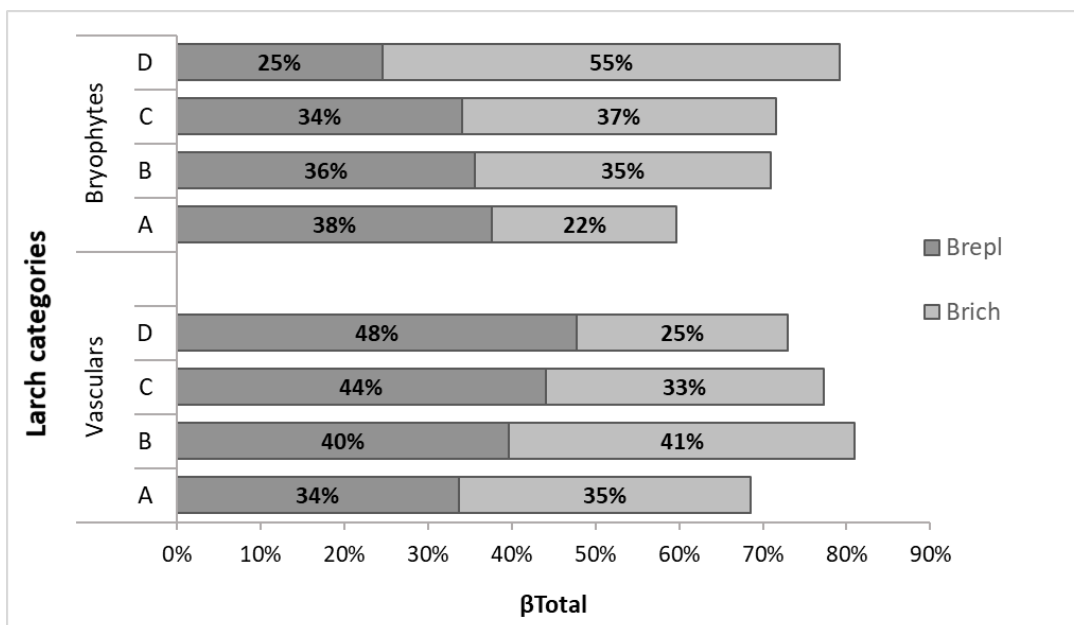


Figure 2.3 β total diversity of vascular plants and bryophytes in 4 m² quadrats among the four LCC (A = 0-25 % ; B = 25-50 % ; C = 50-75 % , D = 75-100 %). The darker section (β repl) of each bar indicates species replacement, that is the degree to which species are replaced by new species among quadrats of the same LCC. The lighter

section (β rich) indicates differences in richness, in other words, differences in the number of species within quadrats of the same LCC.

2.4.3 Understory composition

In bryophyte communities, among species present in 50 % or more of quadrats in at least one LCC, we observed a decrease in frequency of *Dicranum polysetum*, *Sphagnum angustifolium*, *S. russowii* and *Pleurozium schreberi* along the LCC. At the same time, no species increased in frequency along the larch gradient (Table 2). Among species present in only one or two LCC, *Dicranum flagellare* and *S. rubellum* were specific to category A, *D. montanum*, *S. fuscum* and *S. quinquefarium* were specific to categories A and B, *Plagiothecium latebricola* to category B, *Sphagnum* cf. *centrale* to categories B and C, *Hypnum imponens* to category C, *Sciuro-hypnum curtum* to categories C and D and *P. laetum* to category D. We also observed a decrease in the number of common species along the larch gradient (A =4, B= 4, C=3, D=1) (Table 2).

For vascular plants communities, we observed a decrease in frequency of *Gaultheria hispidula*, *Kalmia angustifolia*, *Rhododendron groenlandicum*, *Vaccinium angustifolium* and *Vaccinium myrtilloides*, and an increase in frequency of *Alnus incana* subsp. *Rugosa*, *Carex* sp., *Coptis trifolia*, *Cornus canadensis*, *Lysimachia borealis*, *Maianthemum canadense*, *Rubus idaeus* and *R. pubescens* along the larch gradient (Table 2). *Drosera* sp. and *Rubus chamaemorus* were specific to the category A, *Maianthemum trifolium* to categories A and B, *Galium palustre* to the category B, *Anemone quinquefolia* and *Caltha palustris* to categories B and C, *C. alternifolia*, *C. sericea*, *Fragaria* sp., *Solidago rugosa*, *Symphyotrichum* cf. *ciliolatum* and *Taraxacum* sp. to categories C and D, and *Gymnocarpium dryopteris*, *Lonicera canadensis* et *Thelypteris palustris* var. *pubescens* to the category D. We also observed an increase

in the number of common species along the larch gradient (A =5, B= 5, C=6, D=11)
(Table 2).

Table 2.2 Bryophytes and vascular plants species mean cover when present and its standard deviation, and frequency in 4 m² quadrats across the four LCC (0-25 %, 25-50 %, 50-75 %, 75-100 %). 0 % cover and 0 % frequency indicated a species was absent from that LCC. Frequency of species over 50% in the category is shown in bold. Correlation and G-test that are significant (p <0.05) are followed by an asterisk “*”. The number of quadrats in this category is represented by “n” in brackets.

Species	A (n=51)		B (n=26)		C (n=38)		D (n=24)		Pears on correl ation	G-Test
	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover	G-value
Bryophytes										
<i>Aulacomnium palustre</i>	0.50	11.76	0.50	23.08	0.50	13.16	0.50	8.33	0.00	2.12
<i>Dicranum flagellare</i>	0.50	3.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NA
<i>Dicranum fuscescens</i>	1.17 ± 1.15	5.88	2.50	3.85	0.50	5.26	0.00	0.00	-0.35	NA
<i>Dicranum montanum</i>	0.50	1.96	0.50	3.85	0.00	0.00	0.00	0.00	0.00	NA
<i>Dicranum polysetum</i>	1.54 ± 0.99	82.35	1.52 ± 0.92	80.77	1.64 ± 0.86	76.32	1.54 ± 0.61	45.83	0.01	3.63
<i>Dicranum scoparium</i>	0.50	1.96	0.00	0.00	0.50	7.89	2.50	4.17	0.39	NA
<i>Hylocomium splendens</i>	0.68 ± 0.60	21.57	5.88 ± 12.82	30.77	8.25 ± 0.91	10.53	3.60 ± 0.97	20.83	0.39 *	3.42
<i>Hypnum imponens</i>	0.00	0.00	0.00	0.00	0.50	2.63	0.00	0.00	0	NA
<i>Hypnum pallescens</i>	0.50	1.96	0.00	0.00	0.00	0.00	0.00	0.00	0	NA
<i>Plagiothecium laetum</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.50	16.67	0	NA
<i>Plagiothecium latebricola</i>	0.00	0.00	0.50	3.85	0.00	0.00	0.00	0.00	0	NA
<i>Pleurozium schreberi</i>	39.2 ± 36.94	98.04	18.45 ± 26.79	76.92	4.36 ± 6.92	73.68	1.88 ± 0.73	70.83 *	-0.54 *	2.30
<i>Ptilidium ciliare</i>	0.50	49.02	0.50	26.92	0.50	7.89	0.50	4.167	0	21.66*

Table 2.2 suite

<i>Ptilium crista-castrensis</i>	5.43 ± 13.05	43.14	5.62 ± 12.91	30.77	0.86 ± 0.81	28.95	1.00 ± 1.00	16.67	-0.20	4.04
<i>Sciuro-hypnum curtum</i>	0.00	0.00	0.00	0.00	0.50	10.53	0.50	8.33	0	NA
<i>Sphagnum angustifolium</i>	16.82 ± 14.64	62.75	10.83 ± 13.68	50.00	8.31 ± 8.45	50.00	7.98 ± 2.61	20.83	-0.26*	6.77
<i>Sphagnum capillifolium</i>	11.40 ± 4.07	19.61	14.62 ± 8.88	38.46	9.03 ± 11.46	39.47	9.21 ± 11.27	41.67	-0.13	4.41
<i>Sphagnum cf. centrale</i>	0.00	0.00	3.46 ± 4.80	11.54	2.20 ± 2.54	5.26	0.00	0.00	-0.48	NA
<i>Sphagnum divinum</i>	10.43 ± 12.26	49.02	18.70 ± 18.20	26.92	5.08 ± 3.90	36.84	3.4 ± 2.76	20.83	-0.22	4.60
<i>Sphagnum fallax</i>	2.62 ± 2.94	5.88	0.12	3.85	0.05	2.63	10.45 ± 13.90	12.50	0.40	2.41
<i>Sphagnum fuscum</i>	25.27 ± 7.71	13.73	11.31 ± 0.09	7.69	0.00	0.00	0.00	0.00	-0.42	10.96*
<i>Sphagnum girgensohnii</i>	4.25 ± 2.47	3.92	33.82 ± 32.75	11.54	31.12 ± 42.60	5.26	6.50 ± 8.48	8.33	0.07	1.64
<i>Sphagnum quinquefarium</i>	8.97 ± 14.21	11.76	20.00	3.85	0.00	0.00	0.00	0.00	-0.18	NA
<i>Sphagnum rubellum</i>	9.06 ± 9.28	3.92	0.00	0.00	0.00	0.00	0.00	0.00	0	NA
<i>Sphagnum russowii</i>	16.98 ± 22.72	50.98	18.40 ± 18.08	50.00	16.69 ± 19.12	36.84	16.29 ± 17.29	37.50	0.01	1.44
<i>Sphagnum wulfianum</i>	1.93 ± 0.71	5.88	4.38	3.85	1.56 ± 0.44	5.26	1.01 ± 1.26	8.33	-0.39	0.45
<i>Tomenthypnum nitens</i>	0.00	0.00	0.50	3.85	0.50	2.63	0.50	12.50	0	NA
Vascular plants										
<i>Alnus incana</i> subsp. <i>Rugosa</i>	15.69 ± 30.39	15.69	17.08 ± 18.14	23.08	22.22 ± 23.03	42.11	14.63 ± 15.34	75.00	-0.07	16.80*
<i>Amelanchier</i> sp.	0.50	1.96	0.50	3.85	2.80 ± 0.87	13.16	0.50	4.17	0.23	4.66
<i>Anemone quinquefolia</i>	0.00	0.00	0.50	3.85	0.50	2.63	0.00	0.00	0	NA
<i>Betula nana</i>	0.50	1.96	1.50 ± 1.41	7.69	0.50	7.89	0.00	0.00	-0.04	NA
<i>Caltha palustris</i>	0.00	0.00	0.50	3.85	0.50	2.63	0.00	0.00	0	NA
<i>Carex</i> sp.	4.66 ± 7.76	43.14	2.07 ± 1.01	57.69	2.20 ± 0.98	60.53	8.80 ± 21.68	75.00	0.06	3.18
<i>Chamaedaphne calyculata</i>	5.29 ± 0.86	23.53	3.20 ± 1.02	19.23	0.50	5.26	3.57 ± 0.87	29.17	-0.20	6.93
<i>Clintonia borealis</i>	3.88 ± 1.03	7.84	2.50	3.85	5.00 ± 0.87	7.89	10.17 ± 0.76	12.5	0.42	1.21
<i>Coptis trifolia</i>	2.19 ± 0.90	15.69	0.50	38.46	2.63 ± 0.92	50.00	2.12 ± 1.00	50.00	0.06	10.46*
<i>Cornus alternifolia</i>	0.00	0.00	0.00	0.00	0.50	2.63	0.50	16.67	0	NA
<i>Cornus canadensis</i>	2.59 ± 0.79	21.57	19.90 ± 31.50	38.46	9.04 ± 9.70	36.84	13.31 ± 25.23	54.17	0.13	5.32
<i>Cornus sericea</i>	0.00	0.00	0.00	0.00	3.67 ± 0.29	7.89	2.50	4.17	0.26	NA

Table 2.2 suite

Drosera sp.	0.50	1.96	0.00	0.00	0.00	0.00	0.00	0.00	0	NA
Dryopteris carthusiana	0.00	0.00	1.50 ± 1.15	15.38	0.50	2.63	0.00	0.00	-0.70	NA
Dryopteris cristata	0.00	0.00	0.00	0.00	0.50	2.63	0.50	8.33	0	NA
Equisetum sylvaticum	1.07 ± 0.98	13.72	0.50	7.69	0.50	10.53	0.50	4.17	-0.41	1.84
Eurybia radula	0.00	0.00	0.50	11.54	0.50	7.89	1.00 ± 1.00	16.67	0.46	9.97
Fragaria sp.	0.00	0.00	0.00	0.00	1.30 ± 1.10	13.16	1.07 ± 0.98	29.17	-0.20	20.99*
Galium asprellum	0.00	0.00	0.50	7.69	0.50	13.16	0.50	25.00	0	14.29*
Galium palustre	0.00	0.00	0.50	3.85	0.00	0.00	0.00	0.00	0	NA
Gaultheria hispida	1.66 ± 0.99	56.86	1.85 ± 0.94	50.00	3.52 ± 7.74	57.89	0.78 ± 0.76	29.17	0.05	3.33
Gymnocarpium disjunctum	0.00	0.00	0.00	0.00	1.50 ± 1.41	5.26	0.50	4.17	-0.16	NA
Gymnocarpium dryopteris	0.00	0.00	0.00	0.00	0.00	0.00	0.50	4.17	0	NA
Iris versicolor	0.00	0.00	0.00	0.00	0.50	2.63	0.00	0.00	0	NA
Kalmia angustifolia	5.67 ± 6.08	70.59	3.57 ± 0.97	53.85	4.23 ± 0.93	28.95	2.04 ± 0.88	54.17	-0.24*	7.68
Kalmia Polifolia	1.00 ± 0.92	15.69	0.50	11.54	0.50	5.26	0.00	0.00	-0.31	7.11
Larix Laricina	0.50	1.96	2.50	3.85	0.00	0.00	0.00	0.00	1	NA
Linnaea borealis	0.50	3.92	0.50	19.23	4.25 ± 9.79	36.84	2.45 ± 0.47	41.67	-0.02	18.12*
Lonicera canadensis	0.00	0.00	0.00	0.00	0.00	0.00	0.50	4.17	0	NA
Lonicera villosa	0.00	0.00	0.50	3.85	0.83 ± 0.82	15.79	1.30 ± 1.03	41.67	0.32	25.12*
Lysimachia borealis	1.50 ± 1.15	7.84	0.86 ± 0.81	42.31	1.16 ± 0.94	73.68	0.85 ± 0.78	70.83	-0.17	32.70*
Maianthemum canadense	1.00 ± 0.92	15.69	2.22 ± 0.97	34.62	4.09 ± 0.87	57.89	1.84 ± 0.98	66.67	0.07	16.23*
Maianthemum trifolium	2.06 ± 0.88	17.65	0.50	7.69	0.00	0.00	0.00	0.00	-0.78*	14.06*
Mitella nuda	0.00	0.00	2.50	3.85	5.00 ± 0.87	7.89	1.83 ± 1.03	25.00	-0.33	14.11*
Picea mariana	10.96 ± 13.31	25.49	8.72 ± 11.95	34.62	2.00 ± 1.00	10.53	2.50	4.17	-0.18	9.48*
Poaceae	0.50	3.92	0.50	7.69	0.75 ± 0.71	21.05	1.25 ± 1.04	33.33	0.31	11.83*
Populus tremuloides	0.50	1.96	0.00	0.00	0.00	0.00	0.00	0.00	0	NA
Pyrola elliptica	0.00	0.00	0.50	3.85	0.50	5.26	3.67 ± 0.29	12.50	0.26	NA
Rhododendron groenlandicum	9.88 ± 11.82	82.35	4.89 ± 0.92	73.08	2.89 ± 0.94	57.89	4.93 ± 0.89	58.33	-0.25*	2.43
Ribes glandulosum	0.50	3.92	0.00	0.00	1.50 ± 1.15	10.53	0.50	4.17	0.45	NA

Table 2.2 suite

Ribes lacustre	0.00	0.00	50.55	3.85	0.50	2.63	0.75 ± 0.71	33.33	-0.65*	21.13*
Ribes triste	0.00	0.00	1.17 ± 1.15	11.54	0.50	2.63	2.50	4.17	0.43	NA
Rosa sp.	1.50 ± 1.41	3.92	2.50	3.85	2.50	2.63	2.50	4.17	0.37	NA
Rubus chamaemorus	1.17 ± 1.15	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0	NA
Rubus idaeus	0.00	0.00	21.38 ± 21.22	15.38	31.72 ± 29.96	23.68	8.68 ± 9.63	58.33	-0.42*	32.34*
Rubus pubescens	1.50 ± 1.10	11.76	7.71 ± 13.73	26.92	4.94 ± 0.94	47.37	7.50 ± 11.93	70.83	0.24	19.40*
Salix sp.	1.70 ± 1.10	9.80	2.50	3.85	20.00	2.63	2.50	4.17	0.55	NA
Solidago cf. uliginosa	0.00	0.00	0.50	3.85	0.00	0.00	0.50	4.17	0	NA
Solidago rugosa	0.00	0.00	0.00	0.00	4.33 ± 1.04	7.89	1.50 ± 1.15	16.67	-0.30	NA
Sorbus americana	0.00	0.00	1.17 ± 1.15	11.54	1.30 ± 1.10	13.16	2.50	8.33	0.24	9.32
Spinulum annotinum	5.25 ± 0.35	3.92	14.17 ± 0.29	11.54	13.08 ± 14.91	15.79	18.00 ± 15.94	20.83	0.30	5.43
Symphotrichum cf. ciliolatum	0.00	0.00	0.00	0.00	10.00	2.63	0.50	4.17	-1	NA
Taraxacum sp.	0.00	0.00	0.00	0.00	0.50	5.26	0.50	4.17	0	NA
Thelypteris palustris var. pubescens	0.00	0.00	0.00	0.00	0.00	0.00	0.50	4.17	0	NA
Vaccinium angustifolium	2.72 ± 0.78	60.78	1.10 ± 0.97	38.46	0.50	26.32	0.50	12.50	-0.29*	12.96*
Vaccinium myrtilloides	2.76 ± 0.80	80.39	3.29 ± 0.96	46.15	0.90 ± 0.82	52.63	0.96 ± 0.88	54.17	-0.27*	4.51
Vaccinium oxycoccos	0.50	21.57	0.50	11.54	0.50	5.26	0.00	0.00	0	10.57*
Viburnum cassinoides	0.00	0.00	1.50 ± 1.41	7.69	4.33 ± 1.04	7.89	4.33 ± 1.04	12.50	0.31	NA
Viola sp.	0.00	0.00	0.50	3.85	5.25 ± 0.35	5.26	0.50	8.33	-0.22	NA

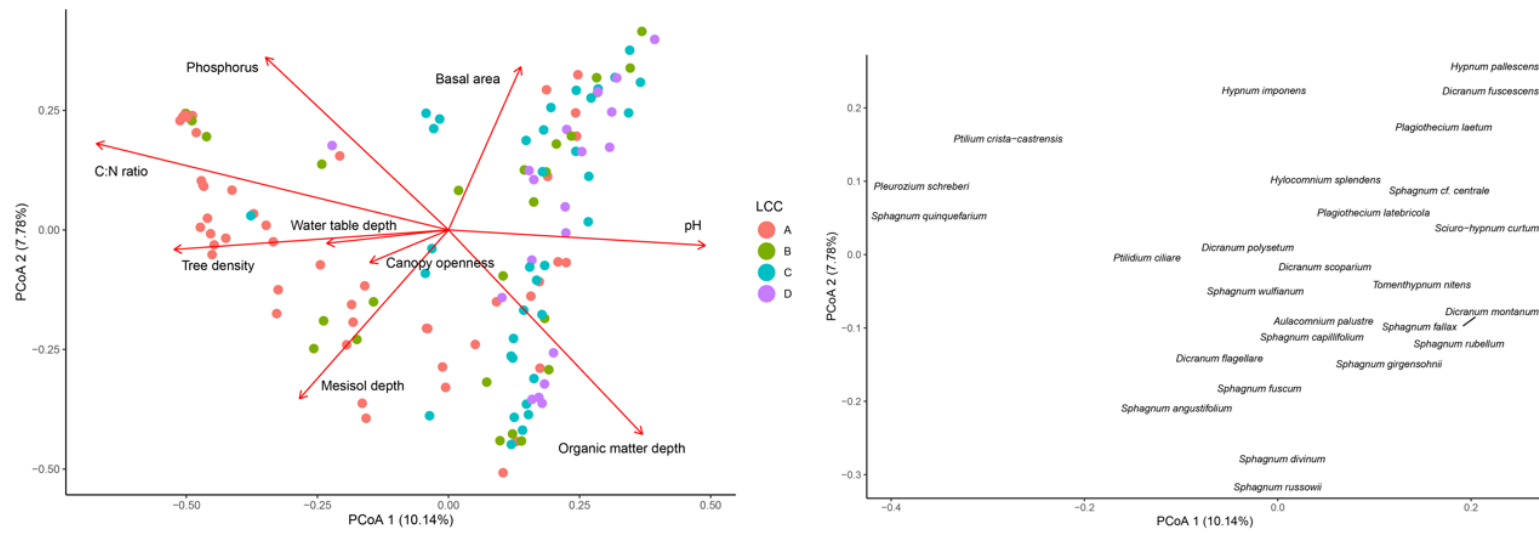
In bryophyte ordinations, we observe a triangular shape of our data. In the upper-left, we observe species and environmental conditions associated with productive black spruce forests on dryer land, in the lower-left part, species and environmental conditions associated with weak productive black spruce forests, and on the right part species and environmental conditions associated with larch forest (figure 4). For vascular plants, we observe the opposite trend in the data distribution on the Y axis of the ordination. Instead of having plants of richer environments in the upper part, we have it in the lower part of the graph. Along axis 1 of PCoA ordination, we observed a trend in herbaceous and bryophyte species composition patterns as a function of the proportion of larch. For bryophytes, the left half of axis 1 contains mostly quadrats with less than 25 % of larch cover proportion (LCC A) associated with species such as: *Pleurozium schreberi*, *Sphagnum quinquefarium* and *Ptilium crista-castrensis* and the right half contains quadrats of other categories with a variety of *Sphagnum* spp (figure 4 a). For vascular plant species, quadrats with less than 50 % of larch cover (LCC A and B) are mostly found on the left half of axis 1 associated with *Rhododendron groenlandicum*, *Maianthemum trifolium* and *Vaccinium angustifolium*, while the quadrats of more than 50 % of larch cover (LCC C and D) are on the right of axis 1 associated with *Mitella nuda* and *Gymnocarpium disjunctum* (figure 4b). However, there is no significant difference in bryophyte and vascular plant composition patterns between all LCC (Vascular plants: $F=7.034$, $p=0.5376$; Bryophytes: $F= 26.449$, $p=0.6194$).

The pH, C:N ratio, mesisol depth and tree density had the strongest relationships with the community patterns for both bryophyte and vascular species communities on axis 1 (Figure 4). For the bryophyte community, nutrients and decomposition rate were associated with axis 2 (Figure 4) while for vascular plants, axis 2 was associated with canopy openness. In terms of the magnitude of effect, nitrogen and organic matter depth had a greater effect on bryophytes than on vascular plants, while the amount of

light in the understory had the opposite pattern. Water table depth didn't have a great impact on quadrat composition.

Figure 2.4. Suite à la page suivante

a)



2.4.4 Needle addition experiment

We found that the abundance and composition of vascular plants (PERMANOVA, 50 % : $F=0.93$; $R^2=0.06$; $p=0.41$, 100 %: $F=0.42$; $R^2=0.03$; $P=0.72$) and bryophytes (PERMANOVA, 50 % : $F=0.77$; $R^2=0.04$; $p=0.48$, 100 %: $F=0.62$; $R^2=0.04$; $p=0.53$) remained the same after the addition of either 50 or 100 % of the needle fall of a >75 % larch site for three years. Furthermore, there was no difference in the abundances of *P. schreberi* (50 %: $F=0.06$, $p=0.80$; 100 %: $F=0.03$, $p=0.87$), *P. crista-castrensis* (50 %: $F=0.39$, $p=0.54$; 100 %: $F=0.01$, $p=0.94$) and *H. splendens* (50 %: $F=NA$, $p=NA$; 100 %: $F=0.15$, $p=0.70$) under the different needle additions. Although there was no significant decrease in bryophyte cover, it was observed that underneath the deposited needle clumps, feather mosses and Sphagnum were black in color and covered with fungi (Figure 5).

a)



Figure 2.5. Suite à la page suivante

b)



c)



Figure 2.5 Bryophyte mortality caused by needle clump in a) *Sphagnum* quadrat and b) Feather moss quadrat. c) Decomposition of needles and feather moss and presence of fungi mycelium.

2.4.5 Functional traits

Higher bryophyte nitrogen content was found in quadrats with a higher proportion of larch, which lead to a lower C:N ratio (Table 3). Vascular plants and *Alnus incana subsp. rugosa* did not follow the same pattern. For vascular plants, there were a higher specific leaf area, a higher nitrogen content and a decrease in carbon content with the increase of larch proportion (Table 4). For *Alnus incana subsp. rugosa*, there was a higher specific leaf area with an increase of larch proportion (Table 5). The other traits did not vary along the larch gradient.

Table 2.3 Bryophyte community traits (mean values \pm standard deviation) and results from linear mixed models with site as a random variable on continuous data of larch proportion showed among the four LCC (A = 0-25 %, B = 25-50 %, C = 50-75 %, D = 75-100 %). Significant variables are shown in bold font ($p < 0.05$). “*n*” is the number of bryophyte samples analyzed with a proportion of larch included in the category.

	A (<i>n</i> =26)	B (<i>n</i> =11)	C (<i>n</i> =17)	D (<i>n</i> =7)	T-value	<i>p</i> -value
Ratio of absorbed water volume to bryophyte volume (ml/cm ³)	1.06 \pm 0.25	1.13 \pm 0.31	1.03 \pm 0.15	0.92 \pm 0.15	-0.11	0.92
Leaf dry matter content (LDMC) (g g ⁻¹)	0.11 \pm 0.05	0.11 \pm 0.06	0.10 \pm 0.05	0.13 \pm 0.01	0.81	0.42
Nitrogen (N) (%)	1.16 \pm 0.25	1.66 \pm 0.50	1.73 \pm 0.28	1.82 \pm 0.32	4.09	2x10⁻⁴
Carbon (C) (%)	46.13 \pm 0.76	45.94 \pm 0.65	45.69 \pm 0.62	45.24 \pm 0.85	-1.81	0.08
Drying rate (log(g)/h)	-0.02 \pm 0.002	-0.02 \pm 0.001	-0.02 \pm 0.001	-0.02 \pm 0.002	-0.21	0.83
Half-drying time (T50) (h)	24.49 \pm 1.78	24.93 \pm 2.05	25.30 \pm 1.58	25.83 \pm 1.31	1.48	0.14
C:N ratio	42.14 \pm 9.61	30.46 \pm 10.50	26.98 \pm 4.30	25.53 \pm 4.22	-4.54	0.00

Table 2.4 Vascular plant community traits (mean values \pm standard deviation) and results from ANOVA of linear mixed models with site as a random variable on site LCC data (A = 0-25 %, B = 25-50 %, C = 50-75 %, D = 75-100 %). Significant variables are shown in bold font ($p < 0.05$). “ n ” is the number of leave scan analyzed with a proportion of larch included in the category.

	A ($n=97$)	B ($n=149$)	C ($n=139$)	D ($n=69$)	F-value	p -value
Specific leaf						
Area (SLA) (cm^2/g)	194.73 \pm 53.63	236.26 \pm 112.91	340.38 \pm 140.34	326.52 \pm 206.65	3.36	0.06
Leaf dry matter content (LDMC) (g g^{-1})	0.39 \pm 0.08	0.32 \pm 0.10	0.30 \pm 0.24	0.47 \pm 0.49	1.58	0.26
Nitrogen (N) (%)	1.86 \pm 0.26	2.13 \pm 0.51	2.83 \pm 0.78	2.92 \pm 0.92	12.94	0.0001
Carbon (C) (%)	55.52 \pm 2.68	52.38 \pm 3.04	50.78 \pm 2.49	50.67 \pm 2.59	5.95	0.01
C:N ratio	30.42 \pm 4.20	26.00 \pm 6.22	18.09 \pm 4.61	18.89 \pm 5.21	6.85	0.001

Table 2.5 *Alnus incana* subsp. *rugosa* traits (mean values \pm standard deviation) and results from ANOVA of linear mixed models with site as a random variable on site LCC data (A = 0-25%, B = 25-50 %, C = 50-75 %, D = 75-100 %). Significant variables are shown in bold font ($p < 0.05$). “ n ” is the number of leaves analyzed with a proportion of larch included in the category.

	A ($n=0$)	B ($n=20$)	C ($n=20$)	D ($n=20$)	F-value	p -value
Specific leaf						
Area (SLA) (cm^2/g)	NA	265.82 \pm 40.21	320.00 \pm 88.62	337.23 \pm 83.14	8.21	0.06
Leaf dry matter content (LDMC) (g g^{-1})	NA	0.31 \pm 0.03	0.46 \pm 0.64	0.40 \pm 0.52	0.41	0.70
Nitrogen (N) (%)	NA	2.92 \pm 0.08	3.18 \pm 0.14	3.24 \pm 0.27	0.95	0.48
Carbon (C) (%)	NA	53.55 \pm 0.97	52.55 \pm 0.18	51.96 \pm 0.46	1.70	0.32
C:N ratio	NA	18.36 \pm 0.15	16.56 \pm 0.78	16.16 \pm 1.48	1.42	0.37

2.5 Discussion

Based on our results, on a thick layer of organic matter, larch would create understory conditions that are both favorable for vascular plant diversity and slightly detrimental for bryophyte diversity. The effect is observable as soon as the proportion exceed 25 % of larch in the canopy and is accentuated with the increase of the proportion of larch. This is an interesting result since a thick layer of organic matter under a spruce canopy is a difficult growing environment for vascular plants due to cold soil temperature, high acidity, low nutrient levels, and shallow water table (Simard et al., 2007). Moreover, it would not be the first time that a larch species has created conditions conducive to herbaceous plants on a low fertility substrate (Arno & Habeck, 1972). The Alpine Larch (*Larix lyallii* Parl.) creates a substrate that allow the establishment of subalpine understory communities in the alpine zone (Arno & Habeck, 1972). According to our results, we identified litter accumulation and canopy openness as the two primary drivers that would explain the observed increase in diversity and the shift from species associated with spruce understory to species associated with mixed hardwood forest understory.

Driver 1: Litter accumulation

Litter accumulation influenced the diversity, compositional pattern, and functional traits of vascular plants and bryophytes. For bryophytes, litter has a deleterious effect in general but its effect is more important for feathermosses. This result can be explained by the fall of needles between the *Sphagnum* mosses as they grow, only partially impairing their growth and causing less mortality than for the slower growing feathermoss species (Turetsky et al., 2010). As seen in the field, larch litter impact is similar to that of a poplar leaf, i.e., blackening of bryophytes and their covering by mycelium. Thus, we hypothesize that larch litter creates a physical barrier to light for

bryophyte communities, as does poplars in the Startsev et al. (2008) study. Larch litter could also release phenolic compounds harmful to bryophytes (Startsev et al., 2008) or promote the establishment of micro and macrofauna feeding on bryophytes (Lindo & Gonzalez, 2010).

When we ignore the site effect in our analyses and look at the overall pattern, we observe a higher litter decomposition rate in quadrats with a higher proportion of larch. Indeed, decomposition is strongly site-dependent, i.e., the same litter can have opposite decomposition rates at two different sites under the same treatment conditions (Sariyildiz, 2003). Since decomposition is generally higher under a larch canopy than under a spruce canopy, we suppose that larch litter is of higher quality since litter quality is one of the primary driver of organic matter decomposition rate in forest ecosystems (Cornwell et al., 2008; Zhang et al., 2008). This result is consistent with Lieffers & Macdonald, (1990) who compared leaf nutrients in larch and black spruce and found equal or greater nutrient concentration in larch than in black spruce. Despite the higher decomposition rate in the quadrats with a high proportion of larch, we did not find a higher concentration of nutrients in the soil. However, we did find a higher foliar concentration of nitrogen and a decrease in carbon in vascular plants and bryophytes. These results suggest a rapid cycling of nutrients.

Moreover, the vascular plant species commonly found (present in more than 50 % of quadrats) in quadrats with less than 25 % of larch are perennial species, that keep their leaves all year long, and have a high leaf carbon content which are nutrient retention strategies for poor environments (Wright et al., 2004). Furthermore, in the guide to recognizing ecological types in our ecological region (Blouin & Berger, 2002), *G. hispidula*, *K. angustifolia*, *R. groenlandicum*, *V. angustifolium*, and *V. myrtilloides* are classified as indicators species for poor to very poor environments. With the increase of larch, these species decrease in frequency and are replaced by *Carex* sp. *C. trifolia*,

M. canadense, *C. canadensis*, *A. incana* subsp. *rugosa*, *L. borealis*, *R. idaeus*, and *R. pubescens*, which are species that are found in moderately to very rich environments (Blouin & Berger, 2002). Thus, we assume a transition from species of poor sites to species of rich sites, which supports our previous results that larch forest soil is richer than spruce forest soil.

An opposite result is observed for bryophytes. There is a decrease in the number of bryophyte species with an increase in the proportion of larch, which agrees with several studies that show that the amount of moss is less with the increase in the amount of litter generated (Jean et al., 2020; Mestre et al., 2017; Startsev et al., 2008). Among others, we observe a decrease in *Dicranum polysetum*, *Sphagnum angustifolium*, *Sphagnum russowii*, and *Pleurozium schreberi* and note a punctual presence of *Sciurohypnum curtum*, *Hypnum imponens* and *Plagiothecium laetum*. However, the mosses that remain present in the quadrats with a more significant proportion of larch are driven by higher pH and lower soil carbon concentration. This suggests that quadrats with more larch are less acidic and have higher nutrient cycling than quadrats with more black spruce. High litter input is known to play an essential role in forming a soil horizon (Stevenson, 1994). Thus, we hypothesize that the high larch litter supply and its rapid decomposition allow the creation of soil on top of bryophytes, thus creating a substrate for the understory plants growth. Then, the establishment of different understory plants in the undergrowth contribute to the litter supply, which changes the soil structure and composition and so, the ecosystem functioning (Hart & Chen, 2006).

2.5.1 Driver 2 : Canopy openness

We measured a less dense stand under a high proportion of larch than under high proportion of spruce. We explain this result by the rapid growth of larch and its larger size than black spruce that competition for more space under surrounding conditions. This rapid growth and large size would allow the transition from an open environment

with a lot of small trees to a more closed environment with bigger trees as shown by the basal area relation in our ordinations. The combination of relatively open canopy in pure larch stand and the low density of trees per m² in comparison of black spruce stands, allow a good light passage to the understory. The mixity of the forest favors a better saturation of the space by the staggering of the tops between the spruces and the larches, which leads to more shade in the undergrowth (Jucker et al., 2020). This shaded environment allows undergrowth plants that are more sensitive to high light levels to colonize the area. In our multivariate analyses, we see that the amount of light reaching the understory strongly impacts the understory floristic composition. This result agrees with the review of Hart & Chen, (2006), which mentions that light is one of the main drivers of understory community composition patterns.

In addition to having a good amount of light in the understory in summer, we measured a significantly greater canopy openness in spring in a closed larch forest than in a closed spruce forest, which we explained by needle loss. This result suggests more rapid spring snowmelt in the larch understory, allowing for a more extended growth period of understory plants. Thus, some plants that require a longer growth period than that found under spruce may colonize the larch understory, like white spruce does under aspen (Lieffers et al., 1996). In our study, we observe an increase in the specific surface of the average leaves of the vascular plant communities with the increase of larch. This result could be explained by the fact that in a rich environment, competition for light increases, which results in above-ground biomass allocation in vascular plants (Poorter & Remkes, 1990).

For future research, we suggest studying the microtopography of the forest floor in the different stands. In stands with a lot of larch, we observed a very variable microtopography due to the large superficial roots of this tree. Since local seed germination microsite and water stress are essential in plant survival and growth in

wetlands (Diamond et al., 2020; Sullivan et al., 2008), we believe that data at this scale would be needed to explain a more significant proportion of the variance. Also, our results showed that a large proportion of larch has a positive impact on the diversity and species composition of vascular plants of rich environments and is detrimental to bryophyte species. Being richer and limiting the spread of bryophytes, these environments could favor the growth of the successive tree layer. Then, to understand better the litter impact, longer term monitoring would allow us to quantify the magnitude of the effects of added litter in the understory and thus estimate the time required to limitate the paludification process.

2.6 Conclusion

In this study, we showed that the proportion of larch in the canopy has an impact on understory composition, diversity and functional traits. We remarked that with an increase in larch proportion, there is a shift of vascular plant species from species associated with spruce (poor and acidic environment) to species associated with mixed hardwood forest (richer and less acidic environment). We also observed an increase in the number of species with an increase of larch in canopy. For bryophytes, we noted a decrease in the number of species and an increase of beta diversity. Finally, we attributed these results to the higher rate of nutrients cycling, lower tree density and closer canopy measured in quadrats with a higher proportion of larch. We assume that the large supply of rapidly decomposing litter allows for the creation of a more suitable surface soil layer for the growth of vascular plants on a thick layer of organic matter. This knowledge is interesting as it shows that larch in medium proportion could have the ability to transform weak productive soils into productive soils. Studies on the optimal planting density and the optimal time after planting for the creation of a productive soil should be conducted.

CHAPITRE III

CONCLUSION GÉNÉRALE

Dans cette étude, nous avons démontré que la proportion de mélèze dans la canopée a un impact sur la composition, la diversité et les traits fonctionnels des plantes vasculaires et des bryophytes en sous-bois. En effet, avec une augmentation de la proportion de mélèze, il y a une transition des espèces de plantes vasculaires associées à l'épinette noire (environnement pauvre et acide) vers des espèces associées à la forêt mixte (environnement plus riche et moins acide). Nous avons également observé une augmentation du nombre d'espèces de plantes vasculaires, de l'azote foliaire et de la surface foliaire avec l'augmentation de la proportion de mélèzes. Pour les bryophytes, nous avons noté une diminution du nombre d'espèces et une plus grande variabilité dans la présence et le nombre d'espèces avec l'augmentation de la proportion de mélèze en canopée. Cependant, nous avons noté une plus grande concentration en azote foliaire dans les mousses persistantes. Enfin, nous avons attribué ces résultats au cyclage plus rapide des nutriments, à la plus faible densité d'arbres et à la canopée plus fermée, mais pas nécessairement moins lumineuse dans les quadrats avec une forte proportion de mélèze. Nous supposons que l'apport important de litière à décomposition rapide permet la création d'une couche superficielle du sol propice à la croissance des plantes vasculaires sur une épaisse couche de matière organique. Cependant, nous suggérons de mettre en relation la composition et la diversité du sous-bois avec les conditions environnementales du microhabitat afin d'avoir une meilleure explication de la présence de certaines espèces de sous-bois. De plus, une prise en compte de la structure

et de la morphologie du mélèze dans la mesure de l'ouverture de la canopée en comparaison avec l'épinette noire serait nécessaire pour mieux comprendre leur impact sur la lumière disponible en sous-bois. Finalement, il serait intéressant d'étudier la relation entre l'âge du peuplement de mélèze et la quantité de litière générée, puisqu'il pourrait potentiellement en avoir plus dans un peuplement jeune et dense.

Ces connaissances sont intéressantes, car elles suggèrent que le mélèze aurait la capacité de créer un sol productif sur un sol organique improductif. Dans un contexte d'aménagement forestier durable, dans la région du nord-ouest du Québec, ces résultats font partie d'une solution à l'enjeu de la paludification qui diminue la productivité forestière. En sylviculture, lorsqu'il y a une coupe forestière dans une forêt tourbeuse avec une épaisse couche de tourbe, il est nécessaire de faire une préparation mécanique du sol. Cette préparation améliore les conditions du sol et réduit la distance entre le semis qui sera planté et la couche de sol minéral, ce qui favorise la croissance du semis (Lafleur et al., 2018; Lavoie et al., 2005; Prevost et al., 1997). Deux types de préparations mécaniques du sol sont couramment utilisées au Québec, soit le scarifiage T26 et le hersage forestier à disques. Le scarifiage consiste à insérer dans le sol deux disques dentés afin de retourner le sol pour éliminer la végétation concurrente et créer des conditions propices à la régénération naturelle et artificielle. Pour ce qui est du hersage forestier, il y a insertion de 6 à 10 disques dans le sol afin de l'ameublir et de le rendre plus propice à la régénération (Bérard et al., 1996). De cette façon, il y a une meilleure croissance du semis (Henneb et al., 2020).

De plus, une forêt mixte est connue pour avoir une strate arborescente plus productive qu'une forêt pure (Pretzsch, 2022; Pretzsch & Schütze, 2021; Richards et al., 2010). Entre autres, le peuplier faux-tremble (*Populus tremuloides*), tout comme le mélèze, améliorerait aussi la productivité de l'épinette noire en forêt boréale (Légaré et al., 2004). Jusqu'à une proportion de 40 % de la surface terrière du peuplement, le peuplier

faux-tremble faciliterait la croissance de l'épinette noire en apportant des nutriments par sa litière, en influençant positivement le taux de décomposition, mais aussi en diminuant la vulnérabilité de l'épinette aux changements climatiques (Chavardès et al., 2021; Légaré et al., 2004). Contrairement au peuplier, le mélèze a plus de résistance à des conditions d'inondations (Blouin & Berger, 2002) et à la présence d'une couche organique épaisse (Gewehr et al., 2014; Lafleur et al., 2015). Ainsi, dans un parterre de coupe où il y a une remontée de la nappe phréatique, le mélèze aura une meilleure croissance que le peuplier et sera donc plus approprié pour améliorer la productivité de l'épinette noire.

En effet, la coupe forestière peut engendrer la remontée de la nappe phréatique et ainsi créer des conditions propices à l'entourbement du site reboisé (Dubé et al., 1995). Le site de coupe devient donc peu productif en matière ligneuse, augmentant par le fait même la proportion de forêts improductive dans la région (Lavoie, 2006). En définissant l'impact de la proportion de mélèze sur les communautés de sous-bois et les conditions environnementales, on peut suggérer que le mélèze pourrait jouer un rôle dans la limitation de la paludification. On pourrait par exemple reboiser les sentiers de débardage après les CPRS ou effectuer des plantations mixtes. Ce projet de recherche est donc une contribution de connaissances à celles nécessaires pour établir une technique de remise en production de sites de coupe tourbeux. De cette manière, l'impact de l'exploitation de ces forêts est moins grand et est ainsi mieux perçu par la population.

ANNEXE A

TABLEAU COMPARATIF DES SITES D'ÉTUDE

Annexe 1 Caractéristiques des sites d'études basées sur les données de la carte écoforestière du 4^e inventaire forestier et de la carte des feux.

Site	Basal area (m ² /ha)	Year of last fire	Woody species group	Density class	Height class	Age class	Slope class	Surfacial materials	Drainage class	Ecotype	Shape Area (m ²)	Larch proportion (%)
5	33,3	1825	ENML	C	4	50	A	4GA	50	RE37	5997	6
6	18,2	1825	ENML	C	4	50	A	4GA	50	RE37	2524	4
7	31,5	1875	ENEN	C	4	50	A	7T	50	RE39	2789	12
8	38,5	1775	ENML	B	3	JIR	A	7E	60	RE39	3052	15
9	27,6	1875	RXR	C	5	50	A	7T	50	RE39	5840	29
10	44,2	1875	ENRX	C	3	50	A	4GA	40	RS26	3865	39
11	35,1	1916	MLEN	B	3	JIR	A	7E	60	RE39	6807	40
13	57,1	1916	MLEN	B	2	JIR	A	4GA	40	ME16	3323	62
14	32,7	1875	MLEN	B	3	JIR	A	7T	53	RE39	4516	42
15	40,1	1916	MLEN	B	3	JIR	A	7T	60	RE39	5653	65
16	33,2	1916	MLEN	B	3	VIR	A	7T	50	RE38	8430	66
17	35,6	1725	MLML	C	2	70	A	7E	60	RE39	7928	78
18	29	1775	MLMLPT	B	3	JIR	A	4GA	40	MS26	4579	93
19	34,8	1916	MLEN	C	3	50	A	7E	60	RE39	4934	66

ANNEXE B

PHOTOS DE L'IMPACT D'UNE FEUILLE DE PEUPLIER ET D'AIGUILLES D'ÉPINETTE NOIRE SUR LES BRYOPHYTES

a)



b)



Annexe 2 Mortalité du *Pleurozium schreberi* et présence de mycélium sous a) une feuille de peuplier et b) sous un amas d'aiguilles d'épinette noire.

ANNEXE C

TABLEAU DES ESPÈCES INDICATRICES

Annexe 3 Espèces indicatrices des différentes catégories de mélèze déterminées selon la proportion de mélèze à l'intérieur d'un rayon de 5m du centre du quadrat (LCC). Les valeurs ont été obtenues avec le package *indicspecies*.

<i>LCC</i>	<i>Type</i>	<i>Specie</i>	<i>A</i>	<i>B</i>	<i>IV</i>	<i>P-Value</i>
A (>0-25%)	Vasculars	Mai_tri	0.90414	0.17647	0.399	0.008
		Rub_cha	1.00000	0.05882	0.243	0.205
		Dro_sp	1.00000	0.01961	0.140	1.000
		Pop_tre	1.00000	0.01961	0.140	1.000
	Bryophytes	Dic_fla	1.00000	0.03922	0.198	0.335
		sph_rub	1.00000	0.03922	0.198	0.415
		Hyp_pal	1.00000	0.01961	0.140	1.000
B (25-50%)	Vasculars	Dry_car	0.94606	0.15385	0.382	0.007
		Gal_pal	1.00000	0.03846	0.196	0.327
		Lar_lar	0.90747	0.03846	0.187	0.524
	Bryophytes	sph_cen	0.77041	0.11538	0.298	0.076
		Pla_lat	1.00000	0.03846	0.196	0.352
C (50-75%)	Vasculars	Ame_sp	0.88078	0.13158	0.340	0.069
		Rib_gla	0.79610	0.10526	0.289	0.154
		Iri_ver	1.00000	0.02632	0.162	0.645
	Bryophytes	Hyp_imp	1.00000	0.02703	0.164	0.629
D (>75%)	Vasculars	Lon_vil	0.78222	0.41667	0.571	0.001
		Cor_alt	0.86364	0.16667	0.379	0.002
		Pyr_ell	0.90961	0.12500	0.337	0.047

		Dry_cri	0.76000	0.08333	0.252	0.104
		Gym_dry	1.00000	0.04167	0.204	0.189
		Lon_can	1.00000	0.04167	0.204	0.173
		The_pal	1.00000	0.04167	0.204	0.172
	Bryophytes	Pla_lae	1.0000	0.2105	0.459	0.001
		sph_fal	0.9113	0.1579	0.379	0.027
		Tom_nit	0.7068	0.1579	0.334	0.028
A + B (>0-50%)	Vasculars	Vac_ang	0.9147	0.5325	0.698	0.001
		Pic_mar	0.9486	0.2857	0.521	0.006
		Vac_oxy	0.8628	0.1818	0.396	0.024
		Kal_pol	0.8907	0.1429	0.357	0.087
	Bryophytes	Pti_cil	0.85029	0.41558	0.594	0.001
		Pti_cri	0.89710	0.38961	0.591	0.189
		sph_fus	1.00000	0.11688	0.342	0.067
		sph_qui	1.00000	0.09091	0.302	0.151
		Dic_mon	1.00000	0.02597	0.161	0.774
C + D (>50%)	Vasculars	Aln_rug	0.76052	0.54839	0.646	0.001
		lin_bor	0.95716	0.38710	0.609	0.001
		Poa_sp	0.90821	0.25806	0.484	0.007
		Fra_sp.	1.00000	0.19355	0.440	0.003
		Mit_nud	0.89870	0.14516	0.361	0.022
		Sol_rug	1.00000	0.11290	0.336	0.036
		Cor_ser	1.00000	0.06452	0.254	0.223
		Vio_sp	0.94297	0.06452	0.247	0.407
		Gym_dis	1.00000	0.04839	0.220	0.247
		Tar_sp	1.00000	0.04839	0.220	0.256
		Sym_cil	1.00000	0.03226	0.180	0.585
	Bryophytes	Bra_cur	1.00000	0.10714	0.327	0.038
		Dic_sco	0.94611	0.07143	0.260	0.187

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