Université du Québec en Abitibi-Témiscamingue

IMPACT DE L'ÉTABLISSEMENT DES PLANTATIONS À CROISSANCE RAPIDE UTILISANT DES PEUPLIERS HYBRIDES (POPULUS SPP.) SUR LA BIODIVERSITÉ DE LA VÉGÉTATION DE SOUS-BOIS

Thèse
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DÉDICACE

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AVANT-PROPOS

Cette thèse est présentée sous forme de trois articles scientifiques représentant les chapitres 1, 2 et 3. Elle est complétée par deux autres sections qui sont l'introduction générale et la conclusion générale. L'introduction générale comprend la mise en contexte, les problématiques, l'état des connaissances, les objectifs et la méthodologie générale. Les trois chapitres ont été rédigés en anglais et visent à répondre aux objectifs et à valider les hypothèses de la thèse. Le Chapitre 1 a été publié dans la revue Forest Ecology and Management en septembre 2023. Le Chapitre 2 sera soumis à une revue et le Chapitre 3 a été publié dans la revue New Forests en novembre 2024. La conclusion générale présente une synthèse des résultats et aborde des ouvertures et perspectives pour des futures recherches.

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Chapitre 1: Randriamananjara, M.A., Fenton, N.J., DesRochers, A. (2023). How does understory vegetation diversity and composition differ between monocultures and mixed plantations of hybrid poplar and spruce? Forest Ecology and Management 549: 1-14

Chapitre 2: Randriamananjara, M.A., Fenton, N.J., DesRochers, A. How clonal identity impacts diversity, composition and functional traits of understory vegetation (A soumettre à une revue)

Chapitre 3: Randriamananjara, M.A., Fenton, N.J., DesRochers, A (2024). Understory vegetation diversity and composition in intensively managed plantations compared to extensively managed forests. New Forests 56 (5)

Les présentations orales à des conférences effectuées dans le cadre de cette thèse sont les suivantes :

Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Plantations *versus* forêts de référence naturellement régénérées et plantées: Réponses de la biodiversité de la végétation de sous-bois. 17e colloque annuel du CEF, Université du Québec ne Outaouais à Gatineau (2024-05-02)

Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Plantations intensivement aménagées *versus* forêts extensivement aménagées: Quelles réponses de la biodiversité de la végétation de sous-bois? 25e colloque de la Chaire AFD. Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec. (2023-11-29)

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Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Diversité végétale dans les plantations de peuplier hybride en plantations pure et mixte. Webinaire thématique 2RLQ (2023-12-20)

Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Diversité végétale dans les plantations de peupliers hybrides en plantation mixte et en monoculture. 15e colloque annuel du CEF, Université de Sherbrooke, Québec (2022-09-29)

Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Impact de l'établissement des plantations à croissance rapide utilisant des espèces exotiques sur la biodiversité de végétation de sous-bois. 1er colloque annuel du GREMA. (2022-05-31)

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Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Diversité végétale dans les plantations de peupliers hybrides en plantation pure et mixte. 24e colloque de la Chaire AFD. Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec. (2022-11-22)

Randriamananjara, M.A., Fenton, N.J., Desrochers, A. Diversité végétale dans les plantations de peupliers hybrides en plantation pure et mixte. 24e colloque de la Chaire AFD. Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec. (2022-11-22)

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Article de vulgarisation :

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C	Carbon
CC	Clear-cutting
CLAAG	Careful logging around advanced growth
Clone1	*Populus trichocarpa* Torrey & A. Gray x *Populus balsamifera* L.
Clone2	*Populus balsamifera* x *Populus maximowiczii* Henry
Clone3	*Populus balsamifera* x *Populus maximowiczii* Henry
Clone4	*Populus maximowiczii* x *Populus balsamifera* L.
DBH	Diameter at breast height
LDMC	Leaf dry matter content
LNC	Leaf nitrogen concentrations
Log	Logarithme
LPC	Leaf phosphorus concentrations
N	Azote
NS	Norway spruce (*Picea abies* (L.) Karst.)
Pl	Plantation
poplar1	*Populus trichocarpa* Torrey & A. Gray × *Populus balsamifera* L.
poplar2	*Populus maximowiczii* Henry × *Populus balsamifera* L.
Rf	Reference forest
SLA	Specific leaf area
TOPIC	Traits Of Plants In Canada database
TRY	Plant Trait Database
VASCAN	Base de données des plantes vasculaires du Canada
WS	White spruce (*Picea glauca* (Moench))

RÉSUMÉ

Les plantations à croissance rapide jouent un rôle important dans la production de bois. Au Québec, les plantations de peupliers hybrides représentent une source potentielle de bois en raison de leur rendement élevé. Toutefois, les plantations sont souvent établies en monocultures et sont perçues comme un type d'aménagement altérant la biodiversité de la végétation de sous-bois. Par conséquent, la diversification des peuplements est préconisée en privilégiant les plantations mixtes par rapport aux monocultures. Cependant, l'effet bénéfique des plantations mixtes sur la biodiversité de la végétation de sous-bois peut varier en fonction des écosystèmes, de la composition de la canopée et des groupes taxonomiques de sous-bois. Les études sur l'effet du mélange d'espèces d'arbres sur la biodiversité de la végétation de sous-bois étaient majoritairement sur le mélange conifère-feuillu. Ainsi, il n'est pas clair si les plantations polyclonales (deux à plusieurs clones) augmentent la biodiversité du sous-bois par rapport aux plantations monoclonales (un seul clone), bien que le mélange de clones d'une même espèce, comme les peupliers hybrides, puisse créer une plus grande hétérogénéité de l'habitat en raison des différences de traits fonctionnels entre clones. En outre, nous ne savons pas si la biodiversité de la végétation de sous-bois est similaire dans les plantations et les forêts qui ont un type de canopée similaire. Il n'est également pas clair si l'origine (exotique *vs* indigène) des espèces plantées influence la naturalité des plantations par rapport aux forêts.

Cette thèse avait comme objectif de déterminer l'impact de la composition et de la complexité de la canopée des plantations sur la biodiversité taxonomique et fonctionnelle de la végétation de sous-bois. Elle visait à évaluer si les plantations mixtes/plantations polyclonales favorisent la biodiversité de la végétation de sous-bois par rapport aux monocultures/plantations monoclonales. Elle évalue également la similarité entre la biodiversité de la végétation de sous-bois des plantations et celle des forêts de référence, en tenant compte de l'origine des espèces (exotiques *vs* indigènes) dans les plantations. Nous avons échantillonné des plantations utilisant des peupliers hybrides et des forêts de référence situées dans les régions d'Abitibi-Témiscamingue et du Nord-du-Québec. Nous avons inventorié la végétation de sous-bois incluant les plantes vasculaires, les bryophytes et les lichens sur le sol, la base et le tronc des arbres dans chaque type de peuplement. Les bryophytes et les lichens ont été récoltés pour identification au laboratoire. Afin d'évaluer l'effet des clones sur les traits fonctionnels de la végétation de sous-bois, nous avons mesuré les traits fonctionnels d'espèces de sous-bois dans les plantations monoclonales et polyclonales établies le long d'un gradient latitudinal.

Nos résultats montrent que la richesse en espèces vasculaires et en lichens était similaire entre les monocultures et les plantations mixtes, tandis que la présence de l'épinette dans les plantations mixtes a favorisé l'établissement des bryophytes au sol. Notre étude justifie l'ajout de l'épinette dans les plantations de peupliers hybrides afin d'accroître la diversité de la végétation de sous-bois lors de la planification de reboisements et de plantations. Elle montre également que la présence des peupliers hybrides dans les plantations mixtes pourrait fournir des habitats temporaires pour les lichens et donc contribuer en partie à l'augmentation de la biodiversité.

En ce qui a trait à la biodiversité de la végétation de sous-bois dans les plantations polyclonales et monoclonales le long d'un gradient latitudinal, les plantations polyclonales favorisaient une plus grande diversité fonctionnelle des plantes, en particulier dans les environnements plus rudes. Les traits fonctionnels des plantes variaient également le long du gradient latitudinal, les plantes des latitudes élevées présentant des traits conservateurs, tandis que celles des basses latitudes présentaient des traits acquisitifs. Les résultats montrent une composition végétale influencée par l'historique d'utilisation des terres, avec davantage d'espèces herbacées sur les anciennes terres agricoles et de végétation forestière sur les anciens sites forestiers. Cette étude recommande l'usage de plantations polyclonales pour améliorer la diversité fonctionnelle, en soulignant l'importance de la diversité clonale et de la dissimilarité des clones pour promouvoir la biodiversité de la végétation de sous-bois.

Comparativement aux forêts de référence, les plantations feuillues et mixtes présentaient une diversité similaire en végétation de sous-bois montrant que les plantations ne sont pas nécessairement des déserts biologiques. La présence d'épinette indigène (épinette blanche) et de peupliers exotiques dans les plantations mixtes a favorisé la diversité des bryophytes et des plantes vasculaires. Les plantations étaient composées d'espèces herbacées rudérales, tandis que les forêts de référence étaient composées d'espèces arbustives et forestières. Les lichens se trouvaient exclusivement dans les plantations. Nos résultats soulignent l'importance de considérer l'origine des espèces dans le cadre d'une planification de plantation et montrent que les plantations mixtes, d'épinette blanche et de peuplier exotique, peuvent représenter une option prometteuse pour améliorer la biodiversité dans les stratégies de reboisement.

Mots-clés : plantation,mélange, végétation de sous-bois, biodiversité, arbre à croissance rapide, peuplier hybride, clone, trait fonctionnel, gradient latitudinal, historique d'utilisation des terres.

Keywords: plantation, mixture, understory vegetation, biodiversity, fast-growing tree, hybrid poplar, clone, functional trait, latitudinal gradient, land-use history.

INTRODUCTION GÉNÉRALE

Mise en contexte. Au cœur du défi que représente la conservation de la biodiversité se situe une demande croissante en bois (Kok *et al.*, 2018; FAO, 2022), ce qui fait croître l'intérêt pour la sylviculture intensive à travers les plantations forestières à croissance rapide (Jürgensen *et al.*, 2014). Au Québec, 100 000 ha de terres agricoles abandonnées ont été recensés entre 1997 et 2007 (Vouligny & Gariépy, 2008). La facilité à remettre en production de ces terres et leur proximité aux villes et villages ont suscité un intérêt pour l'établissement de plantations intensivement aménagées (Ménétrier, 2008; Larocque *et al.*, 2013). Par exemple, il y a 20 ans, un réseau de monocultures et de plantations mixtes utilisant plusieurs clones de peupliers hybrides (*Populus* spp.) a été mis en place par l'Université du Québec en Abitibi-Témiscamingue (UQAT) à travers les régions d'Abitibi-Témiscamingue et du Nord-du-Québec (Guillemette & DesRochers, 2008). Les peupliers hybrides se caractérisent par leur croissance rapide et peuvent atteindre un rendement annuel moyen en bois équivalent à 11 m^3 $ha^{-1}an^{-1}$ (Ménétrier, 2008). Ils peuvent également contribuer à réduire la pression de récolte sur les forêts naturelles dans le cas où ils remplacent le bois qui serait autrement prélevé en forêt (Larocque *et al.*, 2013).

Bien que les plantations à croissance rapide fournissent du bois, leur potentiel à favoriser la biodiversité de la végétation de sous-bois demeure sujet à débat (Lindenmayer & Hobbs, 2004; Brockerhoff *et al.*, 2008). La sylviculture intensive est souvent basée sur des plantations en monoculture, car celles-ci permettent une gestion simplifiée où une seule espèce est cultivée, optimisant les pratiques telles que la plantation, la fertilisation et la récolte (Nichols *et al.*, 2006; Messier *et al.*, 2022). Toutefois, la sylviculture intensive a une connotation négative et est souvent qualifiée de 'déserts de biodiversité' souvent en raison de l'utilisation d'herbicides dans les plantations, entrainant une réduction de la biodiversité de la végétation de sous-bois (Bauhus *et al.*, 2010; Liu *et al.*, 2018). La végétation de sous-bois se définit comme l'ensemble des plantes, d'arbres et des arbustes d'une hauteur inférieure à 1,3 m et se divise en trois différents groupes taxonomiques : les plantes vasculaires, les bryophytes et les lichens (Chen *et al.*, 2004; Hart & Chen, 2008; Faubert, 2012). Elle est une composante importante de l'écosystème forestier qui contribue à différents services écologiques tels que le cycle des nutriments, la séquestration du carbone et la disponibilité des nutriments dans le sol (Gilliam, 2007; Barbier *et al.*, 2008; Rousk *et al.*, 2013; Jean *et al.*, 2021; Grau-Andres *et al.*, 2022). Les communautés de la végétation de sous-bois sont à leur tour influencées par la composition, la structure et le type de canopée (Wang *et al.*, 2021; Stefańska-Krzaczek *et al.*, 2022; Kutnar *et al.*, 2023). L'établissement du réseau de plantations de l'UQAT crée de nouveaux écosystèmes dans le paysage et ces plantations pourraient donc influencer la biodiversité taxonomique et fonctionnelle de la végétation de sous-bois.

Problématique. ***Réponses de la végétation de sous-bois à la diversité de la canopée.*** Les impacts négatifs des monocultures sur la biodiversité de la végétation de sous-bois nous incitent à privilégier les plantations mixtes associant deux ou plusieurs espèces, car elles pourraient favoriser et maintenir la biodiversité (Hisano *et al.*, 2018; Wang *et al.*, 2021). En effet, les canopées plurispécifiques ou mixtes créent un habitat hétérogène (Jucker *et al.*, 2015; Schmid & Niklaus, 2017), fournissant ainsi une variété de substrats et de micro-habitats propices à l'établissement d'une variété d'espèces de sous-bois (Barbier *et al.*, 2008; Nadrowski *et al.*, 2010; Messier *et al.*, 2022). Néanmoins, l'effet positif du mélange d'espèces sur la biodiversité de la végétation de sous-bois par rapport à des forêts monospécifiques n'est pas toujours évident. En effet, des études ont montré que les forêts mixtes pouvaient avoir une diversité de la végétation du sous-bois similaire à celle des forêts monospécifiques (Augusto *et al.*, 2003; Barsoum *et al.*, 2016), tandis que d'autres ont indiqué qu'elles avaient une diversité de sous-bois plus élevée que les forêts monospécifiques (Wang *et al.*, 2021). Ces incohérences sont liées à la difficulté de distinguer le type et la composition de la canopée à d'autres facteurs tels que l'âge du peuplement, le sol, l'historique d'utilisation des terres ou la topographie (Pitkänen, 2000; Gärtner & Reif, 2004; Nadrowski *et al.*, 2010). Il n'y a donc pas de réponse simple à la question de savoir si la biodiversité de la végétation de sous-bois est plus grande dans les plantations mixtes que dans les monocultures. De plus, les études sur la biodiversité de la végétation de sous-bois dans les plantations se concentrent souvent sur un seul groupe taxonomique, comme les plantes vasculaires (Soo *et al.*, 2009), les bryophytes (Pharo & Lindenmayer, 2009) ou les lichens (Hilmo *et al.*, 2009) limitant ainsi l'évaluation de l'impact des plantations sur l'ensemble de la végétation de sous-bois. Par conséquent, il est nécessaire d'intégrer tous les groupes taxonomiques de la végétation de sous-bois afin d'obtenir une vision complète de la manière dont les plantations pourraient influencer la biodiversité.

Effets des plantations polyclonales et monoclonales sur la biodiversité de la végétation de sous-bois. L'effet du mélange d'espèces appartenant à différents genres, tels que les conifères et feuillus, sur la biodiversité de la végétation de sous-bois a fait l'objet de nombreuses études (Brockerhoff *et al.*, 2008; Feng *et al.*, 2022). Les différences phylogénétiques et fonctionnelles entre ces types d'arbres, telles que la tolérance à l'ombre, la phénologie et le type de litière, sont considérées comme des facteurs favorisant l'établissement d'une plus grande diversité d'espèces de sous-bois (Barbier *et al.*, 2008; Brockerhoff *et al.*, 2008; Richards *et al.*, 2010; Cavard *et al.*, 2011a). Cependant, bien que les clones hybrides soient issus d'espèces du même genre, ils présentent des traits différents en termes de productivité, structure de la canopée et de phénologie de feuilles (Benomar *et al.*, 2012; Elferjani *et al.*, 2016; Rabearison *et al.*, 2023). Ces variations intra-clonales suggèrent que le mélange de clones aux traits divergents pourrait accroître l'hétérogénéité des habitats et la disponibilité des nutriments du sol. Par exemple, les plantations polyclonales de peuplier hybride, comprenant deux ou plusieurs clones, ont montré une augmentation de la croissance des arbres, une réduction du rapport biomasse racinaire/biomasse aérienne, ainsi qu'une distribution spatiale des racines différente dans le sol par rapport aux plantations monoclonales (Elferjani *et al.*, 2014). Ces observations suggèrent que les plantations polyclonales pourraient favoriser l'établissement des espèces de sous-bois en fournissant une variété de ressources et un habitat hétérogène. Toutefois, il reste à vérifier si la biodiversité de la végétation de sous-bois est plus élevée dans les plantations polyclonales que dans les monoclonales. Cela permet également d'étudier des espèces appartenant au même genre, mais ayant des traits différents afin de minimiser l'effet potentiel des différences phylogénétiques sur la biodiversité de la végétation de sous-bois.

Outre le type et la composition de la canopée, les gradients latitudinaux peuvent également influencer la réponse des communautés végétales de sous-bois par le biais des facteurs climatiques (Keddy, 1992; Colwell *et al.*, 2008; Sandel *et al.*, 2010). Des conditions environnementales plus difficiles (c'est-à-dire des températures froides, des niveaux de lumière plus faibles et des saisons de croissance plus courtes) aux latitudes septentrionales peuvent conduire à des conditions pauvres en ressources, telles qu'une disponibilité réduite en nutriments (Reich & Oleksyn, 2004). A l'inverse, les latitudes méridionales offrent généralement des conditions riches en ressources et en nutriments. Par conséquent, l'effet du type de plantation (monoclonal ou polyclonal) sur la diversité du sous-bois pourrait varier selon ces gradients environnementaux. Cependant, il reste à déterminer si la biodiversité du sous-bois est systématiquement supérieure dans les plantations polyclonales par rapport aux plantations monoclonales le long d'un gradient latitudinal.

Naturalité des plantations par rapport aux forêts indigènes. Les forêts indigènes abritent généralement plus d'espèces de sous-bois que les plantations, car elles ont une structure complexe, une plus grande variété de substrats et une plus grande diversité de micro-habitats que les plantations (Cole *et al.*, 2008; Fritz *et al.*, 2008; Fritz & Heilmann-Clausen, 2010). Toutefois, certaines études antérieures ont suggéré que les plantations avaient le potentiel d'améliorer la biodiversité forestière dépendamment de leur structure et du type de canopée (Gachet *et al.*, 2007; Bremer & Farley, 2010). Cependant, la plupart des études sur la biodiversité dans les plantations comparent la végétation de sous-bois des plantations à celle des forêts indigènes anciennes (Lindenmayer & McCarthy, 2002; Bauhus *et al.*, 2009). Cette comparaison désavantage généralement les plantations, car les forêts indigènes anciennes sont à un stade de succession plus avancé et ont une structure plus hétérogène et des habitats plus divers que ceux des plantations (Stephens & Wagner, 2007; Paquette & Messier, 2010; Soto & Puettmann, 2020). Ainsi, elles abritent une plus grande variété d'espèces forestières que les plantations (Stephens & Wagner, 2007; Lonsdale *et al.*, 2008; Kremer *et al.*, 2022; Lemessa *et al.*, 2022). Il serait donc plus approprié d'évaluer les effets des plantations sur la biodiversité de la végétation de sous-bois en les comparant à des forêts indigènes présentant une structure et un type de canopée similaires à celles de plantations afin d'isoler et évaluer l'effet du type de gestion forestière (c'est-à-dire plantations intensivement aménagées *vs* forêts extensivement aménagées) sur la végétation de sous-bois (Royer-Tardif *et al.*, 2017).

L'origine des espèces (exotique ou indigène) dans les plantations peut influencer la biodiversité de la végétation de sous-bois (Barbier *et al.*, 2008; Brockerhoff *et al.*, 2008; Gustafsson *et al.*, 2023). Les plantations d'espèces exotiques qui sont issues d'une ou plusieurs espèces non indigènes sont souvent privilégiées pour leur croissance rapide et leur rendement élevé en bois (Elfving *et al.*, 2001; Messier *et al.*, 2022). Cependant, il est souvent recommandé de privilégier les plantations d'espèces indigènes par rapport aux plantations d'espèces exotiques, car elles offrent des habitats pouvant abriter des espèces de sous-bois indigènes et plus diversifiées (Stephens & Wagner, 2007; Bremer & Farley, 2010; Barrette *et al.*, 2014). En outre, les plantations d'espèces exotiques pourraient favoriser l'implantation d'espèces exotiques de sous-bois et sont souvent perçues comme des habitats artificiels contrastant avec les plantations d'espèces indigènes (Simberloff & Von Holle, 1999; Bremer & Farley, 2010; Barrette *et al.*, 2014). Cependant, l'impact de l'introduction d'espèces exotiques sur la biodiversité peut être positif, négatif ou neutre en fonction de l'espèce, du biome, du groupe taxonomique des espèces de sous-bois et de la région (Quine & Humphrey, 2010; Castro-Diez *et al.*, 2019). À titre d'exemple, une méta-analyse a montré une diminution constante de la richesse en espèces du sous-bois lorsque les forêts secondaires étaient converties en plantations d'espèces exotiques à croissance rapide, car la structure de l'habitat des plantations indigènes était relativement similaire à celle des forêts indigènes que celle des plantations d'espèces exotiques (Bremer & Farley, 2010). En revanche, Royer-Tardif *et al.* (2017) ont montré que les plantations de peupliers hybrides exotiques établies dans un paysage forestier abritaient des communautés végétales de sous-bois aussi diverses que celles des forêts secondaires naturellement régénérées et des plantations d'espèces indigènes dans une région du centre du Québec. Cette similarité s'expliquait par les traits fonctionnels partagés entre les clones de peupliers hybrides exotiques et les espèces indigènes, car un des parents des hybrides était originaire du Québec. L'absence de consensus concernant les effets des plantations d'espèces indigènes et exotiques sur la biodiversité de la végétation de sous-bois soulève donc la question de savoir si les plantations utilisant des espèces indigènes favorisent une biodiversité plus proche de celle des forêts indigènes, comparativement à l'utilisation d'espèces exotiques.

Les peupliers hybrides. Il existe plusieurs espèces de peupliers réparties à travers le monde, et ces dernières peuvent se croiser naturellement ou de manière contrôlée pour former des hybrides (Stettler *et al.*, 1996). Ces croisements interspécifiques conduisent souvent à la production d'hybrides ayant une meilleure croissance que leurs parents (Sinha & Khanna, 1975). Ce phénomène est désigné sous le terme de 'vigueur hybride' et il est mis à profit en sylviculture afin de maximiser la productivité des plantations.

La production de descendants hybrides débute par une phase de croisement, qui associe deux espèces parentales, suivi d'un cycle continu de sélection, qui consiste à choisir les arbres présentant des traits d'intérêts tels que la productivité, la plasticité et la résistance aux ravageurs (Riemenschneider *et al.*, 2001; Dillen *et al.*, 2010). La dernière phase est celle des tests, qui consiste à comparer les descendants des arbres présélectionnés (Riemenschneider *et al.*, 2001). Les hybrides performants peuvent ensuite être clonés, multipliés et cultivés à grande échelle à l'aide de boutures de tiges ou de racines (Riemenschneider *et al.*, 2001; Corona *et al.*, 2024). Au Québec, cinq espèces sont utilisées dans le programme d'amélioration génétique des peupliers dont trois sont indigènes : le peuplier baumier (*Populus balsamifera*), le peuplier deltoïde (*Populus deltoides*) et le peuplier de l'Ouest (*Populus trichocarpa*), et deux sont exotiques : le peuplier noir (*Populus nigra*) et le peuplier du Japon (*Populus maximowiczii)* (Richardson *et al.*, 2007; Truax *et al.*, 2014).

Type de canopée: les réponses de la végétation de sous-bois. Les communautés de sous-bois ont des exigences environnementales spécifiques et certaines de ces conditions sont influencées par la composition de la canopée (Nadrowski *et al.*, 2010; Bartels *et al.*, 2018; Barbé *et al.*, 2020). Par exemple, les forêts de feuillus ont une litière riche en nutriments, une décomposition rapide de la matière organique, une plus grande disponibilité de la lumière et une température du sol plus élevée que les forêts de conifères (Laganière *et al.*, 2010; Cavard *et al.*, 2011a; Augusto *et al.*, 2015). Ces conditions favorisent l'établissement des plantes vasculaires, mais limitent généralement l'établissement des bryophytes (Hart & Chen, 2008; Jean *et al.*, 2017). La litière d'aiguilles dans les forêts de conifères contient moins de nutriments et se décompose plus lentement que la litière de feuillus (Laganière *et al.*, 2010; Chomel *et al.*, 2015). Elle a aussi tendance à acidifier le sol et la présence d'une litière d'aiguilles favorise le maintien d'une humidité élevée et d'une température plus basse au niveau du sol (Laganière *et al.*, 2010). Ces conditions sont favorables à l'établissement des bryophytes (Hart & Chen, 2008; Cavard *et al.*, 2011a; Jean *et al.*, 2017). Les forêts de conifères aussi favorisent généralement l'établissement des lichens au sol (Bergeron & Fenton, 2012). Dans les forêts de feuillus, la litière de feuilles et la présence de plantes vasculaires au sol peuvent inhiber l'établissement des lichens (Gilbert, 1993; Bartels & Chen, 2015). En revanche, le tronc des arbres feuillus est favorable à l'établissement des lichens épiphytes. En effet, l'écorce des feuillus tend à être plus rugueuse, plus riche en nutriments et moins acide que celle des conifères, facilitant le développement des lichens épiphytes (Jüriado *et al.*, 2003; Bartels & Chen, 2015; Hämäläinen *et al.*, 2023). Par exemple, les espèces de *Populus* ont une écorce riche en nutriments et peu acide, capable d'abriter une grande diversité de lichens épiphytes (Sheard & Jonescu, 1974; Boudreault *et al.*, 2000; Bartels & Chen, 2015).

Relations entre la diversité spécifique de la canopée et la biodiversité de la végétation de sous-bois. La diversité spécifique et/ou structurelle de la canopée peut influencer la biodiversité de la végétation de sous-bois (Jonsson *et al.*, 2019; Kutnar *et al.*, 2023). Comparées aux forêts monospécifiques, il est généralement admis que les forêts plurispécifiques ou mixtes pouvaient créer un habitat hétérogène et affecter positivement l'environnement biotique et abiotique par une utilisation optimale des nutriments (Jucker *et al.*, 2015; Barsoum *et al.*, 2016; Schmid & Niklaus, 2017), et par ce fait, augmenter la biodiversité de la végétation de sous-bois (Barbier *et al.*, 2008; Nadrowski *et al.*, 2010; Messier *et al.*, 2022). Néanmoins, les effets positifs des forêts mixtes comparées aux monocultures sur la biodiversité de la végétation de sous-bois peuvent dépendre de l'identité et du trait (par exemple, le genre, la tolérance à l'ombre et la phénologie des feuilles) des espèces d'arbres qui composent la canopée (Balvanera *et al.*, 2006; Nadrowski *et al.*, 2010; Messier *et al.*, 2022). En revanche, les canopées mixtes qui combinent des espèces d'arbres ayant les mêmes traits ou le même genre peuvent avoir des besoins en ressources qui se chevauchent et favoriser la concurrence entre les espèces, limitant l'établissement de communautés de sous-bois diversifiées (Cavard *et al.*, 2011b; Jucker *et al.*, 2015; Huang *et al.*, 2018).

Effets de l'intensité de gestion forestière sur la biodiversité de la végétation de sous-bois. Selon le type et l'intensité, l'aménagement forestier peut avoir des effets contrastés sur la végétation de sous-bois. La sylviculture intensive permet de fournir rapidement du bois sur une courte période (Jürgensen *et al.*, 2014). Cependant, l'établissement des plantations intensivement aménagées nécessite une préparation du sol et une utilisation d'herbicides qui peuvent perturber la végétation existante et éliminer les propagules pouvant limiter la régénération des espèces de sous-bois (Battles *et al.*, 2001; Bock & Van Rees, 2002; Newmaster *et al.*, 2007). Il est important de noter qu'au Québec, contrairement à d'autres régions où les herbicides sont couramment utilisés pour contrôler la végétation concurrente, cette pratique n'est pas adoptée, ce qui peut influencer différemment la dynamique de régénération et de compétition dans les plantations.

Les plantations intensivement aménagées créent généralement des conditions telles que l'ouverture de la canopée et l'augmentation de la disponibilité lumineuse qui favorisent l'établissement d'espèces compétitives, rudérales et exigeantes en lumière (Porté *et al.*, 2004; Wei *et al.*, 2019). En revanche, les forêts extensivement aménagées ont peu ou pas de perturbation de sol et offrent des habitats hétérogènes pouvant abriter un large éventail d'espèces de sous-bois (Cole *et al.*, 2008; Fritz *et al.*, 2008; Paillet *et al.*, 2010), typiques d'environnements forestiers (Holl & Aide, 2011; Aubin *et al.*, 2014; Kremer *et al.*, 2021).

Effets de l'historique d'utilisation des terres sur la végétation de sous-bois. La présence des communautés de sous-bois est influencée par la quantité de propagules viables présentes avant l'établissement d'une forêt ou d'une plantation (Newmaster *et al.*, 2007). Par exemple, le recrutement d'espèces forestières dans les sites forestiers est lié à la présence de banques de graines provenant du milieu forestier (Caners *et al.*, 2009). En revanche, la végétation de sous-bois dans les plantations établies sur d'anciennes terres agricoles reflétait l'environnement agricole avant la plantation et était principalement composée d'espèces typiques des milieux ouverts (Bellemare *et al.*, 2002; Ramovs & Roberts, 2005). L'historique d'utilisation des terres des sites et les espèces préexistantes peuvent donc influencer la biodiversité de la végétation de sous-bois (Ross-Davis & Frego, 2002; Soo *et al.*, 2009; Gibson *et al.*, 2011; Mayfield *et al.*, 2013).

Approche par traits fonctionnels sur la végétation de sous-bois. Les traits fonctionnels sont essentiels pour comprendre les réponses des plantes de sous-bois au type et à la composition de la canopée. Ils représentent les caractéristiques morphologiques, physiologiques et phénologiques qui permettent aux plantes d'acquérir les ressources nécessaires à leur survie et à leur croissance (Wright *et al.*, 2004; Violle *et al.*, 2007; Posada *et al.*, 2009). Une approche par traits fonctionnels fournit donc des informations sur la manière dont les plantes réagissent à leur environnement (Lavorel & Garnier, 2002; Naeem *et al.*, 2012; Díaz *et al.*, 2016). Par exemple, les canopées monospécifiques peuvent conduire à des environnements limités en ressources en raison d'une compétition plus intense entre les arbres. Cela peut favoriser l'établissement d'espèces qui ont tendance à investir dans des traits conservateurs tels qu'une croissance lente, une longue durée de vie, une tolérance à l'ombre, une teneur élevée en matière sèche des feuilles et une faible surface foliaire (Muller, 2003; Pérez-Ramos *et al.*, 2012; Reich, 2014). À l'inverse, les canopées mixtes peuvent créer un environnement plus riche en ressources favorisant des espèces présentant des traits acquisitifs tels qu'un taux de croissance élevé, une durée de vie courte, une intolérance à l'ombre, une production abondante de graines et une surface foliaire spécifique élevée qui facilitent une croissance rapide (Poorter & Evans, 1998; Wright *et al.*, 2017).

Une approche taxonomique seule peut s'avérer insuffisante pour évaluer les différences de diversité des plantes vasculaires entre les plantations polyclonales et monoclonales de peupliers hybrides. En effet, ces deux types de plantations utilisent des espèces feuillues qui sont connues pour créer des conditions favorables à l'établissement des plantes vasculaires (Barbier *et al.*, 2008; Augusto *et al.*, 2015). Par ailleurs, la plupart des études sur l'impact des monocultures sur la biodiversité de la végétation de sous-bois par rapport à celui des plantations mixtes se sont concentrées uniquement sur la diversité taxonomique montrant un manque de tendances cohérentes (Augusto *et al.*, 2003; Gamfeldt *et al.*, 2013). Une approche fonctionnelle, axée sur les traits fonctionnels des plantes, serait donc plus pertinente pour comprendre les relations entre la composition de la canopée et la biodiversité de la végétation de sous-bois (Lavorel & Garnier, 2002; Hooper *et al.*, 2005b; Violle *et al.*, 2007).

Objectifs et hypothèses. L'objectif général de cette thèse était d'évaluer comment la biodiversité de la végétation de sous-bois (y compris les plantes vasculaires, les bryophytes et les lichens) était influencée par la composition et la complexité de la canopée. Elle visait également à évaluer si la biodiversité de la végétation de sous-bois dans des plantations intensivement aménagées (plantations) était similaire à celle des forêts extensivement aménagées (forêts de référence).

Le Chapitre 1 avait pour objectif d'évaluer si la diversité et la composition de la végétation de sous-bois dans les plantations mixtes d'espèces de peupliers hybrides et d'épinettes (*Picea* spp.) sont plus élevées et variées par rapport aux monocultures. Nous avons supposé que la diversité spécifique de la végétation de sous-bois serait plus élevée dans les plantations mixtes par rapport aux monocultures en raison de la plus grande variété de micro-habitats qu'elles offrent (Hartley, 2002; Jonsson *et al.*, 2019; Feng *et al.*, 2022). Nous nous attendions à ce que les plantes vasculaires seraient plus présentes dans les monocultures de peupliers hybrides que dans les monocultures d'épinettes parce que la canopée des feuillus laisse passer davantage de lumière et produit une litière riche en nutriments, favorable à l'établissement des plantes vasculaires (Barbier *et al.*, 2008; Augusto *et al.*, 2015). À l'inverse, nous avons supposé que les bryophytes seraient plus présentes dans les monocultures d'épinettes que dans les monocultures de peupliers hybrides parce que la canopée de conifères offre moins de lumière au sous-bois et produit une litière pauvre en nutriments et acidifiante, propice à l'établissement des bryophytes (Laganière *et al.*, 2010). Finalement, nous avons émis l'hypothèse que les plantations mixtes auraient la combinaison des micro-habitats présents dans les monocultures de peupliers hybrides et d'épinette conduisant à une composition intermédiaire entre celles-ci (Hart & Chen, 2008).

Le Chapitre 2 visait à évaluer si la biodiversité de la végétation de sous-bois et les traits fonctionnels des plantes vasculaires de sous-bois sont plus élevés et variés dans les plantations polyclonales que dans les plantations monoclonales, établies le long d'un gradient latitudinal. Nous avons émis l'hypothèse que les plantations polyclonales augmenteraient la diversité taxonomique et fonctionnelle de la végétation de sous-bois par rapport aux plantations monoclonales parce que les différences de traits des clones peuvent augmenter la disponibilité des ressources et créer différents micro-habitats, favorisant la diversité de la végétation de sous-bois (Kunstler *et al.*, 2012; Valencia *et al.*, 2015; Feng *et al.*, 2022). Nous nous attendions à ce que la composition de la végétation de sous-bois et les traits fonctionnels des plantations polyclonales seraient plus diversifiés que ceux des plantations monoclonales parce que le mélange de clones offre des habitats hétérogènes (Elferjani *et al.*, 2014) favorisant la coexistence d'une plus grande diversité d'espèces. Enfin, nous avons émis l'hypothèse que l'effet du type de plantation sur la biodiversité de la végétation de sous-bois varierait le long d'un gradient latitudinal, en raison des variations climatiques et environnementales liées à la latitude qui influencent sur les conditions de croissance et la disponibilité des ressources telles que la lumière, la température et l'humidité (Wright *et al.*, 2004; Colwell *et al.*, 2008). Ces variations pourraient ainsi modifier les réponses de la végétation de sous-bois aux types de plantations.

Le Chapitre 3 a évalué si la diversité et la composition de la végétation de sous-bois sont similaires dans les plantations intensivement aménagées (plantations) et les forêts extensivement aménagées (forêts de référence). Il visait également à évaluer si l'identité des espèces liée à leur origine (c'est-à-dire espèce exotique *vs* indigène) dans les plantations influence la similitude de la biodiversité de la végétation de sous-bois entre les plantations et les forêts de référence. Les forêts de référence offrent des attributs structurels et des micro-habitats plus complexes que les plantations (Ehbrecht *et al.*, 2017; Ehbrecht *et al.*, 2021). Ainsi, nous nous attendions à ce que les forêts de référence aient une plus grande diversité de végétation de sous-bois et une composition distincte par rapport aux plantations. Nous avons également prédit que les espèces rudérales seraient plus fréquentes dans les plantations, tandis que les espèces forestières seraient associées aux forêts de référence parce que ces dernières sont moins perturbées que les plantations, ce qui pourrait être favorable à la repousse des espèces forestières à partir des rhizomes ou des banques de graines présentes dans les forêts préexistantes (Holl & Aide, 2011). A l'inverse, les plantations sont soumises à la préparation du sol, ont une canopée ouverte et une grande disponibilité en lumière, créant des conditions favorables à l'établissement d'espèces rudérales (Klinka *et al.*, 1996; Puettmann & Berger, 2006; Kremer *et al.*, 2022). Enfin, nous avons émis l'hypothèse que la présence d'espèces indigènes dans les plantations contribuerait à la similitude de la biodiversité de la végétation de sous-bois entre les plantations et les forêts de référence, car les plantations d'espèces indigènes offrent un habitat relativement plus proche de celui des forêts indigènes que de celui des plantations d'espèces exotiques (Bremer & Farley, 2010; Barrette *et al.*, 2014).

Méthodologie générale. ***Zones d'étude et sélection des espèces.*** Pour vérifier si la biodiversité de la végétation de sous-bois est plus élevée dans les plantations mixtes que dans les monocultures, nous avons sélectionné des plantations localisées à Amos (48°36'N, 78°04'W), Rivière-Héva (48°1'N, 78°16'W) et Nédelec (47°45'N, 79°22'W) (Abitibi-Témiscamingue, QC, Canada). Les plantations comprenaient deux clones de peuplier hybride (*Populus trichocarpa* Torrey & A. Gray × *balsamifera* L. et *P. maximowiczii* Henry × *balsamifera* L.) ainsi que deux espèces d'épinette, l'épinette de Norvège (*Picea abies* (L.) Karst) et l'épinette blanche (*Picea glauca* (Moench)), plantées en monocultures et en plantations mixtes.

Pour évaluer si les plantations polyclonales améliorent la biodiversité de la végétation de sous-bois par rapport aux plantations monoclonales, nous avons sélectionné quatre clones de peuplier hybride en plantations monoclonales et polyclonales. Un bloc monoclonal contenait une parcelle de chaque clone, tandis qu'un bloc polyclonal contenait une parcelle combinant les quatre clones. Les plantations étaient établies le long d'un gradient latitudinal sur trois sites d'étude situés dans les régions du Nord-du-Québec et de l'Abitibi-Témiscamingue afin de déterminer si l'effet du mélange clonal sur la biodiversité de la végétation de sous-bois varie selon un gradient latitudinal. Le premier site se trouvait près de la municipalité de Villebois (49°09'N, 79°10'O), le deuxième près de la municipalité de Duparquet (48°29'N, 79°26'O) et le troisième dans la municipalité de Duhamel (47°19'N, 79°25'O).

Pour vérifier si les plantations ont une biodiversité de la végétation de sous-bois similaire à celle des forêts de référence, nous avons sélectionné les mêmes plantations que dans le premier Chapitre ainsi que des forêts de référence dont le type de canopée (conifère, feuillu et mixte) et la structure (DHP et hauteur) étaient similaires à celles des plantations. Les forêts de référence étaient réparties dans la région de l'Abitibi-Témiscamingue et étaient composées de peuplements de peuplier faux-tremble, de forêts d'épinette blanche, et de forêts mixtes d'épinettes blanches et de peupliers faux-trembles, représentant respectivement les forêts de référence de feuillus, de conifères et mixtes. Pour évaluer si l'identité des espèces influence la biodiversité de la végétation de sous-bois, nous avons sélectionné des plantations composées d'espèces du même genre, mais d'origines différentes (épinette blanche indigène, épinette de Norvège exotique, clones de peupliers hybrides issus d'espèces indigènes et clones de peupliers hybrides issus d'espèces exotiques).

Inventaire de la végétation de sous-bois. Nous avons inventorié la végétation de sous-bois incluant les plantes vasculaires, les bryophytes et les lichens sur le sol, la base et le tronc des arbres dans les trois chapitres. Les bryophytes et les lichens récoltés ont été identifiés au laboratoire. Afin d'évaluer l'effet des clones sur les traits fonctionnels de la végétation de sous-bois, nous avons mesuré les traits foliaires (SLA, LNC et LDMC) des plantes vasculaires dans les plantations monoclonales et polyclonales. Nous avons également sélectionné des traits impliqués dans la dispersion, la colonisation, la persistance et la compétition à partir des bases de données Traits Of Plants In Canada (TOPIC) et Plant Trait Database (TRY) afin de déterminer les réponses des traits fonctionnels des plantes vasculaires au type de plantation le long du gradient latitudinal.

1. HOW DOES UNDERSTORY VEGETATION DIVERSITY AND COMPOSITION DIFFER BETWEEN MONOCULTURES AND MIXED PLANTATIONS OF HYBRID POPLAR AND SPRUCE?

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1.1 Résumé

Bien que les monocultures soient importantes pour la production de bois, elles sont souvent associées à une diversité biologique plus faible que les plantations mixtes. Ainsi, les plantations mixtes ont été proposées comme un moyen d'améliorer la biodiversité grâce à leur diversité compositionnelle et structurelle. Cependant, les effets des monocultures par rapport aux plantations mixtes sur la diversité et la composition de la végétation de sous-bois peuvent varier d'un écosystème à l'autre. L'objectif de cette étude était d'évaluer l'influence des monocultures et des plantations mixtes sur la diversité et la composition de la végétation de sous-bois dans la région de la forêt boréale du sud du Québec. Nous avons échantillonné des plantations établies avec des feuillus *Populus trichocarpa* Torrey & A. Gray x *balsamifera* L. et *P. maximowiczii* Henry x *balsamifera* L., ainsi que des conifères *Picea abies* (L.) Karst. et *Picea glauca* (Moench) plantés en monocultures et en plantations mixtes sur des terres agricoles abandonnées et sur un site forestier. Nous avons évalué la diversité et la composition de la végétation sous-bois dans chaque type de canopée (conifère, feuillu, mixte) et dans chaque type de plantation. Nous avons également évalué la diversité et la composition des bryophytes et des lichens dans trois microhabitats: le sol, la base et le tronc d'arbres. Nos résultats indiquent que la richesse en plantes vasculaires et en lichens était similaire dans tous les types de plantation, tandis que la richesse en espèces de bryophytes était plus élevée dans les monocultures d'épinettes et les plantations mixtes que dans les monocultures de peupliers. Nos résultats mettent également en évidence l'effet de l'historique d'utilisation des terres sur la composition des plantes vasculaires: les terres agricoles abandonnées étaient composées de plantes vasculaires rudérales, tandis que le site anciennement forestier abritait des espèces présentes dans les forêts naturelles. Dans un contexte de reboisement et de plantation, notre étude suggère de mélanger l'épinette au peuplier pour maximiser la diversité de la végétation sous-bois, car la présence d'épinette dans les plantations de peuplier a favorisé l'établissement de bryophytes terricoles, tandis que la présence de peupliers favorisait l'établissement de lichens épiphytes.

Mots-clés : plantation, végétation de sous-bois, diversité, composition

1.2 Abstract

Although monocultures are important for timber production, they are often associated with lower biological diversity than mixtures. Thus, mixed plantations have been suggested as a way to enhance biodiversity because of their inherent compositional diversity. However, the effects of monocultures versus mixtures on understory diversity and composition can vary in different ecosystems. The objective of this study was to assess how monocultures and mixed plantations influence understory vegetation diversity and composition in the boreal forest region of southern Quebec. We sampled plantations established with deciduous *Populus trichocarpa* Torrey & A. Gray x *balsamifera* L. and *P. maximowiczii* Henry x *balsamifera* L. and coniferous *Picea abies* (L.) Karst. and *Picea glauca* (Moench) species planted in monocultures and in mixed plantations on abandoned farmlands and a previously forested site. We assessed understory vegetation diversity and composition in each canopy type (coniferous, deciduous, mixed) and in each plantation type. We evaluated bryophyte and lichen diversity and composition specifically in three microhabitats: soil, tree bases, and tree trunks. We found that vascular plant and lichen species richness was similar in all plantation types, while bryophyte species richness was higher in spruce monocultures and in mixed plantations compared to poplar monocultures. Our results also highlight how land-use history influenced vascular plant composition as abandoned farmland sites were composed of more ruderal vascular plants, while the previously forested site was composed of species found in natural forests. In the context of reforestation and plantations, our study suggests mixing spruce with poplars to maximize understory vegetation diversity as the presence of spruce in poplar plantations promoted the establishment of terrestrial bryophytes, while poplars favored the establishment of epiphytic lichens.

Keywords: plantation, understory vegetation, diversity, composition

1.3 Introduction

Understory vegetation communities including vascular plants, bryophytes, and lichens contribute to ecological services in forests, such as carbon sequestration, nutrient cycling, and organic matter decomposition (Nilsson & Wardle, 2005; Fenton & Bergeron, 2006; Grau-Andres *et al.*, 2022). Establishment of these species in a forest or plantation depends on environmental conditions and microhabitat availability. Environmental conditions are modified by factors such as soil nutrient availability, pH, and light availability (Anderson *et al.*, 1969; Porté *et al.*, 2004; Reich *et al.*, 2012; Augusto *et al.*, 2015), which are influenced by the overstory composition (Loreau, 2000; Gamfeldt *et al.*, 2013; Wang *et al.*, 2021; Stefańska-Krzaczek *et al.*, 2022). For example, deciduous forests usually have a nutrient-rich broadleaf litter, greater light availability, and warmer soils than coniferous forests (Barbier *et al.*, 2008; Augusto *et al.*, 2015). Greater light availability and warmer soils found under deciduous trees can stimulate organic matter decomposition (Laganière *et al.*, 2010). These conditions are favorable for the establishment of vascular plants (Saetre *et al.*, 1997; Barbier *et al.*, 2008; Hart & Chen, 2008), while bryophyte establishment is constrained by the fall of broadleaf litter (Jean *et al.*, 2017; Bartels *et al.*, 2018). Unlike deciduous forests, coniferous forests have nutrient-poor needleleaf litter that can acidify the soil and have lower light availability and soil temperature (Vance & Chapin, 2001; Laganière *et al.*, 2010) that can further limit organic matter decomposition rates which accumulates and increases soil insulation and limit moisture evaporation (Millar, 1974; Facelli & Pickett, 1991). These conditions are more favorable to bryophyte establishment (Saetre *et al.*, 1997; Fenton *et al.*, 2005; Hart & Chen, 2008) than that of vascular plants. The occurrence of lichen species depends on light availability and on the physical and chemical properties of the bark of trees (Jüriado *et al.*, 2009; Randlane *et al.*, 2017). In addition to environmental conditions, forest bryophytes and lichens establishment also depends on the availability of different types of microhabitats (Cole *et al.*, 2008; Rubio-Salcedo *et al.*, 2015), such as soil, deadwood, or trees (During, 1992; Haughian, 2018; Barbé *et al.*, 2020). Some species are associated with microhabitats created by coniferous forests, while others are associated with those of deciduous forests (Caners *et al.*, 2013; Barbé *et al.*, 2020). Thus, the distinct environmental conditions and microhabitats created by different tree species composing the overstory are key to understanding the biodiversity patterns of understory vegetation diversity and composition in forests.

Because the overstory composition acts as a filter for understory vegetation communities (Kutnar *et al.*, 2023), intensively managed forest plantations of a single tree species (monocultures) provide little to no variability in understory microclimate or microhabitats, and therefore do not allow the establishment of diverse understory communities, making them 'biological deserts' (Brockerhoff *et al.*, 2008). Monoculture plantations have lower levels of biodiversity than native forests (Bremer & Farley, 2010; Brockerhoff *et al.*, 2013). Generally, forest plantations are dominated by a single tree species, and they are managed as even-aged monocultures with an equal spacing between trees (Puettmann *et al.*, 2015; Liu *et al.*, 2018). This management practice results in structurally simplified stands that fail to provide suitable habitats for forest species (Bauhus *et al.*, 2010; Liu *et al.*, 2018; Messier *et al.*, 2022). Consequently, intensively managed forest plantations are perceived as a threat to biodiversity because their use is predicted to grow 37% by 2050 (FAO, 2022).

In contrast, mixed plantations have been shown to enhance levels of biodiversity compared to monoculture plantations (Hartley, 2002; Nichols *et al.*, 2006; Jonsson *et al.*, 2019) due to their compositional and structural diversity (Saetre *et al.*, 1997; Messier *et al.*, 2022). A higher diversity of tree species provides more heterogeneous habitats (Carnus *et al.*, 2006; Brockerhoff *et al.*, 2008), which in turn can support a larger number of associated species (Thompson *et al.*, 2009; Nadrowski *et al.*, 2010; Feng *et al.*, 2022) such as the understory vegetation (Ampoorter *et al.*, 2020; Guo *et al.*, 2021; Messier *et al.*, 2022). Tree species differ in their growth patterns, canopy structures, litter quality and bark characteristics. This diversity results in the formation of various microhabitats within the forest, including different levels of shade, moisture and nutrient availability (Tews *et al.*, 2004; Puettmann, 2011). Consequently, mixed plantations can provide diverse microhabitats and appropriate abiotic conditions leading to the presence and coexistence of a greater number of species (Thompson *et al.*, 2009).

However, for both mixed forests and mixed plantations, there is conflicting evidence on their benefits to understory vegetation diversity compared to monospecific forests. Some authors found that mixed forests had a similar understory vegetation diversity as monospecific forests (Augusto *et al.*, 2003; Barsoum *et al.*, 2016), while others reported that they had higher understory diversity than monospecific forests (Gamfeldt *et al.*, 2013; Wang *et al.*, 2021). Other studies reported that mixed forest understories were compositionally intermediate between deciduous and coniferous stands (Hart & Chen, 2008). This lack of evidence is related to the difficulty in disentangling overstory composition from confounding factors such as age, canopy openness, soil, or topography (Pitkänen, 2000; Gärtner & Reif, 2004; Nadrowski *et al.*, 2010). Furthermore, studies on understory vegetation biodiversity in plantations did not consider the complete understory vegetation (vascular plants, bryophytes, and lichens), as they often focused on only one taxonomic group such as vascular plants (Soo *et al.*, 2009), bryophytes (Pharo & Lindenmayer, 2009) or lichens (Hilmo *et al.*, 2009). Despite the well-documented effects of mixed plantations on the understory vegetation diversity (Wang *et al.*, 2021; Messier *et al.*, 2022), the effects of tree species identity and combinations on the overall forest species diversity and composition are not fully understood, specifically, in the boreal forest region of southern Quebec where mixed plantations are less developed than monoculture plantations.

It is widely recognized that microhabitat availability has an important influence over bryophyte and lichen establishment (Cole *et al.*, 2008; Király & Ódor, 2010; Haughian, 2018). Microhabitats offer a stable substrate that can provide variations in temperature and moisture levels for bryophytes and lichens. The various species composing mixed plantations could provide heterogenous microhabitats (e.g., soils, tree bases, and tree trunks) that may enhance the diversity of bryophyte and lichen specific to each overstory tree species. However, it remains unclear whether the diversity and composition of bryophytes and lichens across various microhabitats are greater and more varied in mixed plantations compared to monocultures within the boreal forest region of southern Quebec. Thus, a better understanding of how tree composition affects understory vegetation diversity and composition related to the microhabitat availability should help guide plantation management to favor plant diversity.

The main objective of this study was to evaluate the understory vegetation (including vascular plants, bryophytes, and lichens) diversity and composition in mixed and monoculture plantations of hybrid poplar (*Populus* spp.) and spruce (*Picea* spp.) species. We also evaluated whether the effect of monocultures or mixed plantations on bryophyte and lichen richness and composition varied among three microhabitats: soil, tree bases and tree trunks. We expected to have more vascular plant and epiphytic lichen species in hybrid poplar and mixed plantations compared to spruce plantations, because mixed plantations provide heterogenous light availability for understory vascular plants and many lichen species are specialized to be epiphytes on deciduous trees only. Conversely, we expected bryophyte diversity to be higher in spruce plantations compared to hybrid poplar and mixed plantations. We expected that the richness of bryophytes, and lichens on soil, tree bases and tree trunks would be greater in mixed plantations compared to monoculture plantations. In terms of composition, we expected that vascular plants would be more dominant in hybrid poplar than in spruce plantations and that bryophytes would be more present in spruce than in hybrid poplar plantations because deciduous forests usually have a nutrient-rich deciduous broadleaf litter, greater light availability, and warmer soils than in coniferous forests which are favorable to the establishment of vascular plants. We expected that lichens would be more dominant in hybrid poplar than in spruce plantations because *Populus* species provide a habitat for a wide range of epiphytic lichens due to their non-acidic bark and nutrient-rich substrate conditions. However, coniferous forests have a low-nutrient needleleaf litter that acidifies the soil and have lower light availability and soil temperature which are more favorable to bryophyte establishment than that of vascular plants. Lastly, we hypothesized that the understory vegetation community in mixed plantations would be compositionally intermediate between spruce and hybrid poplar plantations.

1.4 Materials and Methods

1.4.1 Study sites

Three plantations were established in 2003 near the localities of Amos (48°36’N, 78°04’W), Rivière-Héva (48°1’N, 78°16’W) and Nédelec (47°45’N, 79°22’W) (Abitibi-Témiscamingue, QC, Canada) (Figure 1a). Prior to planting, our study sites had different land-use histories: the Amos and Rivière-Héva sites were abandoned farmland, while the Nédelec site was a forest site previously dominated by trembling aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica* L.) and paper birch (*Betula papyrifera* Marsh.) forests that had been harvested in 2000. The Amos and Rivère-Héva plantations were in a matrix of abandoned farmland, mostly reforested with conifers. The Nédelec plantations were in a forested matrix but surrounded by clearcuts reforested with softwoods and hybrid poplars. The soils of the Amos and Rivière-Héva sites were classified as heavy clay while soils at the Nédelec site had a sandy-loam texture. Based on the 30-year climate average (1981-2010), mean annual precipitation and temperature at the Amos and Rivière-Héva sites were respectively 929 mm and 1.5°C, while, they were 904 mm and 2.2°C at the Nédelec site (Environnement Canada, 2021). We used the same mean annual precipitation and temperature values in the Rivière-Héva site as those in the Amos site because there was no meteorological station specific to Rivière-Héva.

Site preparation at the three sites was carried out in 2002 to remove pre-existing vegetation and tree stumps. At the Amos site, chains and a farm tractor were used to remove shrubs and scattered tree stumps, while a brush shredder was used to remove shrubby vegetation at the Rivière-Héva site. At the Nédelec site, a bulldozer was used to remove the tree stumps and large debris. Soils of the three sites were then plowed to a depth of 30 cm in the fall of 2002 and harrowed in the spring of 2003 to level the soil just before planting rooted hybrid poplar cuttings and spruce seedlings. During the first five years, competitive vegetation was removed annually mechanically by cultivating between trees and rows with a small tractor and discs.

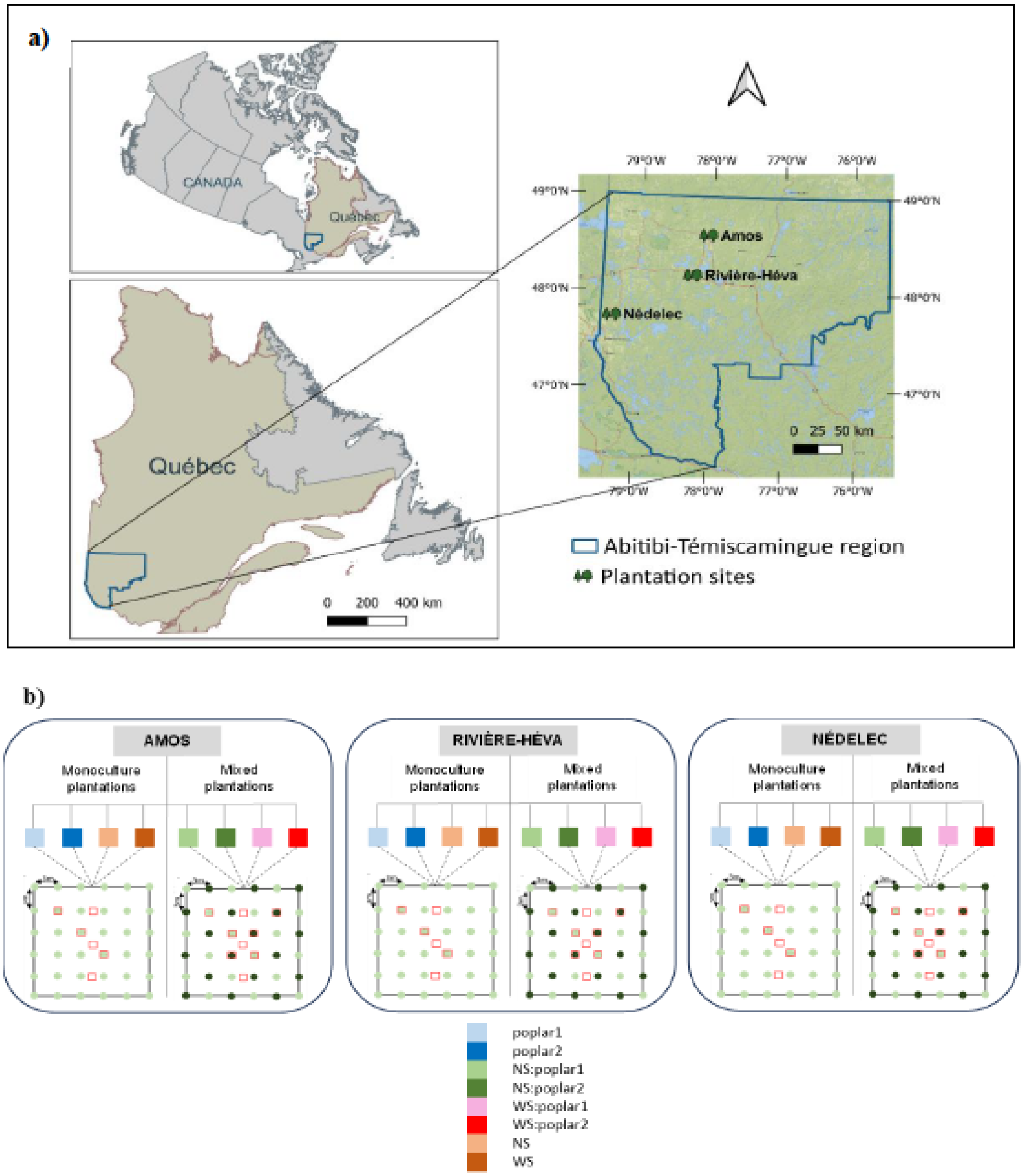

Figure 1
a) Location of the plantation sites within the province of Québec, eastern Canada. Inset the region of Abitibi-Témiscamingue. b) Schematic representation of the experimental design of monoculture and mixed plantations in the three sites (Amos, Rivière-Héva and Nédelec). Each site had eight 15x15m plantation plots (represented by squares of different colors): 4 monocultures and 4 mixed plantations. In each plantation plot, we placed six $1m^2$ quadrats within monoculture or nine within mixed plantations (as red border squares). Trees in monoculture are in light green and in mixed plantations in light and dark greens.

1.4.2 Experimental design

The experiment was designed as a split-plot with the three sites as replicates and plantation type (mixed or monoculture) as a treatment. We selected two hybrid poplar clones: (*Populus trichocarpa* Torrey & A. Gray x *balsamifera* L.) (**poplar1**) and (*P. maximowiczii* Henry x *balsamifera* L.) (**poplar2**) and two spruce families: Norway spruce (*Picea abies* (L.) Karst.) (**NS**) and white spruce (*Picea glauca* (Moench)) (**WS**). Each hybrid poplar clone and spruce species were planted in both monoculture and mixed plantations with a 3x3 m spacing (Figure 1b). Eight plantation types were thus established on each site including four monocultures: poplar1, poplar2, NS, and WS, and four mixed plantations: NS:poplar1, WS:poplar1, NS:poplar2, and WS:poplar2. Each plantation plot measured 15 x 15 m (225 m^2) and contained 36 trees (6 x 6 rows of trees).

1.4.3 Sampling methods

Vegetation surveys. During the spring of 2021, we sampled six or nine 1m^2 quadrats within each treatment (n=6 for monoculture treatment; n=9 for mixed plantation treatment). One plantation type could be adjacent to one or two other types. This condition might act as potential edge effects that our studied plantations could experience. Consequently, we systematically placed three 1m^2 quadrats (no tree boles included) spaced 4.5 m apart in a linear transect established in the center of each plantation type to avoid edge effects (Figure 1b). Within each monoculture plantation, we placed three other 1 m^2 quadrats under trees along a diagonal line. Within mixed plantations, we placed three 1 m^2 quadrats under each species of tree along diagonal lines (total = six). In each quadrat, we inventoried all woody plants less than 1.3 m tall (shrubs and tree seedlings), herbaceous plants (grasses, forbs and ferns), bryophytes and lichens. We expressed the abundance of each vascular plant species as a percent cover per quadrat. We collected bryophytes and lichens in three microhabitats: the soil, the base of trees (0-50 cm) and the trunk of trees (50-150 cm). We did not sample bryophytes and lichens on woody debris or large shrubs as they were absent or minimal in plantations because of the initial mechanical weed control that removed them. We placed all sampled bryophyte and lichen specimens in individual bags and brought to the laboratory for identification under a microscope. We based vascular plant nomenclature on the VASCAN database (Brouillet *et al.*, 2010). We followed Faubert (2012) for bryophyte nomenclature and Brodo *et al.* (2001), Hinds&Hinds (2007) and Brodo (2016) for lichen nomenclature.

Light measurement. Light is one of abiotic variables that depends on the overstory composition and may affect the abundance and presence of understory species (Anderson *et al.*, 1969; Porté *et al.*, 2004). The distinct variability in light created by tree species composing the overstory is likely key to understanding the biodiversity patterns of the understory vegetation.

We measured percent incident light 50 cm above the forest floor using a LAI-2200C plant canopy analyzer (LI-COR Biosciences, Lincoln, NE). We measured incident light in each monoculture above the three quadrats along a diagonal line and above six quadrats in mixed plantations (three under poplar trees and three under spruce trees). We also took reference full light measures in an open field near each treatment. We calculated incident light within the plantations as the ratio of the light measured at 50 cm above the forest floor and the reference light.

1.4.4 Statistical analysis

Taxonomic diversity. We conducted all statistical analyses using R 4.1.0 (2021-05-18) (R Core Team, 2021). We assessed at two scales: first, we focused on the effect of canopy type, i.e., deciduous, mixed, or coniferous to describe general patterns and to better link to the literature. Secondly, to examine the effect of specific clones and species in the plantations, we examined the effect of plantation type.

To evaluate the effect of canopy type (i.e., deciduous, coniferous, and mixed) on species diversity of the understory vegetation, we used Hill numbers which represent a statistically rigorous alternative to other diversity indices as they are expressed in units of effective numbers of species (Chao *et al.*, 2014). We quantified three Hill numbers which were the effective number or number of species (q0), exponential of Shannon or number of frequent species (q1), and Simpson's inverse or number of dominant species (q2) using the «iNEXT» R package (Hsieh *et al.*, 2016). To examine the accumulative and rarefaction of species diversity, we used accumulation curves to represent the cumulative number of species as a function of the number of quadrats sampled. We then compared Hill numbers between canopies using sample-size-based rarefaction and extrapolation (R/E) curves with 95% confidence intervals (Chao *et al.*, 2014). By standardizing samples depending on sample size, integrated curves allow to compare biodiversity data (Chao *et al.*, 2014).

To evaluate the effect of plantation type on species richness, we compared taxonomic diversity between plantation types (i.e., poplar1, poplar2, NS, WS, NS:poplar1, WS:poplar1, NS:poplar2, and WS:poplar2) using GLMMs from the *lme4* package (Bates *et al.*, 2015) for all taxonomic groups combined (i.e., vascular plants, bryophytes, and lichens) and for each taxonomic group separately. The richness referred to the mean richness across all the quadrats sampled in each plantation type (i.e., before the extrapolation curve). We fitted plantation type as a fixed effect for all models while plantation type was nested as a random effect within site which was also a random effect. We checked the estimates of residual deviance and residual degrees of freedom using the function «overdisp_fun» and if it fitted the null hypothesis of equidispersion, we used a Poisson distribution for GLMM; if not, we applied Negative-Binomial distribution to fit over-dispersion. We analyzed all models (except for vascular plant richness) with a negative binomial distribution instead of Poisson distribution because we detected overdispersion. We tested significance of the predictors with a type II Wald chi-square (χ2) tests with the «Anova» function in the *car* package (Fox & Weisberg, 2019). Where categorical explanatory variables had a significant effect, we applied Tukey's multiple comparison tests with the package *emmeans* (Russell, 2022). We considered a *p value* ≤ 0.05 as significant.

We also examined bryophyte and lichen richness in each microhabitat in each plantation type. We expressed richness as the mean number of species found in each microhabitat (soil, base of trees, trunk of trees) within the quadrats of each plantation. We followed the same procedures as in the previous description to analyze the richness by microhabitat.

Community composition. We tested the differences in community composition among plantation types using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations with the «adonis» function from the *vegan* package (Laliberté *et al.*, 2014). We performed a principal coordinates analysis (PCoA) (Borcard *et al.*, 2011) with Jaccard's dissimilarity for all 3 taxonomic groups combined. We then evaluated the composition of each group separately, and we performed a PCoA with Bray–Curtis dissimilarity matrices for vascular plants (abundance data) and a PCoA with Jaccard's dissimilarity for bryophytes and lichens combined (presence/absence data) and as distance measures. We used the PCoA function in the package *vegan 2.6-2* (Laliberté *et al.*, 2014) with the Cailliez correction (Gower & Legendre, 1986) to correct negative eigenvalues. We used the vegan «envfit» function to fit species vectors to ordinations from 999 permutations. We showed the most relevant and influential species in ordination diagrams, and we only represented significant species in all ordinations (envfit, $p \leq 0.05$). We also examined differences in overall community composition between the land-use histories of sites using PERMANOVA to explain our results. We also analyzed the bryophyte and lichen community composition in each microhabitat type per plantation type. We assessed the composition of the bryophyte and lichen communities together because lichens had low occurrence and abundance in our plantations. We followed the same procedures as in the previous description to analyze the composition by microhabitat.

Effect of plantation type on incident light. We used Linear mixed models (LMM) from the package *nlme* (Pinheiro *et al.*, 2021) to test the effect of plantation type on incident light at 50 cm above the forest floor. We took the average of light measurements within each 15 x 15m plantation as the response variable. We verified the independence of residuals, homogeneity of variances, and normality of residuals by diagnostic graphs. We applied log-transformations of incident light to achieve normality. We used the post hoc emmeans method to make pairwise comparisons between plantation types with the package *emmeans* (Russell, 2022).

1.5 Results

1.5.1 Effect of canopy type on species diversity

We identified a total of 115 understory species including 50 vascular plants, 46 bryophytes and 19 lichens. The overall observed species richness, Shannon diversity, and Simpson diversity (i.e., Hill numbers for $q = 0, 1, 2$) for deciduous plantations were, respectively, 61, 36, and 24 (Figure 2). The corresponding observed $q = 0, 1, 2$ were, respectively, 75, 47 and 34 for coniferous plantations and the observed q = 0, 1, 2 were respectively 102, 51 and 34 for mixed plantations (Figure 2).

Sample-size-based rarefaction and extrapolation (R/E) curves showed differences among the canopy types, and deciduous plantations had the lowest diversity (Hill numbers) (Figure 2). Coniferous and mixed plantations were more diverse, and their confidence interval curves overlapped for all Hill numbers (Figure 2) indicating that the number of species (q0), the number of frequent species (q1), and the number of dominant species (q2) were similar between the two canopy types. Although the confidence intervals overlapped, coniferous plantations were more diverse for q2 indicating that they had a higher number of dominant species than mixed plantations (Figure 2).

We did not find low slopes towards the end for q0 in mixed plantations indicating that they could still harbor a higher species richness with an increasing number of quadrats. In contrast, plateaus were reached for coniferous and deciduous plantations in q0. Shannon (q1) and Simpson (q2) diversity curves leveled off for all canopy types.

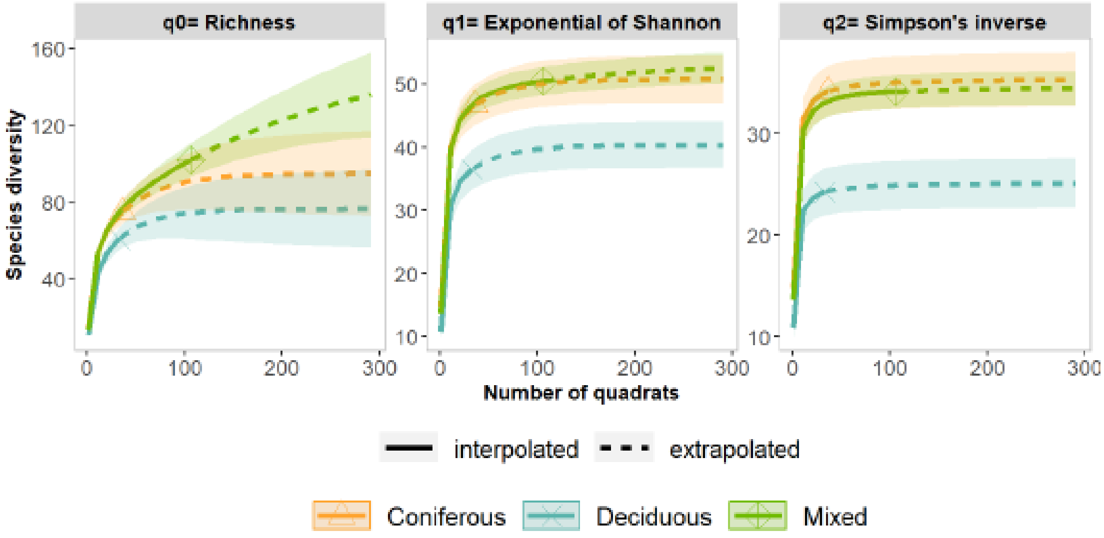

Figure 2
Species diversity (including all 3 taxonomic groups combined: vascular plants, bryophytes, and lichens) for Hill numbers of species (q=0), exponential of Shannon (q=1) and Simpson's inverse (q=2). Solid lines:

interpolation/rarefaction; Dashed curves: Extrapolation. The symbols indicate the observed Hill numbers (q = 0, 1, 2) for each canopy type. Canopy types: coniferous in orange, deciduous in blue and mixed in green.

1.5.2 Effects of plantation type on understory vegetation richness

Mean total species (i.e., all taxonomic groups) richness differed between poplar1 compared to WS:poplar1, WS:poplar2, NS and WS (Figure 3a). The mean total species richness in Poplar1 plantations increased when this clone was mixed with white spruce. Vascular plant species richness did not vary among plantation types (Figure 3b) (ANOVA, $p = 0.22$; see supplementary information Tableau S1). However, bryophyte species richness differed between plantation types (ANOVA, $p < 0.001$; see supplementary information Tableau S1) as it was higher in spruce monocultures (NS and WS) than in hybrid poplar monocultures (poplar1 and poplar2; Figure 3c). All mixed plantations had similar bryophyte species richness as spruce monocultures except for NS:poplar1 which was lower than WS (Figure 3c). There was a difference between NS and WS for bryophytes in mixed plantations, where WS:poplar appeared to be more effective than NS:poplar at harboring bryophyte species. Lichen species richness was similar in all plantation types (Figure 3d) (ANOVA, $p = 0.68$; see supplementary information Tableau S1).

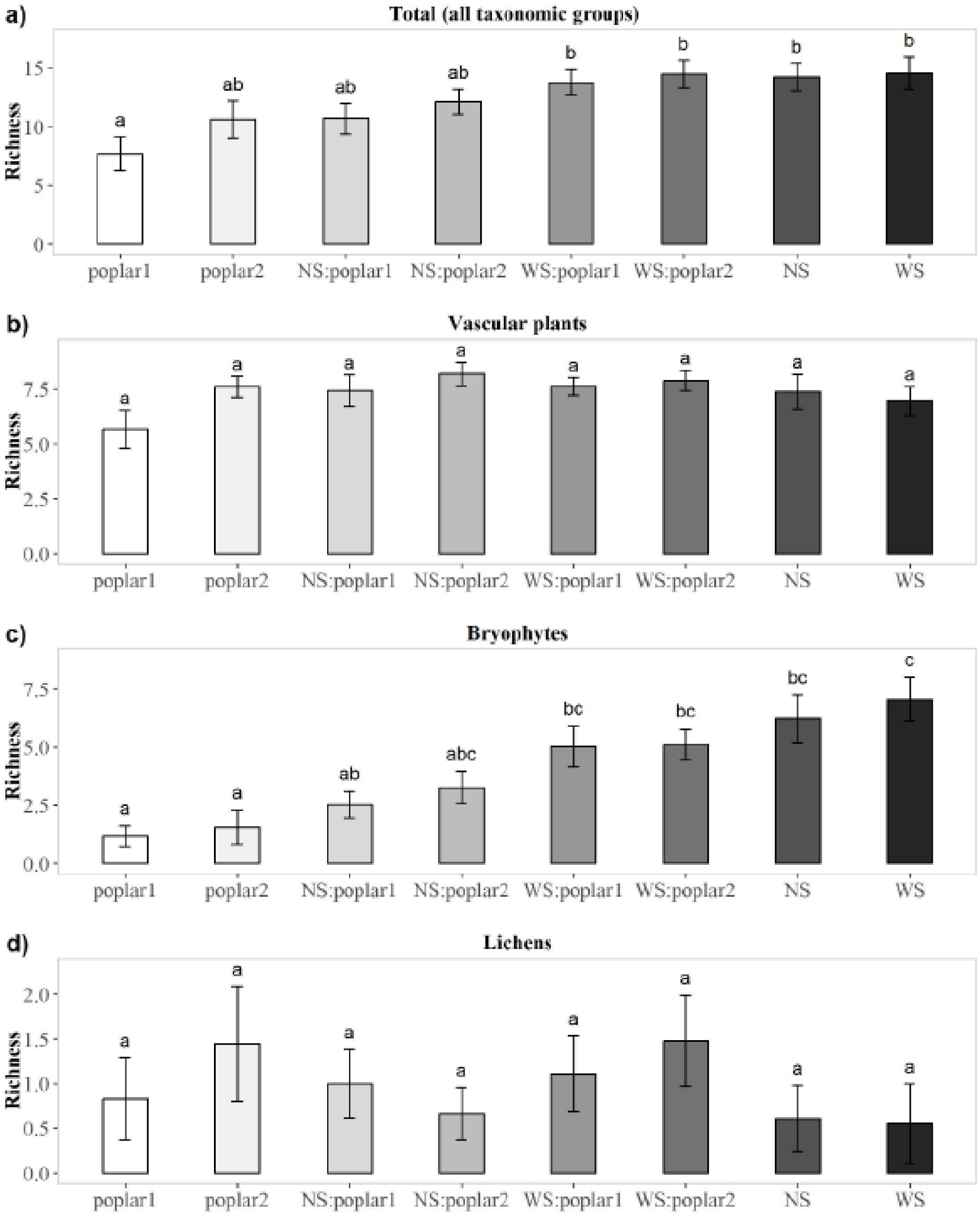

Figure 3
Mean (±SEM) richness of understory vegetation for a) total (all taxonomic groups); b) vascular plants; c) bryophytes; and d) lichens by plantation type. Different letters indicate that mean richness differed significantly between plantation types.

1.5.3 Understory vegetation community composition

The understory community composition varied with plantation type and with land-use history (PERMANOVA; $p = 0.001$; Tableau 1a and Tableau 1b).The PCoA on the total understory vegetation community (all taxonomic groups) and on the vascular plant community showed that there was a gradient from coniferous to deciduous plantations along the second axis (7.39 and 6.24% of variance respectively) with overlapping ellipses (Figure 4a and Figure 4b). Mixed plantations were compositionally intermediate between coniferous and deciduous plantations (Figure 4a and Figure 4b). The first axis of the PCoA (10.91% and 13.40% of variance respectively) was related to the land-use history of sites (Figure 5a and Figure 5b). The land-use history of sites separated along axis 1 showing that abandoned farmland sites (Amos and Rivière-Héva) tended to be associated with species that classified as ruderal vascular plants (i.e., that can colonize and grow rapidly after the plantation establishment) such as *Hieracium* spp. (HIESPP), *Symphyotrichum cordifolium* (SYMCOR) and *Vicia cracca* (VICCRA) (on the left side of the ordination (Figure 5a and Figure 5b)). In contrast, the plantations established on the previously forest site (Nédelec) were composed of forest vascular plant species such as *Diervilla lonicera* (DIELON) *Maianthemum canadense* (MAICAN) and *Vaccinium angustifolium* (VACANG) (on the right side of the ordination, Figure 5a and Figure 5b), ruderal mosses such as *Ceratodon purpureus* (CERPUR) and *Pohlia nutans* (POHNUT) (on the right side of the ordination, (Figure 5a)) and lichens such as *Evernia mesomorpha* (EVEMES), *Hypogymnia physodes* (HYPPHY) and *Parmelia sulcata* (PARSUL) (on the right side of the ordination (Figure 5a)).

The bryophyte and lichen community composition, as represented by PCoA, shifted from coniferous to deciduous plantations along the first PCoA axis (10.84% of variance) and significant differences were found for plantation type (PERMANOVA; $p = 0.001$; Tableau 1a), although there was significant overlap of the ellipses (Figure 4c). The part of the variance explained by the second axis was difficult to interpret (7.52% of variance). There was dissimilarity among canopy types in bryophyte and lichen composition reflected by the presence of mosses in coniferous plantations while epiphytic lichens were present in deciduous plantations. Indeed, coniferous plantations were associated with many mosses such as *Bracythecium acutum* (BRAACT), *B. campestre* (BRACAM), *B.curtum* (BRACUR). *B.falcatum* (BRAFAL), *Pleurozium schreberi* (PLESCH) and *Sanionia uncinata* (SANUNC) (on the left side of the ordination (Figure 4c)), while deciduous plantations (especially poplar2), were associated with lichen species such as *Evernia mesomorpha* (EVEMES), *Bryoria fuscescens* (BRYFUS), *Physcia aipolia* (PHYAIP) and *Usnea* spp. (USNSPP) (on the right side of the ordination (Figure 4c)). In mixed plantations, the bryophyte and lichen community composition were generally intermediate between coniferous and deciduous plantations (Figure 4c).

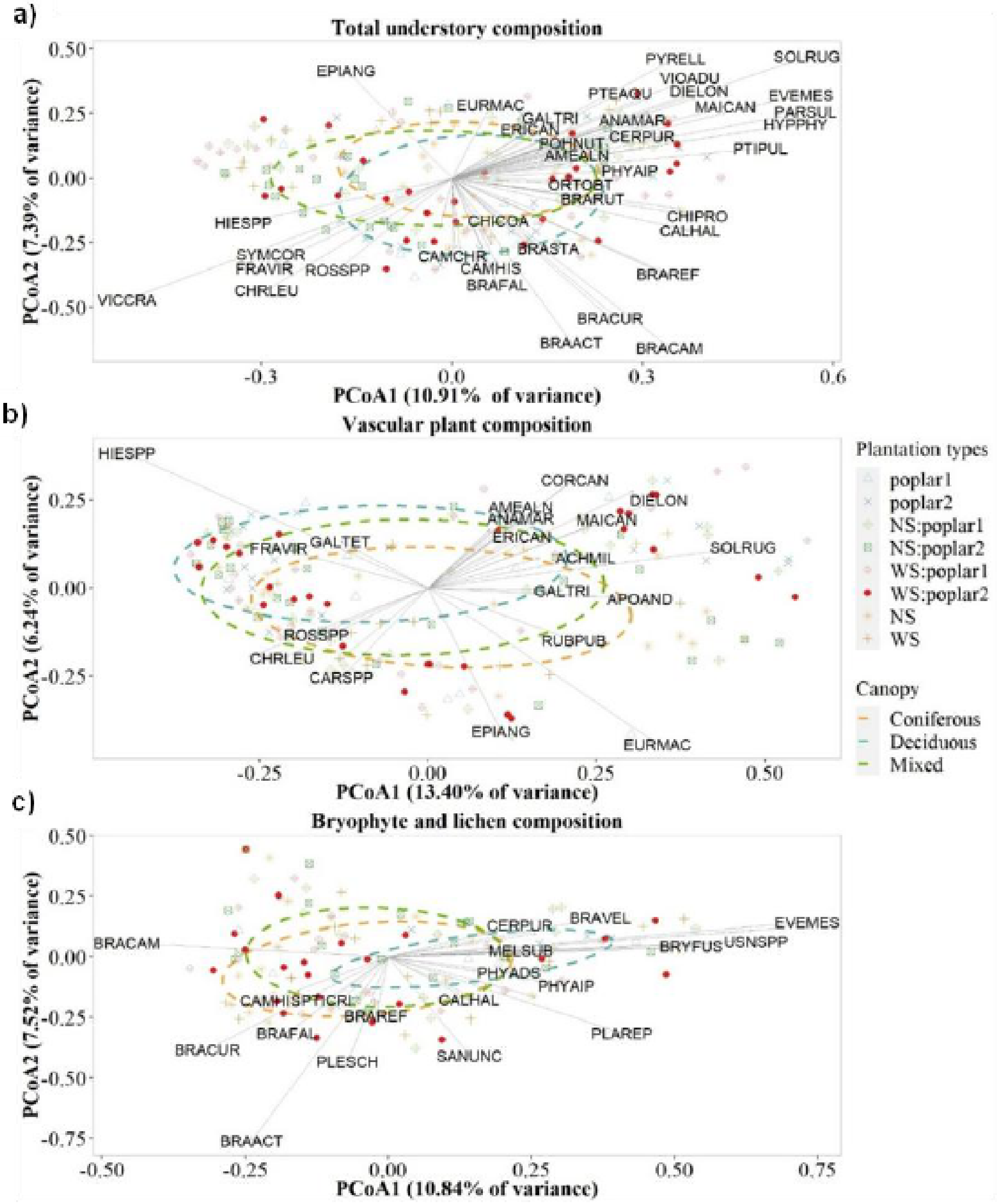

Figure 4

Principal coordinate analysis (PCoA) plots based on a) total vegetation, b) vascular plant, and c) bryophyte and lichen community composition in each canopy (ellipses) and plantation type (symbols). The ellipses are the 95% confidence intervals of the mean positions of canopy types (coniferous, deciduous and mixed as dashed lines in orange; blue and green respectively). Tableau S3 for more details on species names.

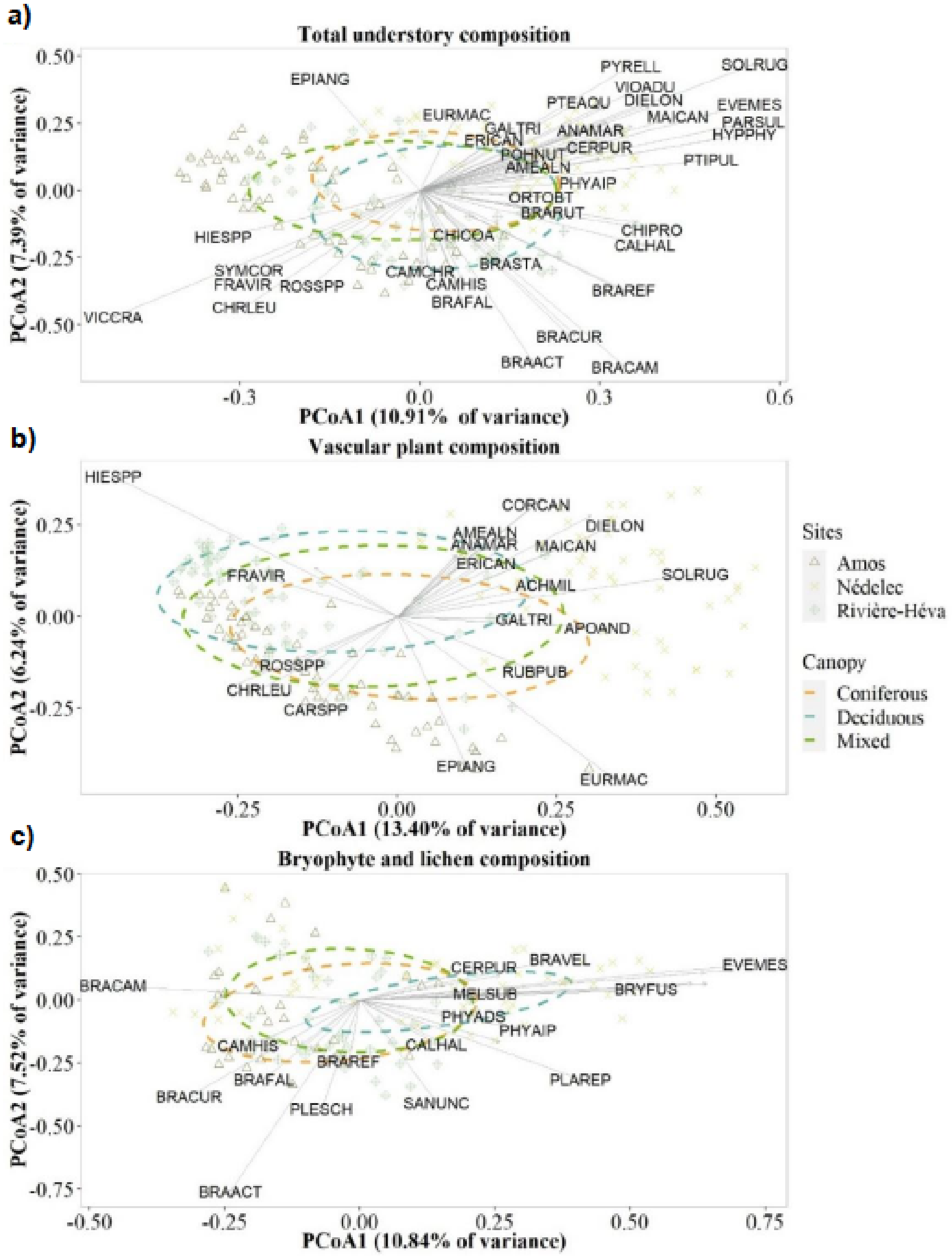

Figure 5
Principal coordinates analysis (PCoA) plots on a) total vegetation, b) vascular plant, and c) bryophyte and lichen community composition in each site represented by symbols (Amos, Nédelec and Rivière-Hiva). The ellipses are the 95% confidence intervals of the mean positioned according to canopy types (Coniferous, deciduous, and mixed as dashed lines in orange, blue and green respectively). Tableau S3 for more details on species names.

1.5.4 Effect of plantation type on bryophyte and lichen richness and composition according to microhabitats

Bryophyte and lichen richness was affected by plantation type only for the soil microhabitat, where deciduous plantations had fewer species than almost all other plantation types (except in NS:poplar1) (Figure 6). Bryophyte and lichen community composition on the soil varied by plantation type (PERMANOVA; $p = 0.001$; Tableau 1c). There was a gradient from coniferous plantations to mixed plantations along the first axis (10.60% of variance) with overlapped ellipses, while the deciduous plantations were explained by the second axis (9.20% of variance) (Figure 7a). Soil in coniferous plantations was dominated by pleurocarpous mosses such as *Bracythecium acutum* (BRAACT), *B. curtum* (BRACUR), *Pleurozium schreberi* (PLESCH) (on the left side of the ordination (Figure 7a)) while deciduous plantations, especially poplar2 were dominated by acrocarpous mosses such as *Ceratodon purpureus* (CERPUR) (on the right side of the ordination (Figure 7a)). Composition of the bryophyte community on the soil in mixed plantations was generally more similar to that of coniferous than to deciduous plantations (Figure 7a). Although there was significant overlap of the ellipses and non-significant effect of plantation type (PERMANOVA; p =0.35; Tableau 1c) on the bryophyte and lichen community composition at the base of trees, *Platygyrium repens* (PLAREP) was associated with the base of hybrid poplar trees, while *Callicladium haldanianum* (CALHAL) was associated with the base of spruce trees (Figure 7b). In mixed plantations, bryophytes and lichens appeared to be compositionally intermediate between coniferous and deciduous plantations at the base of trees (Figure 7b). The bryophyte and lichen community composition on the trunk of trees was significantly different (PERMANOVA; $p = 0.02$; Tableau 1c) between plantation types in the first axis of the PCoA ordination (28.98% of the variance). Trunks of trees were mostly composed of lichens which were more present in hybrid poplar and mixed plantations (Figure 7c).

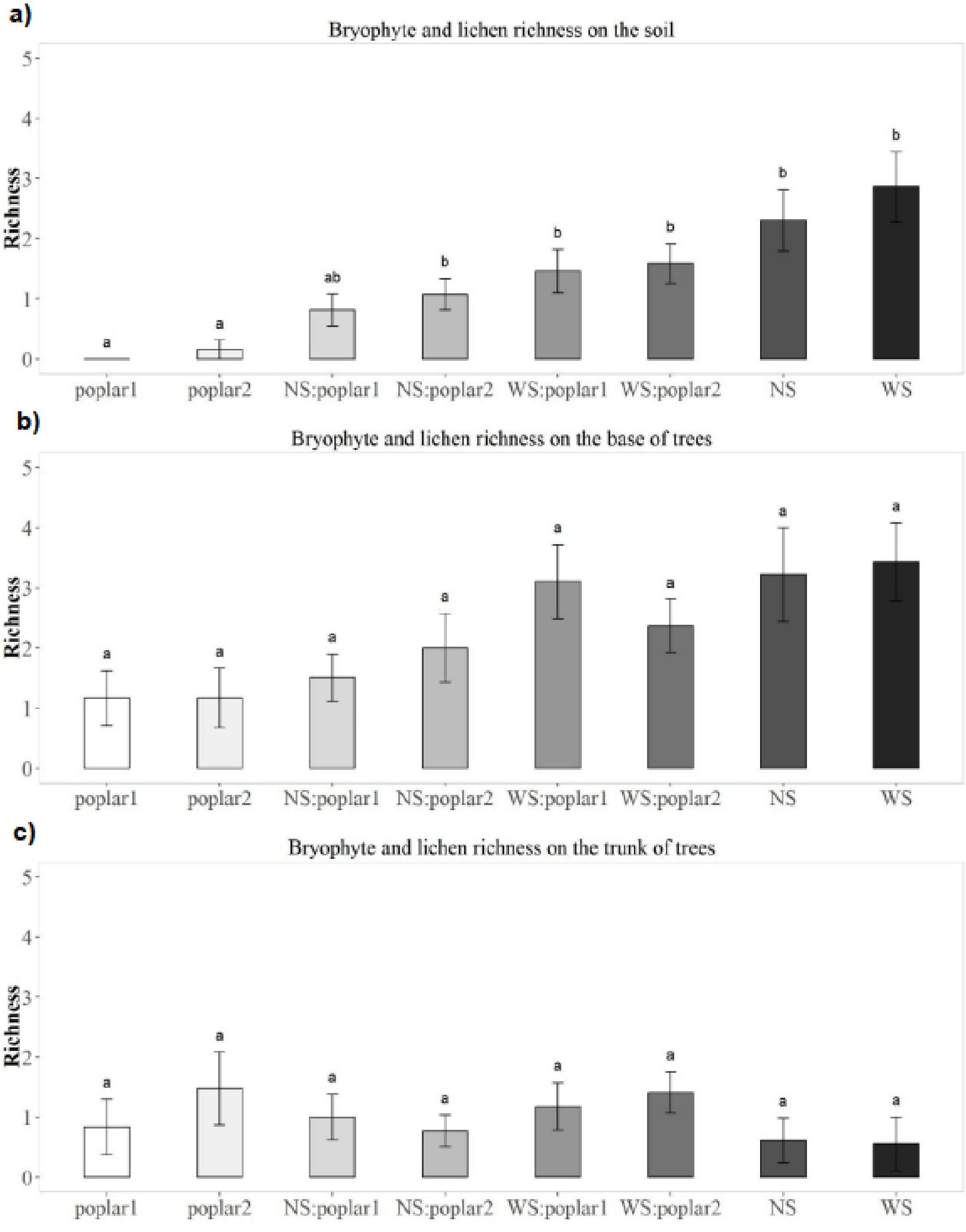

Figure 6
Mean richness (±SEM) of bryophytes and lichens a) On soil; b) At the base of trees; c) On the trunk of trees.

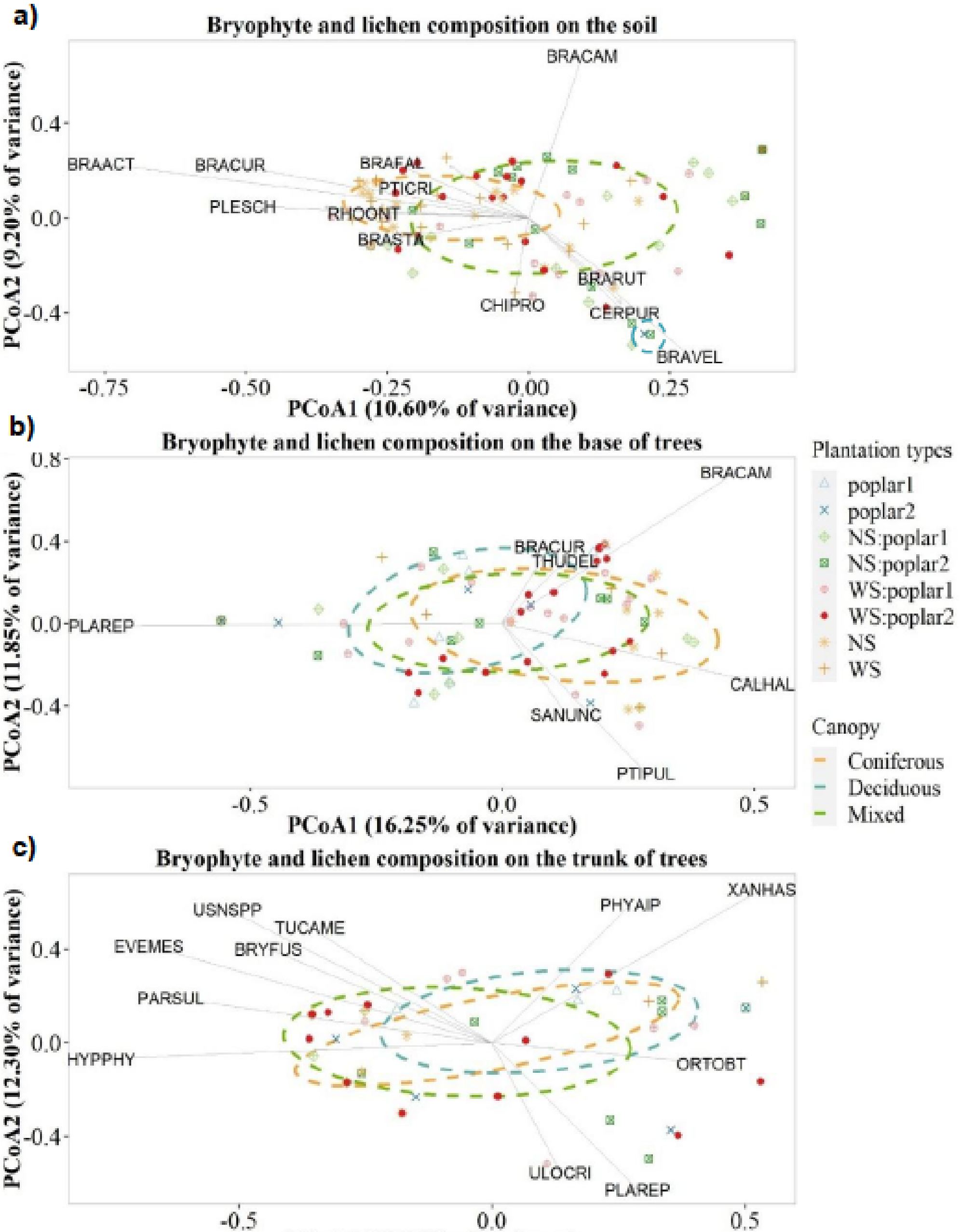

Figure 7

Composition of bryophytes and lichens on each microhabitat for each plantation type. a) Bryophyte and lichen composition on soil; b) Bryophyte and lichen composition at the base of trees; c) Bryophyte and lichen composition on trunk of trees. See supplementary information Tableau S3 for more details on species names.

Tableau 1
Effect of a) plantation type and b) site on the composition of total vegetation, vascular plants, bryophytes, and lichens using the permutational multivariate analysis of variance (PERMANOVA) based on Jaccard (total, bryophytes, and lichens) and Bray-Curtis (vascular plant) transformed community data. c) Effect of plantation type on the composition of bryophytes, and lichens on soil, at base of trees and on trunk of trees using the permutational multivariate analysis of variance (PERMANOVA) based on the Jaccard dissimilarity index.

a)

Communities	**Variable**	**Df**	**Mean square**	**F statictic**	**R^2**	***p value***
Total vegetation	Plantation type	7	4.41	1.97	0.07	**0.001*****
	Residuals	167	53.44			
Vascular plants	Plantation type	7	3.55	2.14	0.08	**0.001*****
	Residuals	166	39.31			
Bryophytes and lichens	Plantation type	7	3.96	1.51	0.07	**0.001****
	Residuals	126	47.19			

b)

Communities	**Variable**	**Df**	**Mean square**	**F statictic**	**R^2**	***p value***
Total vegetation	Site	2	7.86	13.53	0.14	**0.001*****
	Residuals	172	49.80			
Vascular plants	Site	2	11.83	32.59	0.27	**0.001*****
	Residuals	171	31.03			
Bryophytes and lichens	Site	2	4.23	6.21	0.08	**0.001****
	Residuals	131	46.72			

Tableau 1 (suite)

c)

Microhabitats	**Variable**	**Df**	**Mean square**	**F statictic**	**R^2**	***p value***
Soil	Plantation type	7	3.64	1.72	0.09	**0.001*****
	Residuals	96	33.90			
Base of trees	Plantation type	7	2.71	1.05	0.09	**0.35**^{ns}
	Residuals	71	26.27			
Trunk of trees	Plantation type	7	3.17	1.44	0.20	**0.02***
	Residuals	40	12.57			

(*) indicates the levels of significance: ns: nonsignificant. $p > 0.05$; *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$0.0001 < p < 0.001$.

1.5.5 Incident light

Incident light was different between plantation types (ANOVA, $p < 0.001$; see supplementary information Tableau S2) as it was significantly greater in hybrid poplar compared to spruce plantations (Figure 8). NS and WS had the lowest incident light values but were not significantly different from the mixed plantations (Figure 8). Incident light was similar between mixed and deciduous plantations except for WS:poplar1 which was significantly lower than poplar1(Figure 8).

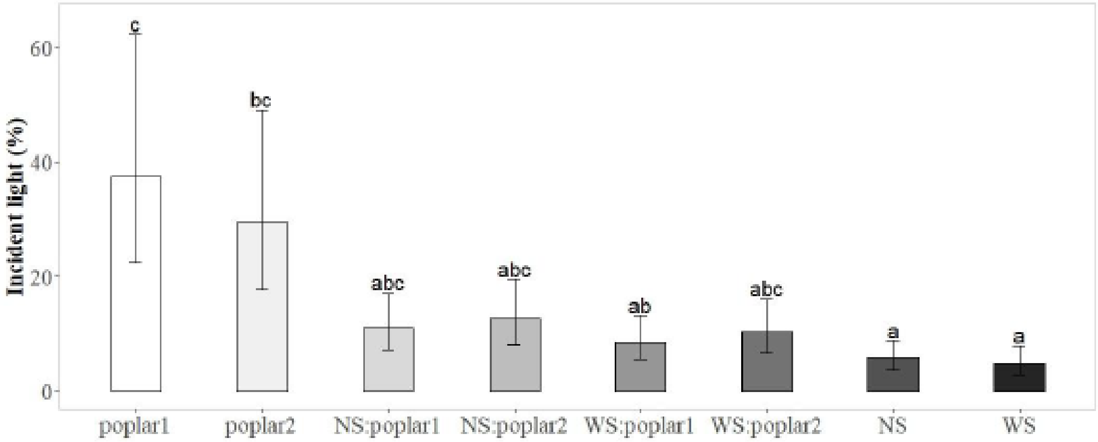

Figure 8
Mean (±SEM) percent incident light (%) for each plantation type. Different letters above bars of SEM indicate that incident light significantly differed between plantation types.

1.6 Discussion

1.6.1 Diversity responses to canopy and plantation types

Mixed and coniferous plantations contained similar understory vegetation diversity, and they had greater Hill numbers than deciduous plantations. These results partially support our hypothesis and indicate that the co-occurrence of hybrid poplar and spruce could increase the diversity of the understory vegetation compared to hybrid poplar monocultures. The most important factors affecting the diversity of forest-floor species, especially bryophytes, are the availability of potential substrates and microhabitats (Mills & Macdonald, 2005; Haughian, 2018). The possible explanation for the similarity of the diversity in coniferous and mixed plantations is that the addition of spruce in mixed plantations created microhabitats and conditions which were favorable for the establishment of species found in coniferous plantations. However, our data suggests that mixed plantation richness could increase with the number of quadrats (Figure 2), indicating that mixed plantations could harbor more species than monocultures.

Conditions created by deciduous forests are normally more favorable to the establishment of vascular plants than coniferous forests (Barbier *et al.*, 2008; Augusto *et al.*, 2015), as deciduous forests have warmer, more nutrient-rich soils and greater light availability, which increase the rate of litter decomposition (Barbier *et al.*, 2008; Laganière *et al.*, 2010; Cavard *et al.*, 2011a). However, our study showed that vascular plant richness was similar in all plantation types which did not support our hypothesis. This finding could be due to the presence of seeds of some species that can persist and remain dormant in the soil (Whittle *et al.*, 1997), allowing rapid recolonization even after a heavy site-preparation and plantation establishment (De Grandpre & Bergeron, 1997; Greene *et al.*, 1999; Ramovs & Roberts, 2005; Soo *et al.*, 2009). The understory layer created by ruderal species can delay the rate of successional change by creating conditions on the ground that inhibit the growth and emergence of many species (Mallik, 2003; Royo & Carson, 2006). Thus, our sites previously dominated by ruderal vascular plants prior to the plantation were probably rapidly re-colonized by species present before the plantation, that may have mitigated the effect of plantation type on vascular plant diversity.

Bryophyte richness was plantation type sensitive as it was higher in spruce and mixed plantations and lower in hybrid poplar plantations, which partially supports our hypothesis, since we expected to have more bryophyte species only in spruce plantations. The low richness of bryophyte species in hybrid poplar plantations could be explained by their inability to grow in the presence of broadleaf litter (Jean *et al.*, 2017; Bartels *et al.*, 2018) due to bryophytes specializing on the acidic and low-light conditions below coniferous canopies (Barbier *et al.*, 2008; Tullus *et al.*, 2015). Recalcitrant needleleaf litter associated with low decomposition rates in spruce plantations (Chomel *et al.*, 2015) had probably produced favorable conditions for bryophytes. Moreover, coniferous plantations created overall shadier conditions than those found in deciduous plantations, which could reduce soil temperatures and organic matter decomposition rates, leading to a high soil insulation and a cool soil surface, typical of coniferous forests (Millar, 1974; Crawford *et al.*, 2003; Laganière *et al.*, 2010; Barbé *et al.*, 2020). These conditions have created suitable microclimate conditions for bryophyte establishment in coniferous plantations. Combined with the microhabitat results, we found that bryophytes growing on the soil were sensitive to plantation type with less species in hybrid poplar plantations than in all other plantation types. Tree bases and tree trunks are in a vertical posture, which may make them less exposed to changes in abiotic factors such as light, litter accumulation, soil moisture, and pH. This indicates that soils are probably more exposed than tree bases and tree trunks to differing abiotic environments caused by canopy composition that mainly affect soil bryophyte communities. The addition of spruce in poplar plantations might have changed the physical properties of litter layers by diluting the quantity of hybrid poplar litter with a slower decomposition rate of spruce litter (Chomel *et al.*, 2015; Chomel *et al.*, 2016), allowing bryophytes to establish on the soil. The presence of spruce in mixed plantations also generated incident light levels similar to those found in coniferous plantations which also promoted shade-tolerant species such as bryophytes.The similarity of lichen richness combined with the low presence of lichens on the soil in all plantation types are probably due to the absence of available free substrate (Randlane *et al.*, 2017) as lichens can not generally compete with ruderal vascular plants and vigorous bryophytes growing on soil microhabitats (Gilbert, 1993).

1.6.2 Community composition

As hypothesized, we found that understory vegetation community composition in mixed plantations were compositionally intermediate between that of coniferous and deciduous plantation types. This indicates that understory vegetation communities in mixed plantations were composed of the same species that were found in hybrid poplar and spruce monocultures. In our study, spruce plantations were associated with bryophytes on the soil while some epiphytic lichens preferred hybrid poplar rather than spruce plantations. Several factors such as available understory light, water-holding capacity, pH and roughness of bark are important for the establishment and growth of bryophytes and lichens in forests (Lõhmus & Lõhmus, 2008; Hilmo *et al.*, 2009). *Populus* species are a substrate for a great number of epiphytic lichens as they possess non-acidic bark and nutrient-rich substrate conditions (Sheard & Jonescu, 1974; Boudreault *et al.*, 2000; Jüriado *et al.*, 2003; Hämäläinen *et al.*, 2023). Thus, this probably favored the occurrence of epiphytic lichens on hybrid poplar trees (e.g., *Evernia mesomorpha* (EVEMES), *Bryoria fuscescens* (BRYFUS) and *Physcia aipolia* (PHYAIP)). Our results suggest that the dissimilarity in the microhabitats generated by hybrid poplar and spruce promoted the establishment of both terrestrial bryophytes (via spruce) and epiphytic lichens (via hybrid poplar) in mixed plantations.

The composition of understory vegetation within plantations is not only affected by the canopy type and composition, it can also be influenced by the silvicultural practices that are applied prior to the plantation establishment and the land-use history (Ross-Davis & Frego, 2002; Brudvig & Damschen, 2011). While both bryophytes and vascular plants can exhibit sensitivity to previous land-use (Ross-Davis & Frego, 2002; Soo *et al.*, 2009; Bremer & Farley, 2010), bryophytes are generally considered to be more sensitive to abiotic changes because unlike vascular plants, bryophytes have no diverse life strategies or vascular tissues for water transport making them sensitive to changing environmental conditions (Bates *et al.*, 2005; Becker Scarpitta *et al.*, 2017). However, our study revealed that vascular plant composition was more sensitive than bryophyte composition to the land-use history. Abandoned farmland sites (Amos and Rivière-Héva) were dominated by ruderal and vascular plants that are disturbance tolerant, while the forest site (Nédelec) was composed of species usually found in natural forests. Our findings concur with those of Ramovs & Roberts (2005) who reported that the understory vegetation in plantations established on abandoned farmland were mostly species found in disturbed and non-forest habitats. This indicates that many plant species composition still reflected the agricultural environment despite the presence of a forest cover in the study area (Bellemare *et al.*, 2002). Recruitment of forest species in the forest site and recolonization of the newly established habitats offered by plantations might be related to the presence of seed banks from the previous forest (Caners *et al.*, 2009). The open canopy and the disturbed area after plantation establishment in forest sites (Nédelec) might have provided opportunities for ruderal and pioneer moss species such as *Ceratodon purpureus* (CERPUR) and *Pohlia nutans* (POHNUT) to establish. These species have been reported as widespread and ruderal moss species which are commonly found in harsh and disturbed habitats (Shaw & Beer, 1999; Rydgren *et al.*, 2004; Ochyra *et al.*, 2008) and they may be persistent for many decades after disturbance (Jonsson & Esseen, 1990).

Because the overstory changes affect the understory vegetation, we can expect that when plantations will become older, the light-demanding and ruderal species will be replaced by shade-tolerant species (Baum *et al.*, 2009). The older the trees will become, the more shade levels increase, leading to a high number of forest species throughout succession.

1.6.3 Tree identity matters

Though not significant, there was a trend that poplar2 appeared to contain greater total understory vegetation (Figure 3) and bryophytes and lichens on soil and trees (Figure 6) than in poplar1 plantations. The understory species richness of poplar1 was also relatively low and improved when mixed with coniferous species. Terminal bud phenology showed significant differences among poplar clones in terms of bud break time, and dormancy period as poplar2 had a longer growing season duration, leafed out earlier and had later onset of dormancy than poplar1 (Elferjani et al., 2016). Thus, the seasonal variations in the canopy associated with leaf budding and defoliation in hybrid poplar trees could affect understory vegetation by influencing abiotic environments such as incident light. Our study focused on current incident light, however, the light-vegetation relationship is likely to be better explained by the light during the whole growing season created by these phenological traits than by current light conditions (Thomas et al., 1999). This might explain a greater number of species as poplar2 plantations created a forest environment (canopy closure) longer and earlier in the year than poplar1. Poplar2 grew faster than poplar1 and leaf nitrogen (N) of poplar2 was greater in mixture than in monocultures (Benomar et al., 2013), suggesting that the presence of poplar2 increased N mineralization at the soil surface and thus, may increase nutrient-loving species richness by promoting a habitat with greater N-availability compared to mixed plantings with poplar1 (e.g., NS:poplar1). However, nitrification could result in the invasion of nutrient-loving species and competition exclusion, which would decrease species diversity (Gilliam, 2006; McClean et al., 2011). The effect of these clone dissimilarities on the biodiversity of understory vegetation is not fully understood and future investigations will be required to evaluate their effects on understory vegetation diversity and composition.

Although this was a non-significant trend, WS harbored greater total bryophyte diversity (Figure 3) and bryophyte richness on soil and trees (Figure 6). In a previous study, WS:poplar2 produced greater aboveground biomass than the other mixture, and the basal diameter of NS was slightly smaller when combined with hybrid poplars (Benomar *et al.*, 2013). This suggests that the high aboveground biomass may lead to taller trees with larger canopies, and lower light availability during the whole growing season in WS than in NS plantations. The low light availability may have limited moisture evaporation and created more suitable microclimate conditions for bryophytes in mixed plantations with WS similar to those in coniferous plantations leading to non-significant differences in bryophyte richness (see supplementary information Tableau S1).

1.7 Conclusion

While the effect of plantations on understory vegetation had been assessed, our study is among the first to evaluate the effect of monocultures and mixed plantations on all taxonomic groups of the understory vegetation (vascular plants, bryophytes, and lichens) in the boreal forest. This study also focused on the impact of different plantation types on bryophyte and lichen richness and composition on three microhabitats: soil, tree base and trunk. We provide evidence that mixed plantations could harbor more bryophyte species compared to hybrid poplar plantations. The presence of multiple tree species in mixed plantations results in greater resource and habitat availability, promoting the growth of different species and increasing overall biodiversity. Short-rotation hybrid poplar plantations in mixed plantations could also provide temporary habitats for lichens and thus, contribute in part to enhance biodiversity in mixed plantations. The lower presence of bryophytes in hybrid poplar plantations compared to spruce plantations, and the well-defined intermediate response of mixed plantations, provide justification for introducing spruce into hybrid poplar plantations to increase understory diversity when planning reforestation and plantation.

One of the limitations of the study is the small size of plantations with relatively few trees. The few trees sampled for epiphytic species may not have captured the full range of species diversity present in larger areas with a greater number of trees. Our studied plantations were also near boundaries, such as forest edges that could potentially act as edge effects. Our results show that land-use histories which were abandoned farmland sites (Amos and Rivière-Héva) and forest site (Nédelec) were an important determinant of future compositional differences in plantations and must be considered when assessing the impact of plantations on the understory vegetation. It could have been better if we had replicated sites for each land use history type to evaluate the overstory effects on the understory vegetation diversity and composition regardless of site origins or land-use histories considering that overstory-understory relationship is not always causal as it may react in parallel with site origins (Berger & Puettmann, 2000).

1.8 Acknowledgments

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2. EFFECTS OF CLONAL IDENTITY AND MIXTURE ON DIVERSITY, COMPOSITION AND FUNCTIONAL TRAITS OF UNDERSTORY VEGETATION

Ce chapitre sera soumis dans une revue

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2.1 Résumé

Les peuplements mixtes sont largement reconnus pour abriter des communautés végétales de sous-bois plus diversifiées que les peuplements monospécifiques. Cependant, les recherches sur l'influence des mélanges d'espèces arborées sur ces communautés se sont principalement concentrées sur les mélanges conifères-feuillus, laissant peu de données pour examiner si le mélange d'espèces au sein d'un même genre favorise davantage la biodiversité de la végétation de sous-bois que les plantations monospécifiques. Cette étude visait à évaluer comment les plantations monoclonales (un clone) et polyclonales (deux clones ou plus) de peuplier hybride (*Populus* spp.) influencent la diversité et la composition de la végétation de sous-bois et de ses traits fonctionnels, le long d'un gradient latitudinal. Quatre clones de peuplier hybride ont été sélectionnés : Clone1 (*Populus trichocarpa* Torrey & A. Gray × *balsamifera* L.), Clone2 et Clone3 (*P. balsamifera* × *maximowiczii* Henry), et Clone4 (*P. maximowiczii* × *balsamifera*). Ces clones ont été établis en plantations monoclonales et polyclonales sur trois sites répartis le long d'un gradient latitudinal. Nous avons évalué la diversité taxonomique et la composition de la végétation de sous-bois, ainsi que la diversité et la composition fonctionnelles des plantes vasculaires dans chaque type de plantation. Nos résultats montrent que les plantations polyclonales favorisaient une plus grande diversité fonctionnelle des plantes que les plantations monoclonales, en particulier dans les environnements plus contraignants. Nous avons observé des effets de l'interaction entre le type de plantation et le site sur la biodiversité du sous-bois. La composition fonctionnelle des communautés végétales dans les plantations polyclonales reflétait un assemblage de traits fonctionnels observés dans chaque plantation monoclonale. La composition des communautés de plantes vasculaires reflétait l'historique d'utilisation des terres avant l'établissement des plantations : les espèces forestières de sous-bois et les arbustes étaient plus abondants sur les sites forestiers, tandis que les espèces herbacées étaient présentes sur les sites agricoles. En outre, le gradient latitudinal a influencé les traits fonctionnels des plantes vasculaires, avec des traits conservateurs plus fréquents aux latitudes élevées et des traits acquisitifs plus courants aux latitudes basses, soulignant le rôle des gradients climatiques et environnementaux. Nous recommandons l’utilisation de mélanges de clones de peuplier pour promouvoir des habitats plus hétérogènes et améliorer la diversité fonctionnelle. Enfin, nous soulignons l’importance de l’identité et de la dissimilarité des traits des clones dans la structuration de la biodiversité du sous-bois.

Mots-clés : peuplier hybride, clone, mélange, végétation de sous-bois, biodiversité, trait fonctionnel.

2.2 Abstract

Mixed forests or plantations are widely recognized for housing more diverse understory plant communities than monospecific stands. However, research on how tree species mixtures influence these communities has largely focused on coniferous–deciduous mixtures, with a lack of studies to support that mixing species of the same genus would also create stands with greater understory vegetation biodiversity than monospecific plantations. This study aimed to assess how monoclonal (one clone) and polyclonal plantations (two or more clones) of hybrid poplar (*Populus* spp.) influence the diversity, composition and functional traits of understory vegetation. Plantations containing four hybrid poplar clones: Clone1, (*Populus trichocarpa* Torrey & A. Gray x *balsamifera* L).; Clone2 and Clone3 (*P. balsamifera* x *maximowiczii* Henry); and Clone4 (*P. maximowiczii* x *balsamifera*), planted in monoclonal or polyclonal blocks across three sites along a latitudinal gradient. We assessed the taxonomic diversity and composition of understory vegetation, and the functional diversity and composition of vascular plants in each plantation type. We found that polyclonal plantations provided greater understory plant functional diversity than monoclonal plantations, particularly in harsher environments. We observed synergistic effects between plantation type and site on understory vegetation biodiversity. The functional composition of plant communities in polyclonal plantations reflected an assemblage of functional traits observed across each monoclonal plantation. The composition of vascular plant communities also reflected the effects of land-use history prior to plantation establishment such that forest specialists, shrubs, and tree species were more abundant at the forested site, while herbaceous and grass species dominated previously farmland sites. Additionally, latitudinal variation influenced functional traits of vascular plants, with conservative traits more prevalent at higher latitudes and acquisitive traits more common at lower latitudes, highlighting the role of climatic and environmental gradients. We recommend mixing poplar clones to promote more heterogeneous habitats and enhance functional diversity. We highlight the importance of clone identity and trait dissimilarity in shaping understory biodiversity.

Keywords: Hybrid poplar, clone, mixture, understory vegetation, biodiversity, functional trait

2.3 Introduction

Forest overstory composition influences resource and microhabitat availability in the understory, which in turn can affect understory vegetation diversity (Gamfeldt *et al.*, 2013; Stefańska-Krzaczek *et al.*, 2022). For example, mixed overstories generally provide a greater variety of resources and microhabitats than monospecific overstories because of their compositional and structural diversity (Messier *et al.*, 2022; Randriamananjara *et al.*, 2023). The greater number of microhabitats allows for the coexistence of a number of species that enhance biodiversity of different taxonomic groups (Brockerhoff *et al.*, 2008; Thompson *et al.*, 2009; Feng *et al.*, 2022). Non-overlapping functional traits of overstory tree species (e.g., shade tolerance and leaf phenology) that are related to phylogenetic differences, such as tree species belonging to different genera (e.g., deciduous and coniferous species) (Barbier *et al.*, 2008; Richards *et al.*, 2010; Cavard *et al.*, 2011a), promote a greater species diversity in the understory compared to monospecific overstories (Brockerhoff *et al.*, 2008; Messier *et al.*, 2022). In contrast, mixed forests that combine tree species of the same genus that may have overlapping resource requirements may favor intra-genus competition, and therefore limit the establishment of diverse understory communities (Cavard *et al.*, 2011b). It has previously been shown that different hybrid poplar (*Populus* spp.) clones may have different functional traits even if they belong to the same genus, especially if they were created from different parental species. For example, productivity, canopy structure and *t*erminal bud phenology can vary between hybrid poplar clones (Benomar *et al.*, 2012; Elferjani *et al.*, 2016; Rabearison *et al.*, 2023). Elferjani et al., (2016) showed that one hybrid poplar clone (*Populus maximowiczii* x *P. balsamifera* L.) leafed out earlier and had a longer growing season than another clone (*Populus trichocarpa* Torrey & A. Gray x *P. balsamifera* L.). Similarly, leaf nutrient concentration varied between hybrid polar clones (Benomar *et al.*, 2011), and these differences in traits between clones could influence understory vegetation diversity by modifying the availability of some resources such as soil nutrients (Kunstler *et al.*, 2012; Valencia *et al.*, 2015). Thus, mixing clones that exhibit different traits could increase resource availability and promote heterogeneous habitats leading to the establishment of a wider variety of species in the understory.

However, the potential of polyclonal plantations (i.e., mixing two or more clones) to support more understory biodiversity than monoclonal plantations (i.e., one clone) remains to be determined.

Overstory composition can also act as a filter on the functional traits of understory plants (Benavides *et al.*, 2019; Happonen *et al.*, 2021). Functional traits include morphological, physiological, and phenological characteristics such as shade tolerance, life cycle duration and seed bank persistence that allow plants to acquire the necessary resources for their survival and growth within their environment (Lavorel & Garnier, 2002; Wright *et al.*, 2004; Violle *et al.*, 2007). Understory species may all have similar functional traits in monospecific overstories, as they have adapted to the same environmental conditions created by the dominant species (Puettmann, 2011; Benavides *et al.*, 2019). In contrast, mixed overstories offer more heterogeneous habitats and varying abiotic conditions that may facilitate coexistence among species occupying specific ecological niches and exhibiting different functional traits (Benavides *et al.*, 2019).

In addition to overstory composition, latitudinal gradients can also influence the functional traits or species composition of understory vegetation through changes in environmental conditions (Wright *et al.*, 2004; Colwell *et al.*, 2008). Harsher environmental conditions (i.e., cold temperatures and shorter growing seasons) of northern latitudes can lead to slow nutrient cycling, resulting in reduced nutrient availability (Hart & Chen, 2008). Resource-poor conditions generally promote the establishment of species that have conservative traits such as slower growth, longer lifespan, shade tolerance, higher leaf dry matter content (LDMC) and lower specific leaf area (SLA) (Pérez-Ramos *et al.*, 2012; Reich, 2014). In contrast, southern latitudes offer resource-rich conditions that tend to favor species that invest in acquisitive traits that facilitate rapid growth such as a high growth rate, a short life span, shade intolerance, abundant seed production, a low LDMC and a high SLA (Wright *et al.*, 2017). Leaf nitrogen and phosphorus concentrations (LNC and LPC) increase from southern to northern latitudes due to environmental and physiological adaptations and to optimize photosynthetic performance in northern regions (Reich &

Oleksyn, 2004). The variation in environmental conditions and resource availability along latitudinal gradients could influence the effect of species mixtures on understory vegetation biodiversity, as the benefits of species complementarity become more pronounced under harsher environmental conditions (Loreau *et al.*, 2001; Hooper *et al.*, 2005b; Del Río *et al.*, 2014). However, it remains uncertain whether understory vegetation biodiversity (functional and taxonomic) are higher in polyclonal plantations than in monoclonal plantations across these latitudinal gradients. A functional trait approach using plant traits as a complement to a taxonomic approach could, therefore, explain the effects of overstory composition on understory vegetation biodiversity along a latitudinal gradient (Lavorel & Garnier, 2002; Violle *et al.*, 2007; Naeem *et al.*, 2012).

The objective of this study was to determine how understory vegetation communities, including vascular plants, bryophytes, and lichens, vary between monoclonal *vs* polyclonal hybrid poplar plantations and along a latitudinal gradient. To do so, we evaluated taxonomic diversity and composition of all groups and the functional diversity and composition of vascular plants. We expected that polyclonal plantations would increase taxonomic and functional diversity in the understory vegetation compared to monoclonal plantations because clonal trait differences can increase resource availability and create different micro-habitats, promoting understory vegetation diversity (Kunstler *et al.*, 2012; Valencia *et al.*, 2015; Feng *et al.*, 2022). We expected the composition of understory vegetation and functional traits of polyclonal plantations to be more diverse than those of monoclonal plantations because clonal mixing can promote nutrient availability and offer heterogeneous habitats (Elferjani *et al.*, 2014), favoring the coexistence of a greater diversity of species. Lastly, we expected to observe a shift towards more conservative traits from the southernmost to the northernmost latitudes and we hypothesized that the effect of plantation type on the biodiversity of understory vegetation would vary along a latitudinal gradient, due to latitudinal-related climatic and environmental variations that influence the availability of resources such as light, temperature and humidity (Wright *et al.*, 2004; Colwell *et al.*, 2008) (Wright et al., 2004; Colwell et al., 2008).

2.4 Materials and methods

2.4.1 Study areas

We selected plantations of four hybrid poplar clones established in June 2005 across three sites located in the Nord-du-Québec and Abitibi-Témiscamingue regions (Québec, Canada) (Elferjani *et al.*, 2016): Clone1 (*Populus trichocarpa* Torrey & A. Gray x *balsamifera* L.), Clone2 and Clone3 (*P. balsamifera* x *maximowiczii* Henry), and Clone4 (*P. maximowiczii* x *balsamifera*). Although Clone2 and Clone3 were created from the same parental species, they are different as these two clones came from a different seed (i.e., genetically distinct). The three sites were distributed along a latitudinal gradient (Figure 9). The first site was in the black spruce (*Picea mariana* (Mill.) BSP) and feather moss (*Pleurozium* spp.) (Grondin, 1996) bioclimatic domain near the municipality of Villebois (49°09'N, 79°10'W). Before plantation establishment, the site was cultivated for cereals and hay. The second site was in the western balsam fir (*Abies balsamea* L.)-paper birch (*Betula papyrifera* Marshall) (Grondin, 1996) bioclimatic domain and near the municipality of Duparquet (48°29'N, 79°26'W). The second site was forested before being harvested in 2004. The third site was in the western sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britton) (Grondin, 1996) bioclimatic subdomain and located in the municipality of Duhamel (47°19'N, 79°25'W). The site was previously cultivated for hay.

Site preparation and planting treatments are detailed in Elferjani *et al.* (2014). Briefly, Villebois and Duhamel were ploughed with an agricultural tractor in fall 2004, while stumps and debris were removed in the Duparquet site, followed by deep ploughing with a skidder and disc harrowing before planting. Trees were then planted at a spacing of 4 x 3 m, corresponding to a density of around 833 trees ha^{-1}.

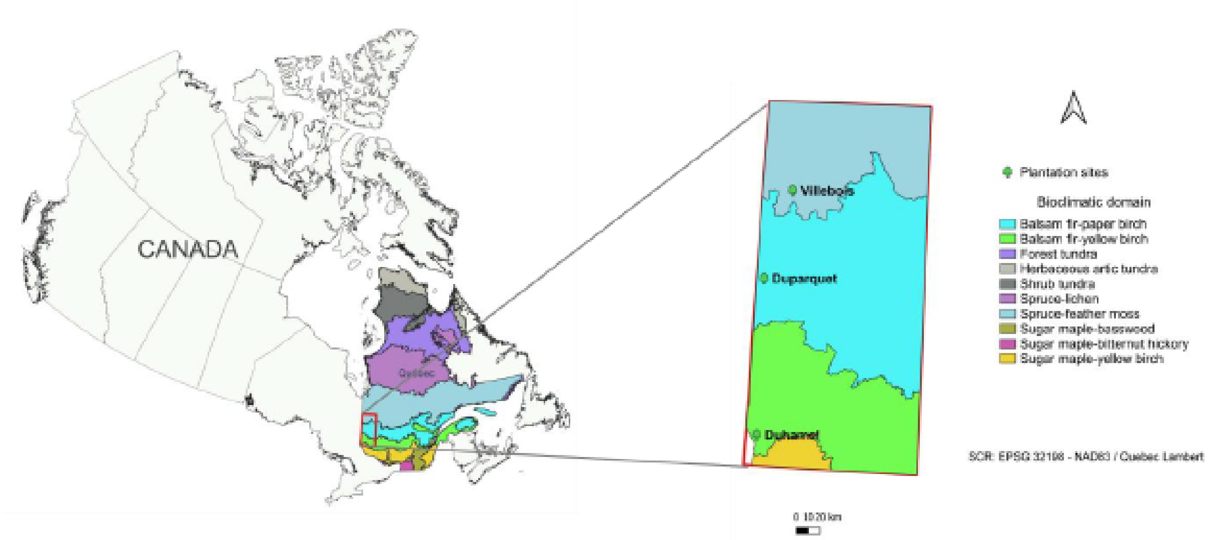

Figure 9
Location of the study sites within the province of Québec, eastern Canada. Insets are the Nord-du-Québec and Abitibi-Témiscamingue regions. Red triangles represent the three sites (Villebois, Duparquet and Duhamel).

2.4.2 Experimental design

Three monoclonal and polyclonal blocks (replicates) were randomly distributed in each of the three sites. A monoclonal block contained one plot of each clone (subplots), while a polyclonal block contained one plot of all four clones combined. Each monoclonal plot consisted of five rows of five trees of a single clone. Each polyclonal plot was composed of eight rows of eight trees. The position of the four clones was randomly attributed within the row, and each clone had two trees per row. Overall, across the three sites, a total of 1476 trees were planted.

2.4.3 Vegetation sampling

Within each monoclonal plot, two 1 m^2 quadrats were systematically placed in a linear transect established in the center of each plot to avoid edge effects, while two other 1 m^2 quadrats were directly placed under trees along a diagonal line (Figure 10). Within polyclonal plots, two 1 m^2 quadrats were placed between four different clones while two other 1 m^2 quadrats were placed under each clone (Figure 10). We placed a total of four to ten 1 m^2 quadrats within each plot, i.e. n=4 for monoclonal plots where two were placed under trees and two in the center of plot, while n=10 for polyclonal plots where two were under trees of each clone (2 x 4 clones) and two between four different clones (Figure 10). We inventoried all woody plants less than 1.3 m tall (shrubs and tree seedlings), herbaceous plants, bryophytes, and lichens in each quadrat. We collected bryophytes and lichens in three microhabitats: soil, base of trees (0-50 cm) and tree trunks (50-150 cm). We identified bryophyte and lichen specimens in the laboratory under a binocular microscope. We used nomenclature based on VASCAN database (Brouillet *et al.*, 2010) for vascular plants, Faubert (2012) for bryophytes and Brodo *et al.* (2001), Hinds&Hinds (2007) and Brodo (2016) for lichens.

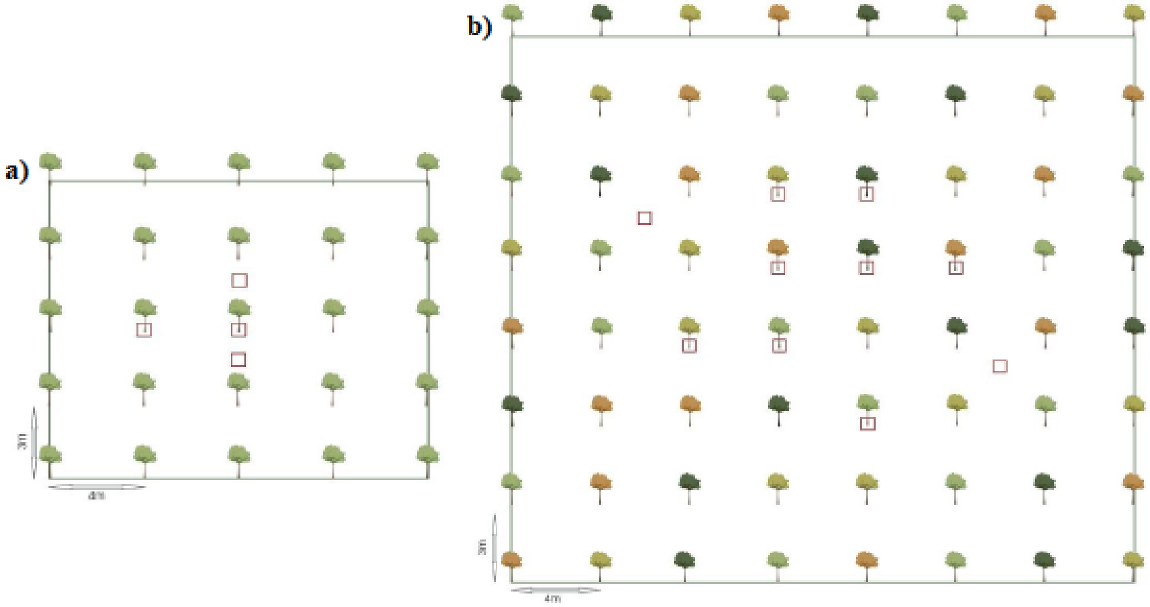

Figure 10
Schematic representation of the experimental design of a) monoclonal and b) polyclonal plots at each site. Quadrats are represented by red border squares. Clones are represented by tree symbology (similar color in the monoclonal plantation and four different colors in the polyclonal plantation).

2.4.4 Functional traits

Trait selection. First, we estimated the abundance of each vascular plant species by evaluating their percent cover in the quadrat. We then cumulated the average percent cover of the most abundant species of each plot in each site until we obtained at least 80% total cover (Garnier *et al.*, 2004). To measure plant functional traits, we selected 10 leaves per species included in the 80% of the vascular plant cover across each plot. We selected a total of 16 different species representing the most abundant species considering the three sites. We selected leaf functional traits classified as functional markers by Garnier *et al.* (2004), because they respond to resource availability and show the impact of community changes on ecosystem functioning (Garnier *et al.*, 2004; Díaz *et al.*, 2016). The first trait was specific leaf area (SLA), which is the ratio of leaf area (cm^2) to leaf dry mass (g) (Reich *et al.*, 1992). SLA represents a proxy for the assimilation rate and relative growth rate of the plant (Shipley, 2002). The second trait was leaf dry matter content (LDMC), which is the ratio of leaf dry mass to leaf fresh mass (saturated fresh mass) (Poorter & Garnier, 1999). LDMC approximates leaf tissue density and plant retention of nutrients (Smart *et al.*, 2017). Lastly, we measured two chemical trait of the leaves: leaf nitrogen content (LNC), which indicates the leaf nitrogen concentration or total amount of N per unit dry leaf mass, and leaf phosphorous content (LPC), which is the phosphorous concentration or total amount of P per unit dry leaf mass, expressed in $mg.g^{-1}$.

We also selected traits involved in dispersal, colonization, persistence and competition to determine how functional traits of vascular plants change in response to plantation type along the latitudinal gradient (Tableau 2). We obtained information on functional traits from the Traits Of Plants In Canada database (TOPIC) (Aubin *et al.*, 2021) and the Plant Trait Database (TRY) (Kattge *et al.*, 2020).

Tableau 2
Functional traits compiled from TOPIC and TRY databases and leaf traits measured in the field (in italics).

Trait type	Trait	Code	Description	Trait role
Morphological traits	Raunkiaer life form (ra)	Ra.ch	Chamaephyte (buds between 1 mm & 25 cm from ground)	Persistence
		Ra.g	Geophyte (herbaceous, buds located in the ground)	
		Ra.h	Hemicryptophyte (herbaceous, buds on the surface of the ground)	
		Ra.mc	Micro & nano phanerophyte (buds between 25 cm & 8 m from ground)	
		Ra.mg	Mega & meso phanerophyte (woody perennial, buds located ≥ 8m from the ground)	
		Ra.p	Phanerophyte (woody perennial, no information regarding bud location)	
		Ra.t	Therophyte (annual plant)	
	Maximum height	0	0-50 cm	Persistence
		1	51-100 cm	
		2	101-200 cm	
		3	201-1000 cm	
		4	> 1000 cm	

Tableau 2 (suite)

	Leaf dry matter content (LDMC)	mg/g	Linked to adaptability to environmental conditions	Persistence
	Specific leaf area (SLA)	cm^2/g	Linked to adaptability to environmental conditions	Persistence
Regeneration and dispersal traits	Lateral extension	0	Absence of vegetative propagation	Dispersal, colonization, persistence
		1	Compact propagation Phanerophytes: propagation by sprouting or root collar sprouts Non-phanerophytes: propagation by bulbs/bulbettes, corm/caudex, tubers	
		2	Intermediate propagation Phanerophytes: propagation by layering, root suckers or rhizomes Non-phanerophytes: propagation by bulbils or layering	
		3	Extensive propagation Phanerophytes: propagation by root suckers or rhizomes	

Tableau 2 (suite)

			Non-phanerophytes: rhizomes, stolons, plant fragments	
	Seed weight	0	< 0.1g	Dispersal, colonization
		1	0.11-0.5g	
		2	0.51-2 g	
		3	2.01-4 g	
		4	4.01-10 g	
		5	>10 g	
	Seed dispersal	D.ins	Dispersal by insects	Dispersal
		D.bir	Dispersal by birds	
		D.end	Dispersal by animals other than birds (endo zoochorous)	
		D.hum	Dispersal by humans	
		D.win	Dispersal by wind	
		D.exo	Dispersal by animals (exo-zoochorous)	
Longevity traits	Seed persistence	1	Short viability: ≤ 1 year Transient or absent	Persistence
		2	Semi-persistent: > 1 – 5 years	
		3	Persistent: > 5 years	
	Life cycle	1	Annual	Persistence

Tableau 2 (suite)

		2	Bi-annual	
		3	Perennial	
Habitat and resource utilization traits	Water preference	0	Habitat mesic-xeric or xeric	
		1	Habitat mesic	
		2	Habitat humid or humid-mesic	
	Light requirement	0	Shade intolerant	Competition
		1	Shade mid-tolerant	
		2	Shade tolerant	
	Leaf nitrogen content (LNC)	%	Nitrogen concentration per unit dry leaf mass	Competition
	Leaf phosphorous content (LPC)	%	Phosphorous concentration per unit dry leaf mass	Competition

Trait measurements. To measure SLA and LDMC, we selected young, fully exposed leaves with no significant damage caused by herbivores or pathogens. The leaves were wrapped in moist paper before being placed in sealed plastic bags. We then immersed leaves in deionised water during 24h to 48h as soon as we arrived at the laboratory to obtain the saturated fresh mass. Each leaf was dried with tissue paper before weighing to remove surface water and immediately weighed to determine saturated fresh mass. We measured leaf area with a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE), and oven-dried each leaf at 80°C for 48h and to determine dry mass.

We referred to the leaf collection procedure described above for LNC and LPC measurement. We cut off all petioles prior to LNC and LPC analysis (Cornelissen *et al.*, 2003). We then oven-dried leaves at 80°C for 48h and ground each dried leaf for subsequent nitrogen and phosphorous analysis in the laboratory (Laurentian Forestry Centre, Québec, Canada). LNC was determined using a LECO CNS analyzer (Leco 928 CNS, LECO Corporation, St. Joseph, MI, USA) after sample combustion. LPC was determined by extracting available phosphorus with an acid fluoride solution, followed by colorimetric quantification using a Lachat Quickchem 8500 Series 2 autoanalyzer (Lachat Instruments, Loveland, CO, USA).

2.4.5 Environmental variables

To assess the effects of climate variables related to latitudinal gradient on functional traits, we selected mean annual temperature (T_a) and annual rainfall (P_a). We obtained meteorological data of the three sites from nearby stations in the National Climate Data and Information database (Environnement Canada, 2021). At the Villebois, Duparquet and Duhamel sites, mean annual precipitation were respectively 909.1mm, 889.8mm and 836.5mm, while mean annual temperatures were respectively 0°C, 0.7°C and 3.1°C (Climate normals 1981-2010).

We measured the percentage of incident light 50 cm above the forest floor in each plantation type at each site using a LAI-2200C plant canopy analyzer (LI-COR Biosciences, Lincoln, NE) based on Légaré *et al.* (2002). We measured full reference light in an open field near each plantation. Lastly, we calculated the incident light within the plantations as the ratio between the percentage of incident light 50 cm above the forest floor and the reference light. We used ANOVA within linear models from the package *nlme* (Pinheiro *et al.*, 2021) to test the effects of plantation type on incident light at each site. We used the post hoc emmeans method with the package *emmeans* (Russell, 2022) to make pairwise comparisons between plantation types (Tableau 3).

Tableau 3
Mean (±SEM) incident light for each plantation type at each site. Significant differences ($p \leq 0.05$) between stand types are indicated by different letters.

Site	Plantation type	Light (%)
Villebois	Clone1	35.30 (±10.2) ^{b}
	Clone2	25.70 (±5.87) ^{ab}
	Clone3	9.15 (±2.90) ^{a}
	Clone4	10.90 (±3.34) ^{a}
	Polyclonal	9.28 (±1.44) ^{a}
Duparquet	Clone1	64.80 (±4.79) ^{a}
	Clone2	69.80 (±9.62) ^{a}
	Clone3	48.80 (±4.78) ^{a}
	Clone4	44.20 (±15.3) ^{a}
	Polyclonal	49.20 (±5.62) ^{a}
Duhamel	Clone1	12.10 (±2.87) ^{a}
	Clone2	7.99 (±3.20) ^{a}
	Clone3	15.5 (±4.99) ^{a}
	Clone4	9.75 (±3.07) ^{a}
	Polyclonal	10.30 (±2.22) ^{a}

2.4.6 Statistical analyses

Taxonomic diversity: Understory vegetation responses. We conducted all data processing and analyses using R 4.1.0 (2021-05-18) (R Core Team, 2021). To evaluate the effects of plantation type at each site on understory vegetation, we quantified the zero-order Hill number (q=0) representing the effective number of species (Chao *et al.*, 2014) using the «iNEXT» R package (Hsieh *et al.*, 2016). To represent the cumulative number of species, we used accumulation curves as a function of the number of quadrats sampled. We then compared q=0 between plantation types at the three sites for each taxonomic group using rarefaction and extrapolation (R/E) curves based on sample size with 95% confidence intervals (Chao *et al.*, 2014).

Understory vegetation community composition. To assess the interacting effects of plantation type and site on understory vegetation community composition, we performed permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations with the "adonis" function from the *vegan* package (Laliberté *et al.*, 2014). To visualize community composition, we performed principal coordinate analyses (PCoAs) (Borcard *et al.*, 2011) using the "PCoA" function from the *vegan* package (Laliberté *et al.*, 2014) with Bray–Curtis dissimilarity matrices for vascular plants only and for bryophytes and lichens combined at each site (i.e., Villebois, Duparquet, and Duhamel). We analysed the bryophyte and lichen communities together, as lichens had low occurrence in our plantations. We corrected the negative eigenvalues using the Cailliez correction (Gower & Legendre, 1986). We used the vegan "envfit" function to fit the most significant species in ordination diagrams with 999 permutations (envfit, $p \leq 0.05$). We followed the same procedures as in the previous description to analyze and visualize understory vegetation community composition by site.

Functional traits: Vascular plant responses. To assess plant functional trait responses to plantation type along the latitudinal gradient, we performed multivariate and univariate functional responses. First, we created a matrix representing the percentage cover per species in each plot ("species x traits") and a matrix containing species trait values ("species x traits"). We assigned a value per species for the categorical and quantitative traits from the TOPIC and TRY databases. We calculated the average value per trait, per species, and per plantation type for the four traits we measured in the field (i.e., SLA, LDMC, LNC and LPC). We then created a matrix representing the information on plantation type and site. We calculated community weighted means (CWMs) of trait values using the «functcomp" function from the *FD* package (Laliberte & Legendre, 2010; Laliberté *et al.*, 2014) to determine which proportion of the total plant abundance is composed by a given trait in a plot (Garnier *et al.*, 2004).

We computed Rao's index as a functional diversity index using the dbFD function from the *picante* package (Kembel *et al.*, 2010). Rao's index describes the variability or the dissimilarity between species traits within a community and represents the sum of pairwise distances between species weighted by their relative abundance. We evaluated the effect of plantation type on functional diversity using analysis of variance models (ANOVA). We then applied Tukey's multiple comparison tests with the package *emmeans* (Russell, 2022).

We tested the interacting effects of plantation type and site on community functional composition using PERMANOVA with 9999 permutations with the «adonis2» function from the *vegan* package (Laliberté *et al.*, 2014). We then performed a principal component analysis (PCA) on the CWM matrix to represent the trait composition patterns of each plantation type by site and each site.

To evaluate the effects of environmental variables on community functional composition, we performed multimodel selection that included individual and combined models of three explanatory variables (i.e., site, mean annual temperature and precipitation). We used linear mixed models from the *lme4* and *lmerTest* packages (Bates *et al.*, 2015; Kuznetsova *et al.*, 2017). We extracted the scores of the first and second PCA axes and fitted them as response variables. We then put block as a random effect. We ranked candidate models based on Akaike's information criterion (AICc;(Burnham & Anderson, 2002)) using the package aiccmodavg 2.3-1 (Mazerolle, 2020) and selected the model with the lowest AICc.

2.5 Results

2.5.1 Taxonomic diversity

Overall, our monoclonal and polyclonal plantations had similar numbers of species at each site for all taxonomic groups as their confidence interval curves overlapped (Figure 11), except for vascular plants at Duhamel, where the number of vascular plant species for Clone1 was lower than for the other plantation types (Figure 11f). In addition, although it is a non-significant trend, Clone4 harbored a greater number of vascular plants and bryophyte species than the other plantation types at Villebois and Duhamel (Figures.11a, 11b, 11f and 11g). Lastly, lichens were only present at Duparquet, and the number of lichen species was similar among plantation types (Figure 11e).

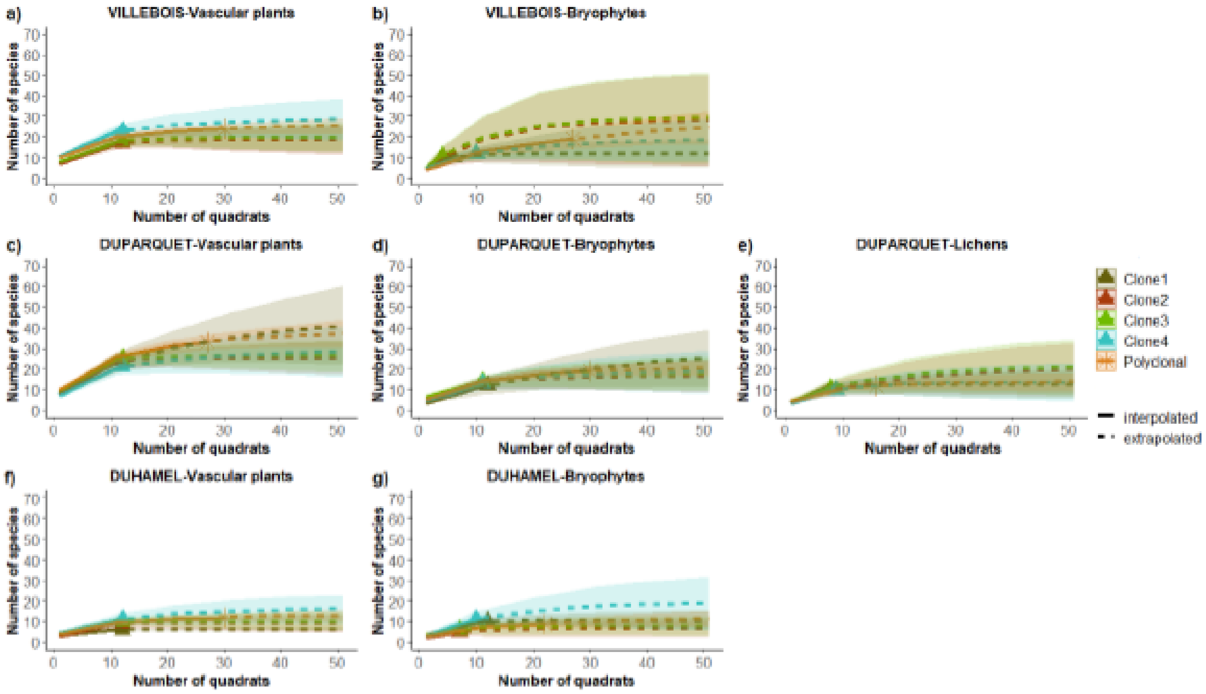

Figure 11

Rarefaction and extrapolation showing the total number of vascular, bryophyte and lichen species for each plantation type (Clone1 in dark green, Clone2 in light brown, Clone3 in light green, Clone4 in light blue and Polyclonal in orange) at a) and b) Villebois; c), d) and e) Duparquet; and f) and g) Duhamel sites. Sample-size-based rarefaction and extrapolation are respectively in solid and dashed lines with 95% confidence intervals for number of species. The symbols indicate the observed numbers of species.

2.5.2 Understory vegetation community composition across sites along a latitudinal gradient

We found an interaction effect between plantation type and site on understory vegetation community composition (PERMANOVA; $p = 0.001$; Tableau 4). The first and second axes of vascular plant community composition PCoA (all plantation types combined) explained respectively 13.40% and 7.87% of the variance (Figure 12). The first axis separated previously forested (i.e., Duparquet) from previously cereal-growing and haying (i.e., Duhamel and Villebois) sites. The differences between the northernmost (i.e., Villebois) and southernmost (i.e., Duhamel) sites were captured on the second axis (Figure 12a). Plantations established at Duparquet were associated with shrubs (e.g., *Alnus incana* (ALNINC), and *Sorbus americana* (SORAME)) and trees (e.g., *Abies balsamea* (ABIBAL) and *Picea glauca* (PICGLA)), while plantations established at Villebois and Duhamel were associated with herbaceous and graminoids species (e.g., *Carex aurea* (CARAUR), *Chrysanthemum leucanthemum* (CHRLEU) and *Elymus repens* (ELYREP)) (on the right side of the ordination (Figure 12a)). However, the composition of herbaceous species at the Duhamel and Villebois sites differed along the second axis. Species such as *Linnaea borealis* (LINBOR) and *Veronica persica* (VERPER) versus *Achillea millefolium* (ACHMIL) and *Trifolium pratense* (TRIPRA) were associated with the Duhamel and Villebois sites respectively.

The first and second axes of the bryophyte and lichen community PCoA (all plantation types combined) explained 15.02% and 8.08% respectively. The first axis separated the Duparquet site from the Duhamel and Villebois sites (Figure 12b). Both moss (e.g., *Ceratodon purpureus* (CERPUR), *Brachythecium erythrorrhizon* (BRAERY) and *Sanionia uncinata* (SANUNC)) and lichen species (e.g., *Cladonia chlorophaea* (CLACHL) and *Cladonia verticillate* (CLAVER)) were associated with the Duparquet site, while only moss species were associated with the Duhamel and Villebois sites. However, the northernmost (i.e., Villebois) and southernmost (i.e., Duhamel) sites differed in associated species along the second axis as *Brachythecium campestre* (BRACAM) was associated with the Villebois site, while *Campyliadelphus* *chrysophyllus* (CAMCHR) and *Fissidens osmundoides* (FISOSM) were associated with the Duhamel site (Figure 12b).

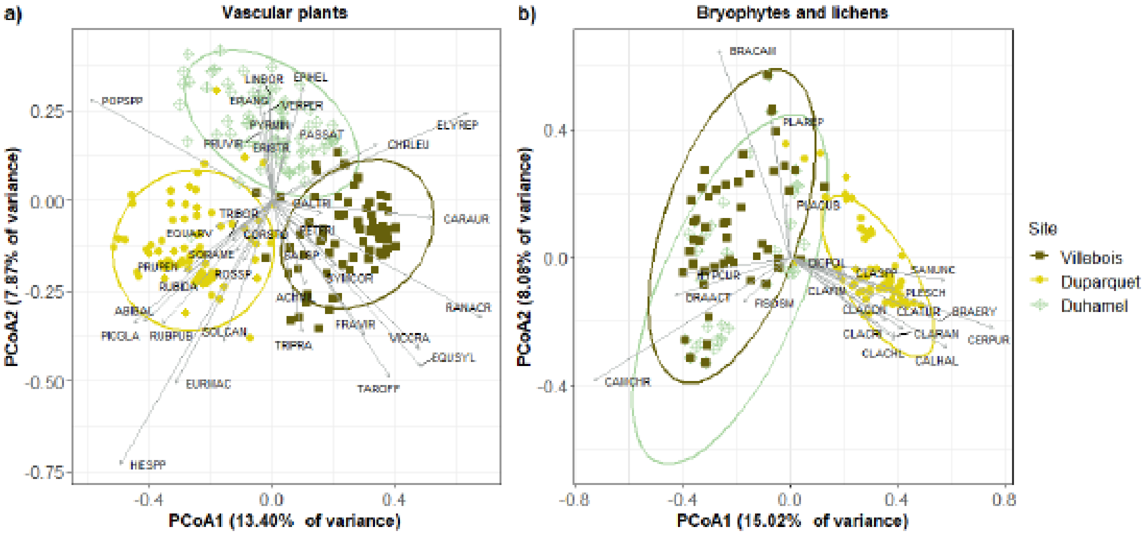

Figure 12
Principal coordinates analysis (PCoA) plots on a) vascular plant community composition and b) bryophyte and lichen community composition at each site represented by symbols. The ellipses represent the 95% confidence intervals of the mean positioned according to sites (Villebois in dark green, Duparquet in yellow, Duhamel in light green). See Tableau S8 for more details on species names.

2.5.3 Understory vegetation community: differences among plantation types at each site

When analyzed separately by site, the first PCoA axis of the vascular plant community at the Villebois, Duparquet, and Duhamel sites explained 16.37%, 9.37% and 11.84% of the variance respectively, while the second axis explained 11.70%, 8.64% and 8.95% of the variance respectively (Figure 13). At Villebois, the first PCoA axis illustrated the variability of species assemblages within monoclonal plantations, while the second axis highlighted differences between monoclonal and polyclonal plantations (Figure 13a). *Chrysanthemum leucanthemum* (CHRLEU), *Trifolium pratense* (TRIPRA) and *Taraxacum officinale* (TAROFF) were associated with polyclonal plantations (Figure 13a).

At Duparquet, the vascular plant community composition in monoclonal plantations was also different from that of polyclonal plantations, despite the overlapping ellipses (pairwise PERMANOVA; Tableau S4) (Figure 13c). The monoclonal plantations also differed from one another in terms of vascular plant community composition, with Clone1 differing from Clone4 (pairwise PERMANOVA; Tableau S4). Ruderal and light-demanding species such as *Eurybia macrophylla* (EURMAC), *Rubus ideaus* (RUBIDE), and *Taraxacum officinale* (TAROFF) were associated with Clone1 but little present in Clone4 plantations (Figure 13c).

At Duhamel, there was a gradient from Clone1 to polyclonal plantations along the first axis, despite the overlapping ellipses (Figure 13e). The species *Epilobium angustifolium* (EPIANG) was associated with Clone1, while polyclonal plantations were associated with graminoids (e.g., *Carex aurea* (CARAUR)), shrubs (e.g., *Prunus virginiana* (PRUVIR)) and forage plants (e.g., *Pastinaca sativa* (PASSAT)) (Figure 13e). The effect of clone identity on vascular community composition was stronger at the Duhamel site, as the vascular community composition differed between all monoclonal plantations except between Clone2 and Clone3 (pairwise PERMANOVA; Tableau S4).

Bryophyte and lichen community composition were similar among plantations at all sites, except at Villebois where bryophyte and lichen community composition in Clone2 plantations differed from that in Clone4 plantations (pairwise PERMANOVA; Tableau S4). In this site, *Brachythecium campestre* (BRACAM) was associated with Clone2 while *Campyliadelphus chrysophyllus* (CAMCHR) was associated with Clone4 (Figure 13b).

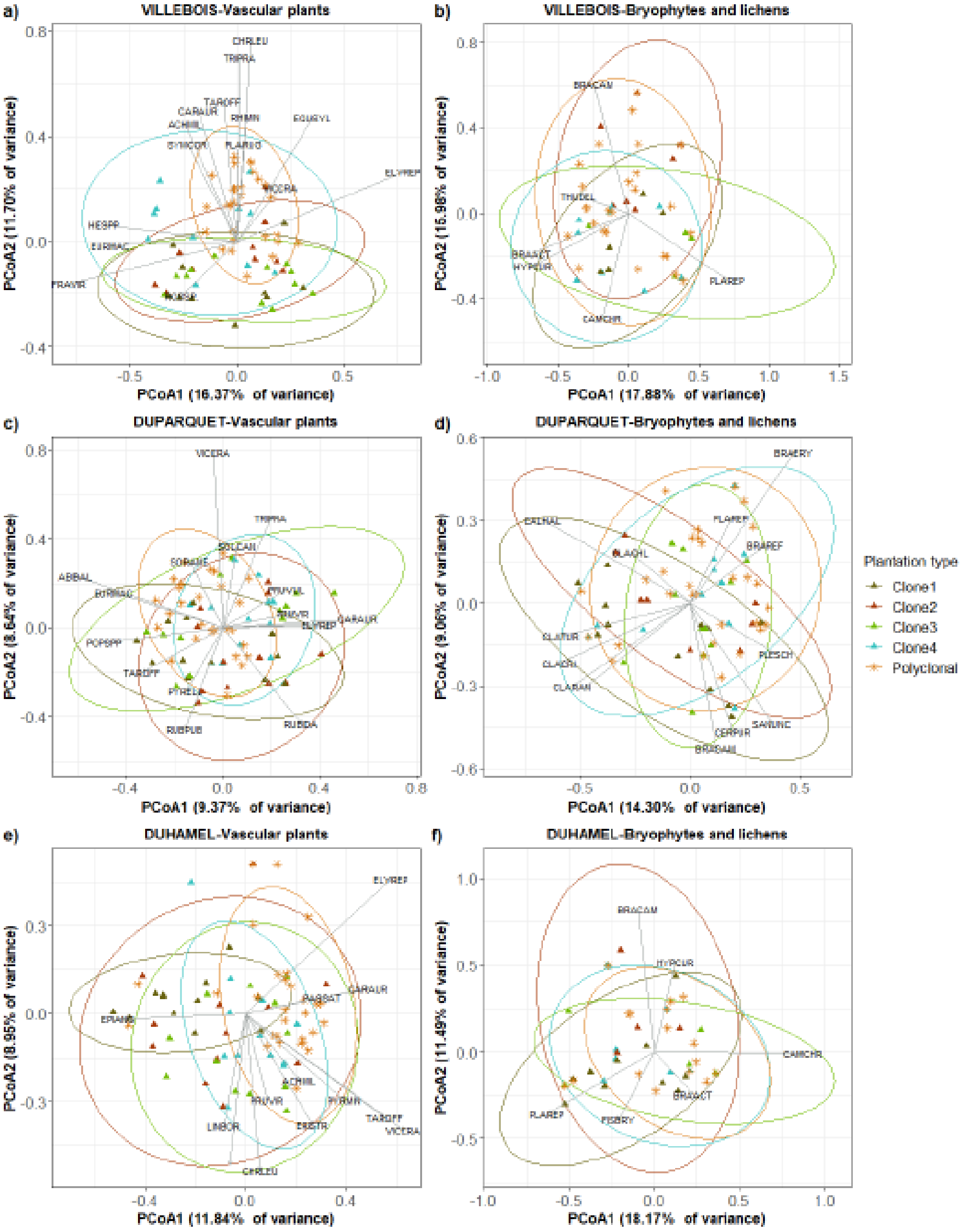

Figure 13
Principal coordinates analysis (PCoA) plots on vascular plant community composition and bryophyte and lichen community composition at a) and b) Villebois; c) and d) Duparquet; and e) and f) Duhamel sites. The ellipses are the 95% confidence intervals of the mean positioned according to plantation types (Clone1 in dark green, Clone2 in light brown, Clone3 in light green, Clone4 in light blue and Polyclonal in orange). See Tableau S8 for more details on species names.

Tableau 4
Effects of plantation type, site and their interaction on understory vegetation community composition using permutational multivariate analysis of variance (PERMANOVA) based on Jaccard's index.

Communities	Variable	Df	Sum of squares	F statistics	R^2	*p*
Vascular plants	Plantation type	4	2.90	3.11	0.04	**0.001*****
	Site	2	15.94	34.19	0.21	**0.001*****
	Plantation type: Site	8	5.27	2.82	0.07	**0.001*****
	Residuals	216	50.35		0.67	
Bryophytes and lichens	Plantation type	4	1.85	1.43	0.02	**0.029***
	Site	2	13.42	20.71	0.18	**0.001*****
	Plantation type: Site	8	4.65	1.79	0.06	**0.001*****
	Residuals	167	54.13		0.73	

(*) indicates the levels of significance: $p > 0.05$; *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$0.0001 < p < 0.001$.

2.5.4 Functional trait responses of vascular plant communities

Responses of functional diversity. Functional diversity of vascular plants shifted with plantation type at each site (ANOVA, *p* =0.001and 0.004; Tableau 5). Although some monoclonal plantations were as functionally diverse as polyclonal plantations, mixing clones generally increased functional diversity compared with monoclonal plantations (Figure 14). At Villebois, functional diversity was higher in polyclonal plantations than in all monoclonal plantations (Figure 14a). At the Duparquet site, some monoclonal plantations showed similar functional diversity to that of polyclonal plantations, as in the case of Clone1. At Duhamel, polyclonal plantations had similar functional diversity to monoclonal plantations, except for Clone1 which had lower functional diversity (Figures. 14b and 14c).

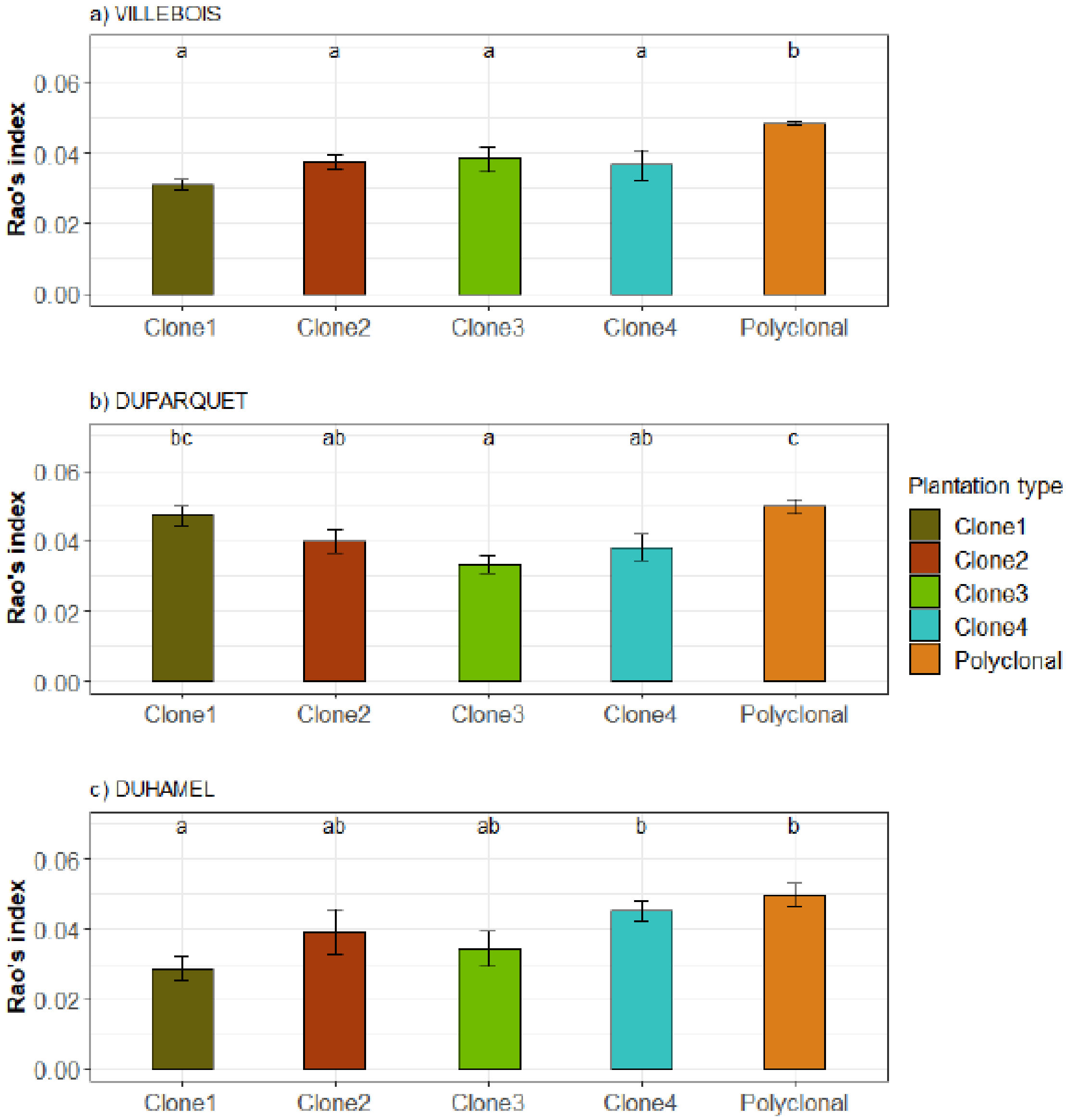

Figure 14
Mean (±SEM) Rao's index (functional diversity of vascular plants) for a) Villbeois; b) Duparquet; c) Duhamel by plantation type. Different letters indicate that mean Rao's index differed significantly between plantation types.

Tableau 5
Results of the ANOVA models on the effects of plantation type on functional diversity of vascular plants at each site.

Site	**Variable**	**Functional diversity index**	**Df**	**Sum of squares**	**Mean squares**	**F value**	***p***
Villebois	Plantation type	Rao's index	4	0.003	0.0008	11.51	**0.001*****
Duparquet	Plantation type	Rao's index	4	0.003	0.0007	6.35	**0.001*****
Duhamel	Plantation type	Rao's index	4	0.004	0.001	4.10	**0.004****

Community functional composition across sites along a latitudinal gradient. The interaction between site and plantation type affected the functional composition of the vascular plant community (PERMANOVA; $p = 0.001$; Tableau 6). The first axis of the all plantation PCA (24.85% of variance) explained the dissimilarity between sites, with the Duhamel and Villebois plantations on the left side and the Duparquet plantations on the right side of the ordination (Figure. 15). This axis was associated with geophyte species with greater lateral extension, higher LNC and SLA, and a preference for higher soil moisture on the left side, and species with higher seed persistence and life cycle on the right side (Figure 15). Overall, the second axis of the all plantation PCA (21.23% of variance) separated the northernmost (i.e., Villebois) and southernmost (i.e., Duhamel) sites (Figure 15). Geophyte species with higher seed weight, LDMC and more shade intolerance were positively correlated with axis 2 and the Villebois site. In contrast, mega and meso phanerophytes, tall plants and species with higher LPC and SLA were negatively associated with axis 2 and more abundant at Duhamel.

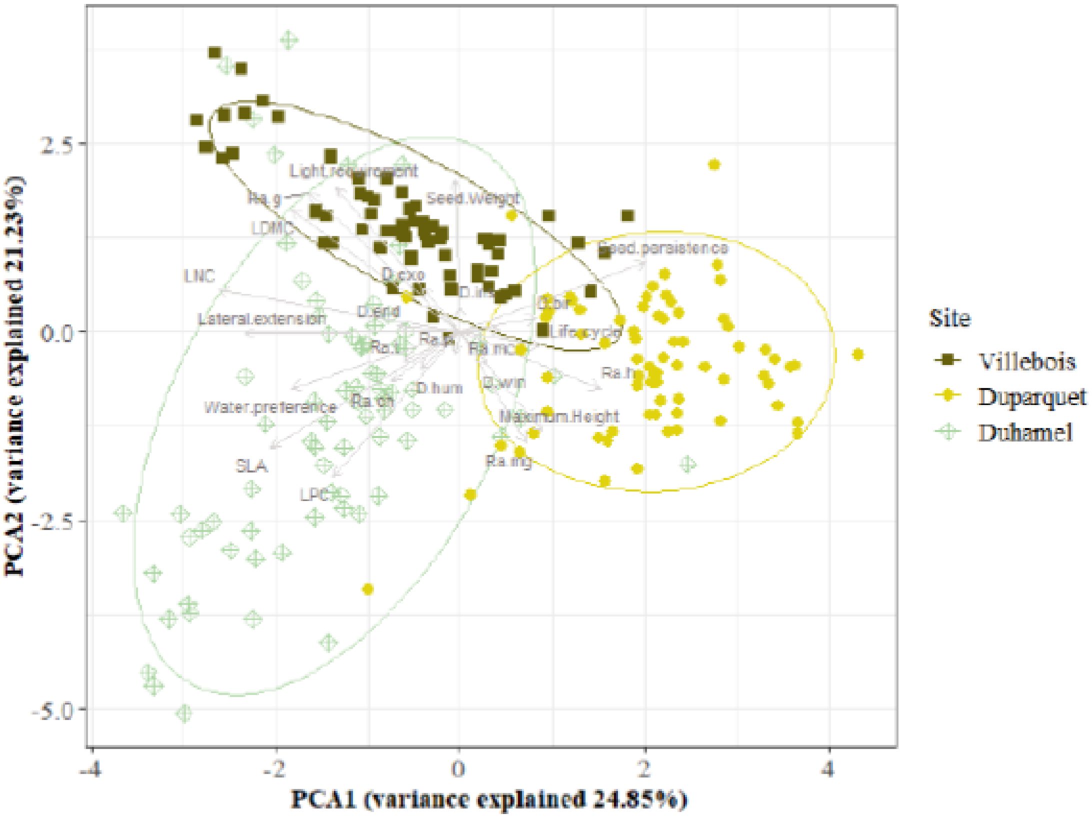

Figure 15
Trait occurrence patterns from a Principal component analysis (PCA) performed on the Community Weighted Mean (CWM) trait × site (Villebois, Duparquet and Duhamel) matrix. The direction and strength of relationships between site and functional trait are represented by light grey arrows and their length. The ellipses represent the 95% confidence intervals of the mean positioned according to sites (Villebois in dark green, Duparquet in yellow, Duhamel in light green). See Tableau 2 for trait descriptions.

Responses of community functional composition to plantation type at each site. At the site level, the PCA of Villebois, polyclonal plantations were generally centered in the middle of the PCA and had no specific traits to distinguish them from monoclonal plantations except for species with a preference for wetter soil which had a higher abundance in polyclonal plantations than in monoclonal plantations (Figure 16a). The first axis (38.43% of variance) explained the differences between Clone1 and Clone3 and the other plantation types in terms of colonization, persistence, dispersal, and competition traits (Figure 16a). Vascular plant communities in Clone1 and Clone2 were composed of geophytes and shade-intolerant species with higher LNC, LDMC, seed weight, extensive propagation and maximum height than in other plantation types (Figure 16a). Hemicryptophytes and species that had lower seed weight, and higher seed persistence were abundant in all plantation types (Figure 16a).

At Duparquet, the first axis of the PCA (22.36% of variance) separated Clone3 from all other plantation types (Figure 16b). The functional composition of vascular plant communities was related to seed persistence, lateral extension, water preference, LPC and LDMC at the Duparquet site. Hemicryptophytes with high viability of seed banks were abundant in Clone3 plantations, while species with high lateral extension, higher LPC and LDMC and a preference for higher soil moisture dominated Clone1 and Clone2 plantations (Figure 16b). There was an evolution of vascular plant community acquisition strategies along the second axis (17.09% of variance), distinguishing Clone1 and Clone2 from Clone4 (Figure 16b). Communities in Clone1 and Clone2 had smaller height and lower SLA, while those in Clone4 were taller and exhibited higher SLA (Figure 16b). Communities in polyclonal plantations were distributed along both axes, indicating that abundant traits in monoclonal plantations were also found in polyclonal plantations (Figure 16b).

At Duhamel, the first axis of the PCA (30.91% of variance) separated Clone1 and Clone4 on the left side from Clone3 and Polyclonal plantations on the right site (Figure 16c). Communities in Clone1 and Clone4 plantations exhibited more acquisitive traits such as higher SLA, LPC and LNC, while Clone3 and Polyclonal plantations were associated with shade-tolerant species with higher LDMC and seed weight and with insect-dispersed species (Figure 16c). Hemicryptophytes and chamaephytes had higher abundance in Clone1 and Clone4, while geophytes and therophytes were more abundant in Clone3 and polyclonal plantations (Figure 16c). Vascular plant communities in Clone2 plantations were distributed along the first axis, indicating that traits that were abundant in other plantation types associated with the first axis were present in Clone2. The second axis (20.33% of variance) reflected variability in the functional composition of traits within each plantation (Figure 16c). Variability along the second axis was predominantly associated with persistence traits such as seed persistence, life cycle and lateral extension.

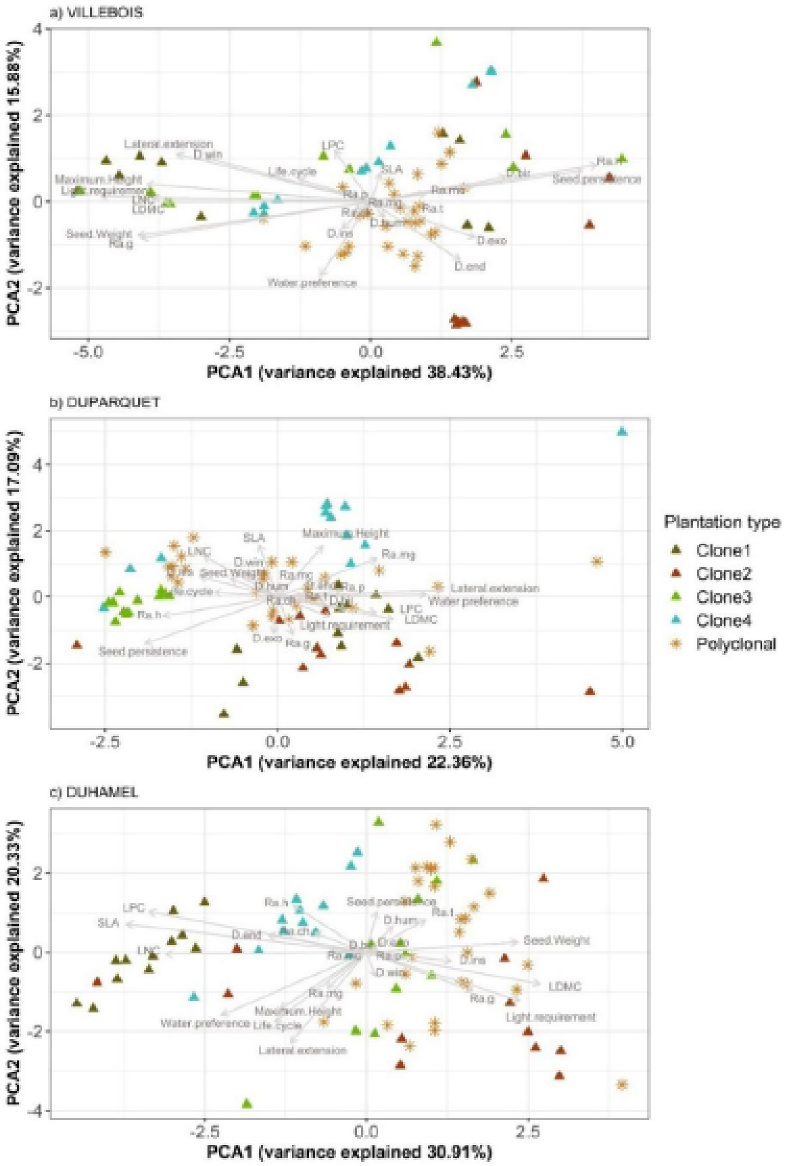

Figure 16
Trait occurrence patterns from a Principal component analysis (PCA) performed on the Community Weighted Mean (CWM) trait × plantation type (Clone1, Clone2, Clone3, Clone4 and Polyclonal plantations) matrix at each site (Villebois, Duparquet and Duhamel). The direction and strength of relationships between plantation type and functional trait are represented by light grey arrows and their length. The symbol colors represent the plantation types (Clone1 in dark green, Clone2 in light brown, Clone3 in light green, Clone4 in light blue and Polyclonal in orange). See Tableau 2 for trait descriptions.

Tableau 6
Effect of plantation type, site and their interaction on the functional composition of vascular plant community using the permutational multivariate analysis of variance (PERMANOVA).

Variable	Df	Sum of squares	F statistics	R^2	*p*
Plantation type	4	0.25	53.26	0.14	**0.001*****
Site	2	0.72	309.85	0.42	**0.001*****
Plantation type: Site	8	0.51	54.53	0.29	**0.001*****
Residuals	216	0.25		0.14	

(*) indicates the levels of significance: ***$0.0001 < p < 0.001$.

2.6 Discussion

2.6.1 Taxonomic and functional diversity of understory vegetation between plantation types

We found evidence of changes in functional diversity of vascular plants related to plantation type, indicating the effects of the overstory composition on functional diversity (Pitman *et al.*, 2014; Barsoum *et al.*, 2016). We showed that polyclonal plantations increased functional diversity compared to monoclonal plantations, which is consistent with our hypothesis and aligns with the theory that mixing species with different canopy traits has a positive effect on understory vegetation biodiversity. A previous study in the same plantations showed that macronutrients in poplar leaves were higher in polyclonal plantations than in monoclonal plantations at all three sites (Elferjani *et al.*, 2014), suggesting a positive effect of mixing clones on nutrient uptake and a reduction in competition for nutrients. These conditions probably led to greater use of limited resources and favored the availability of resources in polyclonal plantations which increased the functional diversity of vascular plants (Turnbull *et al.*, 2016; Barry *et al.*, 2019). Light is one of the most important factors explaining the understory vegetation community composition (Messier *et al.*, 2009; Wei *et al.*, 2019). We expected polyclonal plantations to create more heterogeneous light conditions from that of monoclonal plantations, as the canopy structure of the clones is different, which could support a broader diversity of plant species and functional traits (Härdtle *et al.*, 2003; Barbier *et al.*, 2008; Forrester *et al.*, 2019). However, in our study, incident light was generally similar between monoclonal and polyclonal plantations (Tableau 3). Light availability measured throughout the entire growing season is probably more relevant for understory vegetation composition than single-period measurements (Thomas *et al.*, 1999; Augspurger, 2008). Thus, because clones have different phenological traits (Elferjani *et al.*, 2016), clones that emerge later but lose their leaves earlier may allow more incident light to reach the understory during understory plant growth periods. Conversely, clones that leaf-out earlier and have a later dormancy period have a longer growing season and offer a longer period of time when canopy closed. Therefore, this dynamic canopy phenology in polyclonal plantations may have contributed to more heterogenous light conditions, that could explain the increased functional diversity of vascular plants. In contrast, single clones create uniform light conditions in the understory leading to consistent light penetration that have been shown to reduce functional diversity of communities (Scherer-Lorenzen, 2014; Ampoorter *et al.*, 2020).

The positive effects of mixing clones on functional diversity were more noticeable at the northernmost site (i.e., Villebois) than at the other sites, indicating that the effects of plantation type on functional diversity depended on site. Northernmost latitudes typically experience harsher environmental conditions (e.g., shorter growing season, and lower temperatures) (Chapin *et al.*, 2002). This suggests that mixing clones when environmental conditions become harsher resulted in positive effects of mixed overstories, as complementarity becomes more effective (Loreau *et al.*, 2001; Hooper *et al.*, 2005a; Del Río *et al.*, 2014).

Our findings highlight the importance of a functional approach to assess the effects of overstory composition on understory vegetation (Hooper *et al.*, 2005a), because based on taxonomic diversity, polyclonal plantations had similar numbers of understory vegetation species as monoclonal plantations, regardless of site. The absence of any remarkable effects of polyclonal plantations on understory vegetation diversity could result from the difficulty of distinguishing the effects of understory composition from other factors such as site characteristics, topography, biotic interactions and environmental filtering (Nadrowski *et al.*, 2010; HilleRisLambers *et al.*, 2012; Cardou *et al.*, 2022).

2.6.2 Effects of interaction between plantation type and site on understory vegetation community composition

Our results show that plantation type and site had interacting effects on understory vegetation community composition. Vascular plant community composition in polyclonal plantations was always different from that in monoclonal plantations across the three sites which is consistent with our hypothesis (Tableau S4). However, vascular plant community composition was similar between monoclonal plantations at the Villebois site, while it differed between all monoclonal plantations except for Clone2 and Clone3 at the Duhamel site (Tableau S4). In resource-rich environments, the effects of species traits (linked to species identity) on biodiversity can be more pronounced than those of the overstory diversity or composition (Loreau & Hector, 2001; Cavard *et al.*, 2011b). Soil nutrients were more available at the Duhamel site than at Villebois and Duparquet (Elferjani *et al.*, 2014), which suggests that the similarity in vascular plant community composition between Clone2 and Clone3 at Duhamel may be due to the fact that they are crossbreeds (*P. balsamifera* x *maximowiczii* Henry) were similar but were different from those of the other clones.

The abundance of ruderal and light-demanding species in Clone1 at the Duparquet site may be explained by the effect of incident light, which was greater in Clone1 than in Clone4 plantations, although this was not significant (Tableau 3). This has probably generated opportunities for colonisation by light-demanding species in Clone1 plantations. It is therefore possible to link the greater functional diversity in Clone1 at the Duparquet site, which was similar to that of polyclonal plantations, to the persistence of shade-intolerant species in addition to the pre-established forest plant species before planting (De Grandpre & Bergeron, 1997; Fahey & Puettmann, 2007).

Bryophyte and lichen community composition was similar between plantation types across the three sites except between Clone2 and Clone4 at the Villebois site, where Clone2 was associated with *Brachythecium campestre* (BRACAM), while Clone4 was associated *Campyliadelphus chrysophyllus* (CAMCHR). *Brachythecium campestre*

(BRACAM) is a generalist moss species that grows on various substrates and in different microclimatic conditions, while *Campyliadelphus chrysophyllus* (CAMCHR) prefers calcareous substrates, more consistently moist environments and semi-shaded conditions (Faubert, 2012). This indicates that at Villebois, Clone2 and Clone4 might have created differing abiotic environments due to their various traits and produced incident light (higher in Clone2 than in Clone4, although not significant, Table 2) that mainly affect bryophyte communities. However, further measurements would be needed to evaluate substrate characteristics and soil moisture under each clone to fully understand the effects of these clones on bryophyte composition at the Villebois site. The four clones we studied were from deciduous trees that are known to modify forest floor conditions through the nutrient-rich broadleaf litter which favors litter decomposition and increases soil temperature and humidity (Hart & Chen, 2008; Laganière *et al.*, 2010; Augusto *et al.*, 2015). Thus, the consistency of environmental conditions and the similarity of microhabitats across all plantation types probably favored the establishment of similar bryophyte and lichen communities. Moreover, generalist and common species dominated bryophyte assemblages in all plantation types, leading to limited differences in community composition between plantations on the same site. The similarity in bryophyte and lichen community composition between plantation types could also be related to the greater effect of site, which resulted in a dilution of the effect of plantation type on bryophyte and lichen community composition at each site.

2.6.3 Effects of plantation type and site interaction on vascular plant functional composition

The disparity of functional composition between monoclonal and polyclonal plantations was more pronounced at the southernmost site (i.e., Duhamel), where Clone1 and Clone4 differed from polyclonal plantations and Clone3. The divergence in vegetal communities has been found to be greater in resource-rich environments compared to resource-poor environments (Royer-Tardif *et al.*, 2017). Soil nitrogen availability was higher at the Duhamel site compared to the Duparquet and Villebois sites (Elferjani *et al.*, 2014). Thus, this may explain why plantations on more productive sites (i.e., Duhamel) exhibited greater differences in the functional composition of plant communities between plantation types. We showed that vascular plant community had acquisitive traits (i.e., higher SLA, LPC and LNC) in Clone1 and Clone4 at the Duhamel site. Ruderal species are known to acquire the most resources and dominate available space (Grime, 2006). Plant understory species such as *Epilobium angustifolium* (EPIANG) are qualified as ruderals and strong competitors for light and nutrients (Hangs *et al.*, 2003; Balandier *et al.*, 2006). Therefore, the dominance of this species in Clone1 plantations at the Duhamel site probably explained the abundance of species with higher SLA, LNC and LPC and the lower vascular plant diversity. Thus, the low abundance of species with conservative traits in Clone1 could be explained by the combination of a greater number of species with higher SLA, LPC and LNC, which compete conservative species. Clone4 is a higher yielding clone and has a denser canopy that could offer a longer closed-canopy environment than the other clones (Elferjani *et al.*, 2014, 2016). Thus, this might have increased humidity under canopies and enhanced nutrient cycling (Forrester & Bauhus, 2016). Moreover, this clone has low soil C/N ratios which could stimulate organic matter decomposition (Rabearison *et al.*, 2023) and favor nutrient-loving and acquisitive species in Clone4 at the Duhamel site through rapid mineralization of organic matter.

In general, mixing species has positive effects on soil nutrient availability, which generally results in shifts towards more acquisitive traits such as higher SLA, LPC and LNC, and lower LDMC (Puettmann, 2011; Maxwell *et al.*, 2020; Shovon *et al.*, 2020). However, our study showed that vascular plants exhibited conservative traits such as lower leaf N and P and higher LDMC shade tolerance, and seed weight in polyclonal plantations at the Duhamel site. Clones grown in mixtures tended to have greater leaf macronutrients than monoclonal plantations, suggesting an increase in the proportion of resources captured on a site (Richards *et al.*, 2010; Elferjani *et al.*, 2014). Our findings could therefore be due to fact that soil nutrients in a resource-rich environment (i.e., Duhamel) were mainly allocated to poplar leaves, which may have limited nutrient uptake by understory plants and promoted vascular plant species with conservative traits. The presence of shade-tolerant, heavy-seeded plant species in polyclonal plantations could also reflect their adaptation to the closed-canopy forest environment (Bergeron *et al.*, 2014; Barsoum *et al.*, 2016).

At Villebois and Duparquet, the traits of vascular plants associated with each monoclonal plantation were generally present in polyclonal plantations. This suggests that on these sites, mixing species favored the co-occurrence of species with a wider range of traits (e.g., resource acquisitive and conservative strategies) (Nichols *et al.*, 2006; Liu *et al.*, 2018; Feng *et al.*, 2022). Thus, polyclonal plantations might limit the dominance or redundancy of a vascular plant traits and favor the establishment of species with more diverse strategies to thrive in the niche space due to increasing resource availability (Bernard-Verdier *et al.*, 2012; Barsoum *et al.*, 2016).

2.6.4 Understory vegetation composition along a latitudinal gradient

We found evidence that the understory vegetation community composition exhibited sensitivity to site along the latitudinal gradient. Vascular plant community composition varied between agricultural and forest sites which concur with our previous study (Randriamananjara *et al.*, 2023). Forest plant, tree and shrub species were commonly present at the Duparquet site, which was probably related to the regrowth of their stumps or root particles and the presence of seed banks from the previous forest. This could explain the community composition, which reflected the forest environment prior to planting (Bremer & Farley, 2010; Brudvig & Damschen, 2011). In contrast, ruderal and herbaceous species were dominant at the Duhamel and Villebois sites. Our findings might be explained by the proximity of plantations to seed sources and the surrounding environment (Hartley, 2002; Felton *et al.*, 2010), leading to a plant species composition that reflected the surrounding agricultural environment at the Duhamel and Villebois sites. *Brachythecium campestre* which is a colonizing and perennial species and is known as field cushion moss (Crum & Anderson, 1981; Gignac & Dale, 2005; Takala *et al.*, 2012) was associated with the Villebois site. The presence of this moss species at the Villebois site therefore reflected previous habitat type and characteristics, as the site was previously dominated by cereal and hay crops. Our study showed that lichens were commonly found at the Duparquet site. Lichens thrive in sunlit areas, thus, the possible explanation is the availability of incident light

(Palmqvist & Sundberg, 2000; Jüriado *et al.*, 2009), since it was greater at Duparquet than at the other sites (Tableau 3). At Duparquet, soil nitrogen was less available than at the Duhamel and Villebois sites (Elferjani *et al.*, 2014), and soil exposure after soil preparation was more intense leading to slower tree growth rates at Duparquet. This probably favored the establishment of terricolous lichens by creating environments with reduced competition for space, as their establishment is generally constrained by the persistence of dense vegetation (Gilbert, 1993; Randlane *et al.*, 2017). The presence of pioneer and ruderal moss species such as *Ceratodon purpureus* (CERPUR) at the Duparquet site might also be linked to the open canopy and bare soil in the previously forest site. *Fissidens osmundoides* often thrives in specific microhabitats, such as wet, shaded, and nutrient-rich environments (Faubert, 2012-2014). Its presence at the Duhamel site may therefore indicate specific ecological conditions, such as high humidity, stable moisture levels, and low light availability.

2.6.5 Functional composition of vascular plant communities along a latitudinal gradient

As expected, the functional composition of vascular plant communities varied along the latitudinal gradient which was represented by sites. Vascular plant communities at the northernmost site (i.e., Villebois) were associated with conservative traits such as higher LDMC and seed weight. We showed that mean annual temperature and precipitation influenced the functional composition of vascular plant communities across sites along the second axis of the PCA (Tableau S7). This suggests that the shorter growing season and lower temperature at Villebois may affect and adjust photosynthetic activity. Adjustment of plant photosynthetic activity to lower temperatures could lead to efficient carbon assimilation and resource conservation through thicker leaves (Sultan, 2000; Wright *et al.*, 2004; Ordoñez *et al.*, 2009). This probably explained the abundance of species with higher LDMC at the Villebois site. Moreover, the abundance of species with higher seed weights at the Villebois site might be due to an adaptation to cope the harsher environmental conditions in northern latitudes, as higher seed weights allow species to conserve metabolic reserves (Westoby *et al.*, 1996). Our results confirm that dominant species generally have conservative traits to optimize resource use in resource-limited environments

(Pérez-Ramos *et al.*, 2012; Reich, 2014; Wright *et al.*, 2017). In contrast, dominant species exhibited acquisitive traits such as higher SLA in resource-rich environments such as at the southernmost site (i.e., Duhamel). All plantation types had greater growth rates at Duhamel than at other sites due to favorable environmental conditions. (Elferjani *et al.*, 2014), which probably explained the shadier environment than at the Duparquet and Villebois sites due to canopy closure (Tableau 3). In shadier environments, plants acclimatize their leaves by increasing their SLA to intercept more light (Barbier *et al.*, 2008; Ames *et al.*, 2016). Thus, a higher SLA at Duhamel may represent a morphological adjustment to the competition for light to increase the amount of intercepted radiation that has been reduced by the shading effect related to the canopy closure.

Our study showed that vascular plant communities at the Villebois and Duhamel sites were both associated with higher leaf N and P concentrations. At Villebois, the possible explanation is that leaf nitrogen and phosphorus concentrations generally increase from southern to northern latitudes to maintain metabolic efficiency and photosynthetic activity (Körner, 1995; Reich *et al.*, 2009). At Duhamel, this could be explained by differences in the chemical characteristics of each site, as soil N and P concentrations were higher at Duhamel than at Duparquet and Villebois (Elferjani *et al.*, 2014). The availability in soil nutrients could have favored better nutrient uptake, leading to higher leaf nutrient content (Ågren, 2004). At Duparquet, the functional composition of vascular plant communities was related to the previous forest site where species with higher seed persistence and life cycle were abundant and reflected the vascular plant community composition (i.e., forest specialist, tree and shrub species) at this site.

2.7 Conclusion

Our study is among the first to assess the effects of mixing clones created from a similar genus on understory vegetation biodiversity. We showed that polyclonal plantations increased plant functional diversity and provided justification that a functional approach allowed us to understand changes in understory vegetation and compare different ecosystems (Aubin *et al.*, 2007). Our results highlight a more pronounced positive effect of polyclonal plantations on functional diversity in more difficult environments (i.e., Villebois).

We found interactive effects of plantation type and site on understory vegetation biodiversity suggesting that site characteristics should be considered when assessing the effect of plantation type on understory vegetation. The community functional composition in polyclonal plantations was generally more diverse than in all monoclonal plantations suggesting a decrease in the dominance of specific functional traits that are often prevalent in monoclonal plantation understories. Lastly, our results showed that understory vegetation can exhibit different diversity, composition and functional traits in each monoclonal plantation from site to site.

Based on this study, we recommend mixing poplar clones that have different phenological and morphological traits to promote more heterogeneous habitats and favor functional diversity. Our results support polyclonal plantations as a management recommendation for functional diversity in resource-limited conditions. Our findings suggest considering the effects of clone identity and dissimilarity on understory vegetation biodiversity. Here, we showed that Clone4 was the best clone for increasing the number of vascular plant species at previous agricultural sites, while Clone1 favored the establishment of light-demanding species in previous forested sites and increased function diversity by favoring this type of species combined with pre-planting forest species.

2.8 Acknowledgments

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3. UNDERSTORY VEGETATION DIVERSITY AND COMPOSITION IN INTENSIVELY MANAGED PLANTATIONS COMPARED TO EXTENSIVELY MANAGED FORESTS

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3.1 Résumé

Les plantations sont reconnues pour leurs avantages en production de bois, mais il reste à déterminer si elles peuvent soutenir une diversité de végétation de sous-bois comparable à celle des forêts indigènes. L'influence de l'identité des espèces de la canopée liée à leur origine (exotiques *vs* indigènes) sur la naturalité des plantations en termes de biodiversité de la végétation de sous-bois par rapport aux forêts indigènes demeure également incertaine. Dans cette étude, nous avons évalué la diversité et la composition des bryophytes, des lichens, et des plantes vasculaires dans des plantations de peupliers hybrides (*Populus* spp.) exotiques et indigènes, ainsi que dans des plantations d'épinettes (*Picea* spp.) exotiques et indigènes. Nous avons comparé ces plantations à des forêts de référence ayant des types de canopée similaires (conifère, feuillu, mixte) dans la forêt boréale méridionale du Québec. Nous avons également examiné si l'identité des espèces d'arbres dans les plantations influence la biodiversité de la végétation de sous-bois par rapport aux forêts de référence. Nos résultats montrent que les plantations ne sont pas des déserts de biodiversité, car les plantations mixtes présentaient une diversité de bryophytes et de plantes vasculaires comparable à celle des forêts mixtes de référence. La présence d'épinettes indigènes et de peupliers exotiques dans les plantations mixtes a augmenté la diversité des bryophytes et des plantes vasculaires, respectivement. Cela suggère que l'effet des plantations sur la diversité des espèces de sous-bois, comparé aux forêts de référence, était lié à l'identité des espèces d'arbres dans les plantations. Les plantations étaient associées à des espèces végétales rudérales, tandis que les forêts de référence abritaient principalement des espèces forestières. La composition des bryophytes était similaire entre les plantations et les forêts de référence, tandis que les lichens étaient présents uniquement dans les plantations. Nos résultats soulignent que les plantations, en particulier les mélanges d'épinette blanche et de peuplier exotique, constituent une option prometteuse pour maintenir la biodiversité dans les stratégies de reboisement.

Mots-clés : plantation, forêt, végétation de sous-bois, biodiversité, identité des espèces

3.2 Abstract

The benefits of plantations for wood production are well known, but it is unclear whether they have a clear negative effect on biodiversity, compared to native forests. It is also unclear how overstory species identity (i.e., exotic, compared to native) would interact with the simple plantation effects on understory vegetation biodiversity. Here, we assessed bryophyte, lichen, and vascular plant diversity and composition in mono-specific and mixed plantations of exotic and native hybrid poplars (*Populus* spp.) and exotic and native spruces (*Picea* spp.). We compared these plantations to reference forests with similar overstory types (coniferous, deciduous, mixed) to those of the plantations in the southern boreal forest of Quebec. We also assessed whether the overstory species identity in plantations influenced understory vegetation biodiversity compared to reference forests. Our results show that plantations were not biological deserts, since mixed plantations contained similar bryophyte and vascular plant diversity as reference mixed native forests. The presence of native spruces and exotic poplars in mixed plantations increased bryophyte and vascular plant diversity respectively. This suggests that the influence of plantations on understory species diversity, compared to reference forests, was linked to the overstory species identity. Plantations were associated with ruderal plant species, while reference forests were composed of forest species. Bryophyte composition was similar in plantations and reference forests, while lichen species were only present in plantations. Our findings highlight that plantations, especially mixtures of white spruce and exotic poplar, are a promising option for planting strategies to enhance biodiversity.

Keywords: plantation, forest, understory vegetation, biodiversity, species identity

3.3 Introduction

Wood production from plantations is predicted to grow 37% by 2050 to meet increasing global wood demand (Jürgensen *et al.*, 2014; FAO, 2022). However, despite their utility because of high wood production, plantations raise concerns about their implications for biodiversity (Bremer & Farley, 2010; Barrette *et al.*, 2014). Establishment of plantations commonly requires intensive management practices such as mechanical site preparation, which can disturb the forest floor, expose mineral soils and eliminate or modify substrates that are favorable to understory vegetation species (Battles *et al.*, 2001; Ódor & Standovár, 2001; Bock & Van Rees, 2002; Bauhus *et al.*, 2009; Chaves Cardoso *et al.*, 2020). Plantations generally have a homogenous structure (e.g., tree size or crown architectures) and an open canopy, which may increase light availability in the understory (Klinka *et al.*, 1996; Kremer *et al.*, 2022). These conditions likely favor ruderal and pioneer species and limit the presence of forest specialist species (Puettmann & Berger, 2006; Wilson & Puettmann, 2007; Brockerhoff *et al.*, 2008). Thus, plantations generally fail to provide suitable habitats for understory species (Simberloff & Von Holle, 1999; Duan *et al.*, 2010; Barrette *et al.*, 2014).

In contrast, native or extensively managed forests are characterized by minimal soil disturbances and without intensive silvicultural interventions (Bengtsson *et al.*, 2000; Paillet *et al.*, 2010). They are commonly structurally complex, have a larger variety of substrate types and a higher diversity of microhabitats (e.g., deadwood, soil and tree bases) than plantations (Cole *et al.*, 2008; Fritz *et al.*, 2008; Fritz & Heilmann-Clausen, 2010). Thus, a broader variety of understory species, and specifically more forest species are found in native or extensively managed forests compared to plantations (Stephens & Wagner, 2007; Lonsdale *et al.*, 2008; Kremer *et al.*, 2022; Lemessa *et al.*, 2022). The presence of forest plant species in native or extensively managed forests could be explained by the proximity to seed sources (including seed banks) in surrounding forested landscape (Hartley, 2002; Felton *et al.*, 2010; Kremer *et al.*, 2021).

Although there is evidence that plantations generally harbor fewer species than native forests (Berg *et al.*, 1994; Angelstam, 1996), some previous studies suggested that plantation forests have the potential to support forest biodiversity depending on their structure and overstory composition (Gachet *et al.*, 2007; Bremer & Farley, 2010; Randriamananjara *et al.*, 2023). However, most biodiversity studies in plantations compared the understory of plantations to native old-growth forests whose structure and overstory type were different from those of plantations (Lindenmayer & McCarthy, 2002; Bauhus *et al.*, 2009). This comparison is often not relevant for plantations, as native old-growth forests represent ecosystems at a more advanced stage of succession and thus provide more heterogeneous habitats compared to those found in plantations or younger native forests (Stephens & Wagner, 2007; Paquette & Messier, 2010; Soto & Puettmann, 2020). Thus, it may be more appropriate to assess the effects of plantations on understory vegetation biodiversity by comparing them to native forests with similar structures and overstory types (Royer-Tardif *et al.*, 2017).

Aspects of overstory species identity related to species origin (i.e., exotic *vs* native species) could also be an important driver of the effects of plantations on understory vegetation biodiversity (Barbier *et al.*, 2008; Brockerhoff *et al.*, 2008; Gustafsson *et al.*, 2023) compared to native forests. Plantations of exotic tree species (i.e., originating from at least one non-native parental species) are likely to be increasingly used due to their rapid growth and high wood production (Elfving *et al.*, 2001). However, a previous study showed that plantations of exotic species (*Quercus rubra*) generally contained lower bryophyte and lichen diversity compared to plantations of native species (*Q. robur* and *Q. petraea*) (Gustafsson *et al.*, 2023). Moreover, plantations of exotic species could favor the establishment of exotic understory species and are perceived as artificial habitats compared to plantations of native species (Bremer & Farley, 2010; Barrette *et al.*, 2014). Thus, it is suggested that native tree species should be favored over exotic tree species to reduce differences in understory vegetation biodiversity between plantations and native forests (Brockerhoff *et al.*, 2008).

However, the impact of introducing exotic tree species on biodiversity is highly variable and appears to depend on species, biome and region (Castro-Diez *et al.*, 2019). For example, exotic tree species had positive, negative, or neutral effects on biodiversity compared to native tree species, depending on species, region, and taxonomic group in the United Kingdom (Quine & Humphrey, 2010). A global meta-analysis revealed a consistent decline in understory species richness following the conversion of secondary forests into fast-growing exotic tree plantations, while the study showed a general increase in understory species richness when these secondary forests were replaced by native tree plantations (Bremer & Farley, 2010). In contrast, Royer-Tardif et al. (2017) found that fast-growing exotic tree plantations supported understory vegetation that was as diverse as plantations with native species and naturally regenerated native forests in a region of central Quebec, Canada. Thus, it remains uncertain whether plantations of native species harbor levels of biodiversity similar to those of native or extensively managed native forests, compared to plantations of exotic species.

Here, we compared understory vegetation diversity and composition in two different management types in the southern boreal forest of Quebec: intensively managed plantations and extensively managed native forests. For the sake of simplicity, we referred to intensively managed plantations as “plantations” and extensively managed native forests as “reference forests”. We also evaluated if the differences between plantations and reference forests depended on the overstory species identity (i.e., exotic *vs* native tree species) of plantations. We assessed species diversity and composition of three taxonomic groups: bryophytes, lichens, and vascular plants across three overstory types (coniferous, deciduous, mixed) in both plantations and reference forests. We expected that reference forests would exhibit greater understory vegetation diversity and a distinct community composition compared to plantations, because reference forests offer more complex structural attributes and microhabitats than plantations (Ehbrecht *et al.*, 2017; Ehbrecht *et al.*, 2021). We expected that ruderal species would be more common in plantations while forest species would be associated with reference forests (Puettmann & Berger, 2006). Lastly, we hypothesized that the difference between the biodiversity in the understory vegetation in plantations compared to reference forests would depend on the overstory species identity within the plantations (Brockerhoff *et al.*, 2008). We expected that the presence of native species in plantations would be a key factor contributing to the similarity of understory vegetation biodiversity between plantations and reference forests.

3.4 Materials and Methods

3.4.1 Study sites

The study areas were primarily in the balsam fir (*Abies balsamea*)-paper birch (*Betula papyrifera* Marsh.) bioclimatic domain of Quebec. We used three plantation sites established in 2003 near the localities of Amos (48°36'N, 78°04'W), Rivière-Héva (48°1'N, 78°16'W) and Nédelec (47°45'N, 79°22'W) (Abitibi-Témiscamingue, QC, Canada) (Figure 17). The three sites had different land-use histories prior to planting: the Amos and Rivière-Héva sites were abandoned farmland, whereas the Nédelec site was a forest site previously dominated by trembling aspen (*Populus tremuloides*), pin cherry (*Prunus pensylvanica* L.), and paper birch. The Amos and Rivière-Héva plantations were surrounded by abandoned farmland with a large proportion that was reforested with conifers, while the Nédelec plantations were surrounded by natural coniferous forests and plantations. Site preparation consisted of removing stumps and deep ploughing prior to planting (Randriamananjara *et al.*, 2023). A small tractor and discs were used to cultivate between trees and rows, controlling competitive vegetation every year for the first five years after planting.

The reference forests were located near the localities of Amos (48°34'N, 78°08'W), Duparquet (48°27'N, 79°25'W) and (48°29'N, 79°26'W), La Motte (48°17'N, 78°13'W), Launay (48°35'N, 78°26'W), Saint-Dominique-du-Rosaire (48°45'N, 78°11'W) and (48°45'N, 78°11'W), and lastly, Trécesson (48°39'N, 78°15'W) and (48°35'N, 78°16'W) (Figure 17). We selected stands with no or little slope (similar to plantations) based on the government publicly accessible database, Forêt ouverte (Gouvernement du Québec, 2021).

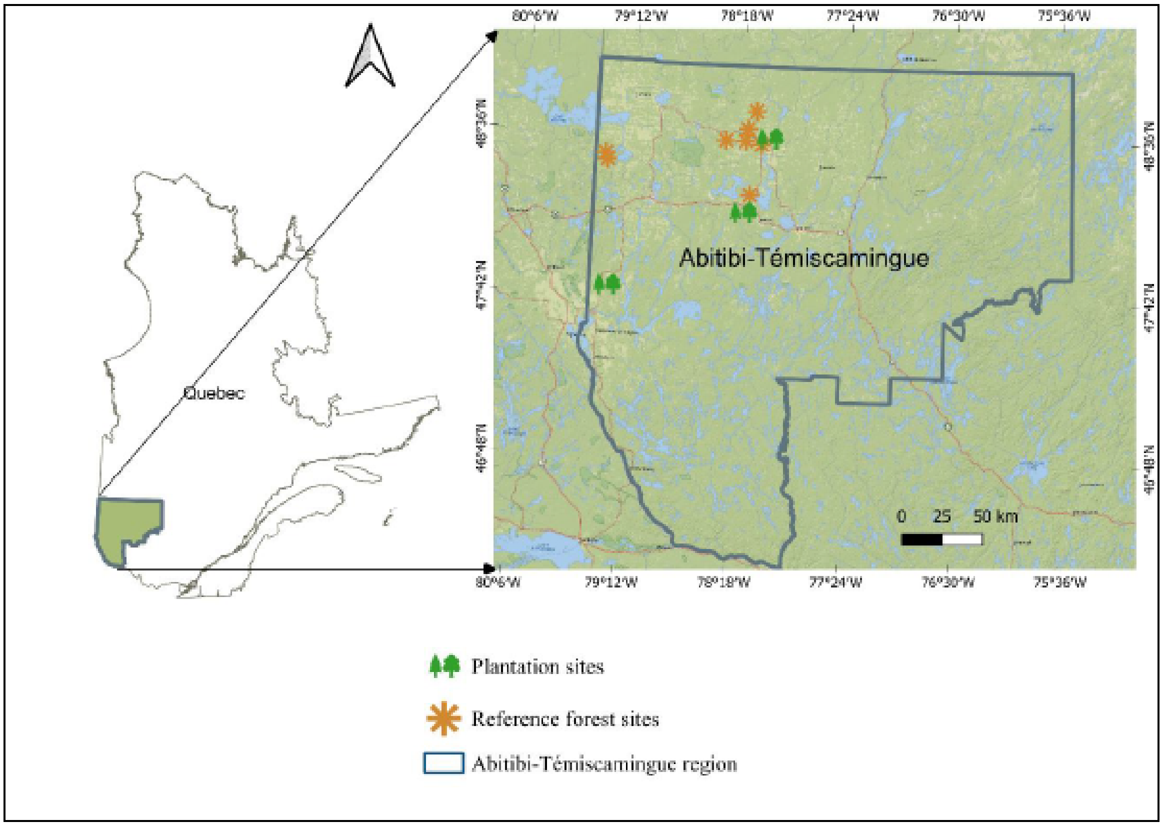

Figure 17
Location of the sites within the province of Québec, eastern Canada. Inset the region of Abitibi-Témiscamingue within Québec. Coniferous and deciduous tree symbology represents the plantation sites. Orange stars represent the reference forest sites.

3.4.2 Experimental design

Our plantations were established in three sites (replicates), split to accommodate each plantation type. Each plantation type was further split into 15x15 m plots (Randriamananjara *et al.*, 2023). Each plantation type contained 36 trees (6x6 rows of trees) with a 3x3 m spacing.

To evaluate the effects of management type on understory vegetation diversity and composition, we compare plantations to reference forests with similar overstory types (coniferous, deciduous, and mixed). First, we selected two monocultures of native species: white spruce (*Picea glauca* (Moench)) ($\mathbf{WS}_{\mathbf{pl}}$), hybrid poplar clone (*Populus trichocarpa* Torrey & A. Gray x *balsamifera* L.) ($\mathbf{poplar}_{\mathbf{native}}$), and one mixed plantation:

WS:poplar$_{native}$ (Tableau S9). To evaluate the effects of overstory species identity (native/exotic) on understory vegetation diversity and composition, we selected plantations using exotic species which were: Norway spruce (*Picea abies* (L.) Karst.) (**NS$_{pl}$**), a second hybrid poplar clone containing an exotic poplar species from Japan (*P. maximowiczii* Henry x *balsamifera* L.) (**poplar$_{exotic}$**) and three mixed plantations: **NS:poplar$_{native}$**, **NS:poplar$_{exotic}$**, and **WS:poplar$_{exotic}$** (Tableau S9). Thus, in total, we selected eight plantation types/species combinations established at each site, including four monocultures and four mixed plantations.

We then chose reference forests that had similar overstory types (coniferous, deciduous, and mixed) as the plantations. We selected three trembling aspen (**Aspen**), three white spruce (**WS$_{rf}$**), and three mixed (**WS:aspen**) forests, representing reference deciduous, coniferous and mixed forests respectively (Tableau S9). Reference deciduous forests were naturally established after clear-cutting (CC), or careful logging around advanced growth (CLAAG) operations conducted between 1995 and 1999. Reference coniferous forests were established after CC or CLAAG (1996-2004) and reforested with white spruce in 2004-2008. Reference mixed forests were composed of aspen that regenerated naturally after CLAAG (1999-2004) and were fill planted with white spruce (2004-2005). We delimited a 15x15 m area in each reference forest to have the same sample size as our plantations (Tableau S9).

Within each stand type (i.e., NS$_{pl}$, WS$_{pl}$, WS$_{rf}$, poplar$_{native}$, poplar$_{exotic}$, Aspen, NS:poplar$_{native}$, NS:poplar$_{exotic}$, WS:poplar$_{native}$, WS:poplar$_{exotic}$ and WS:aspen), we measured the diameter at breast height (DBH) and the height of trees. To reduce the influence of stand structure on understory vegetation diversity and composition, we chose reference forests with DBH and height values similar to those of our plantations. However, we had difficulty locating comparable stands in the region and most had smaller DBH values than plantations (Tableau 7).

3.4.3 Vegetation survey

We systematically placed three 1 m^2 quadrats under trees along a diagonal line within each plantation and reference forest except for mixed stands where we placed six 1 m^2 quadrats (3 under poplar trees and 3 under spruce trees). We put three 1 m^2 quadrats (without tree trunks) spaced 4.5 m apart along a linear transect established in the center of each stand type to avoid edge effects. Within each quadrat, we identified all woody plants less than 1.3 m tall, herbaceous plants, bryophytes, and lichens at the species level whenever possible. We used the VASCAN database (Brouillet *et al.*, 2010) to identify vascular plants. We collected all terricolous bryophytes and lichens and those found at the base of trees (0-50 cm) and on the trunk of trees (50-150 cm). We identified bryophyte and lichen species under a binocular microscope based on Faubert (2012) for the bryophyte nomenclature and Brodo *et al.* (2001), Hinds&Hinds (2007) and Brodo (2016) for the lichen nomenclature.

3.4.4 Light measurement

We used a LAI-2200C plant canopy analyzer (LI-COR Biosciences, Lincoln, NE) to systematically measure the incident light 50 cm above the forest floor in each stand type. First, we took full light measures in an open field as a reference (Légaré *et al.*, 2001). We then measured incident light above the quadrats under trees along a diagonal line. We calculated incident light within the stand type as the ratio of the light measured at 50 cm above the forest floor and the reference light (Légaré *et al.*, 2001). We compared the mean of incident light between each stand type of plantations and reference forests in Tableau S10.

3.4.5 Statistical analyses

Effects of management type on the understory vegetation diversity. We performed all statistical analyses using R 4.1.0 (2021-05-18) (R Core Team, 2021). We evaluated the effects of management type on the species diversity of each overstory type (i.e., coniferous, deciduous, and mixed) and each taxonomic group (i.e., bryophytes, lichens, and vascular plants) using Hill numbers, which expressed diversity indices in units of effective number of species (Chao *et al.*, 2014). We calculated the effective number or number of species (q=0), exponential of Shannon or number of frequent species (q=1), and Simpson's inverse or number of dominant species (q=2) using the «iNEXT» R package (Hsieh *et al.*, 2016). We used accumulation curves to represent the cumulative number of species as a function of the number of observations/quadrats sampled. We then compared species diversity between management types for each taxonomic group calculating sample-size-based rarefaction and extrapolation (R/E) curves with 95% confidence intervals (Chao *et al.*, 2014).

Community composition. We conducted permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations with the «adonis» function from the *vegan* package (Laliberté *et al.*, 2014) to assess the effects of management type and stand type on understory community composition. We converted understory vegetation communities into a Bray-Curtis distance matrix. We performed a visual analysis of community composition using principal coordinate analysis (PCoA) (Borcard *et al.*, 2011) with Bray–Curtis dissimilarity matrices for all 3 taxonomic groups combined. We then conducted PCoA with Bray–Curtis dissimilarity matrices for bryophytes and lichens combined and for vascular plants only of each overstory type (i.e., coniferous, deciduous, and mixed). We evaluated the composition of bryophyte and lichen communities together because lichens had very low occurrence and abundance. We used the PCoA function from the *vegan* package (Laliberté *et al.*, 2014) with the Cailliez correction (Gower & Legendre, 1986) to correct negative eigenvalues. We used the vegan «envfit» function to fit species and incident light vectors onto the ordinations with 999 permutations. We displayed only the most influential species in all ordination diagrams for clarity (envfit, $p \leq 0.05$).

Stand structure. To take into account the nested data structure, we used linear mixed models (LMM) from the package *nlme* (Pinheiro *et al.*, 2021) to assess DBH and height of tree species by overstory type. Stand DBH and height were the response variables and the overstory species of each stand type was the explanatory variable. We verified the independence of residuals, homogeneity of variances, and normality of residuals by diagnostic graphs. We tested significance of the predictors with the «Anova» function in the *car* package (Fox & Weisberg, 2019). We used the post hoc emmeans method with the package *emmeans* (Russell, 2022) when explanatory variables had a significant effect (*p value* ≤ 0.05).

Tableau 7
Mean (±SEM) DBH (cm) and height (m) of all species by overstory type. Different letters indicate that mean DBH (cm) and height (m) differed significantly between species within each overstory type. Subscripts $_{(pl), (rf), (native), (exotic)}$ respectively mean plantations, reference forests, native species, and exotic species.

Overstory type	Species	DBH (cm)	Height (m)
Coniferous	NS$_{pl}$	11.71±1.12^{b}	5.18±0.36^{a}
	WS$_{pl}$	12.87±1.12^{b}	7.38±0.45^{b}
	WS$_{rf}$	6.51±0.30^{a}	5.72±0.25^{ab}
Deciduous	poplar$_{native}$	13.27±0.97^{a}	10.06±0.93^{a}
	poplar$_{exotic}$	14.62±1.60^{ab}	13.57±0.98^{a}
	Aspen	10.05±0.38^{a}	13.48±0.31^{a}
Mixed			
NS: poplar$_{native}$	NS$_{pl}$	11.38±1.16^{bc}	5.18±0.38^{ab}
NS:poplar$_{exotic}$	NS$_{pl}$	8.32±0.86^{b}	4.68±0.48^{a}
WS: poplar$_{native}$	WS$_{pl}$	13.65±1.15^{c}	7.72±0.36^{c}
WS:poplar$_{exotic}$	WS$_{pl}$	10.02±0.63^{b}	7.21±0.39^{bc}
WS:aspen	WS$_{rf}$	4.40±0.28^{a}	4.23±0.28^{a}
NS: poplar$_{native}$	poplar$_{native}$	16.60±1.60^{ab}	9.94±1.17^{a}
NS: poplar$_{exotic}$	poplar$_{exotic}$	21.95±1.84^{c}	17.20±0.65^{b}
WS: poplar$_{native}$	poplar$_{native}$	13.42±1.55^{a}	10.61±0.98^{a}
WS: poplar$_{exotic}$	poplar$_{exotic}$	19.25±3.72^{bc}	15.04±1.53^{b}
WS:aspen	Aspen	7.40±0.36^{a}	9.67±0.37^{ab}

3.5 Results

3.5.1 Species diversity

Bryophyte diversity was similar between reference coniferous forests (WS_{rf}) and coniferous plantations (NS_{pl} and WS_{pl}) as their confidence interval curves overlapped (Figure 18a). However, reference coniferous forests exhibited higher vascular plant diversity compared to coniferous plantations. The confidence intervals of reference coniferous forests did not overlap with those of coniferous plantations for q=1 and q=2, indicating that reference coniferous forests harbored more frequent and dominant vascular plant species than coniferous plantations (Figure 18c). In contrast, bryophyte and vascular plant diversity in deciduous plantations ($poplar_{native}$ and $poplar_{exotic}$) was similar to that of reference deciduous forests (Aspen) as the confidence intervals overlapped (Figures 19a and 19c).

There was a trend that WS:poplar and WS:aspen plantations were more effective than NS:poplar plantations at harboring bryophyte species (Figure 20a). This indicates that mixed plantations containing the native WS appeared to have higher bryophyte species diversity than the exotic NS. Diversity of frequent and dominant vascular plant species was higher in reference mixed forests than in mixed plantations except in the $WS{:}poplar_{exotic}$ plantation (Figure 20c). This indicates that, native spruce (WS) and exotic poplar ($poplar_{exotic}$) had more diverse vascular plant communities than the other mixtures. Overall, no lichen species were found in any of the reference forests, while lichen diversity was consistently similar across coniferous, deciduous, and mixed plantations (Figures 18b, 19b, 20b).

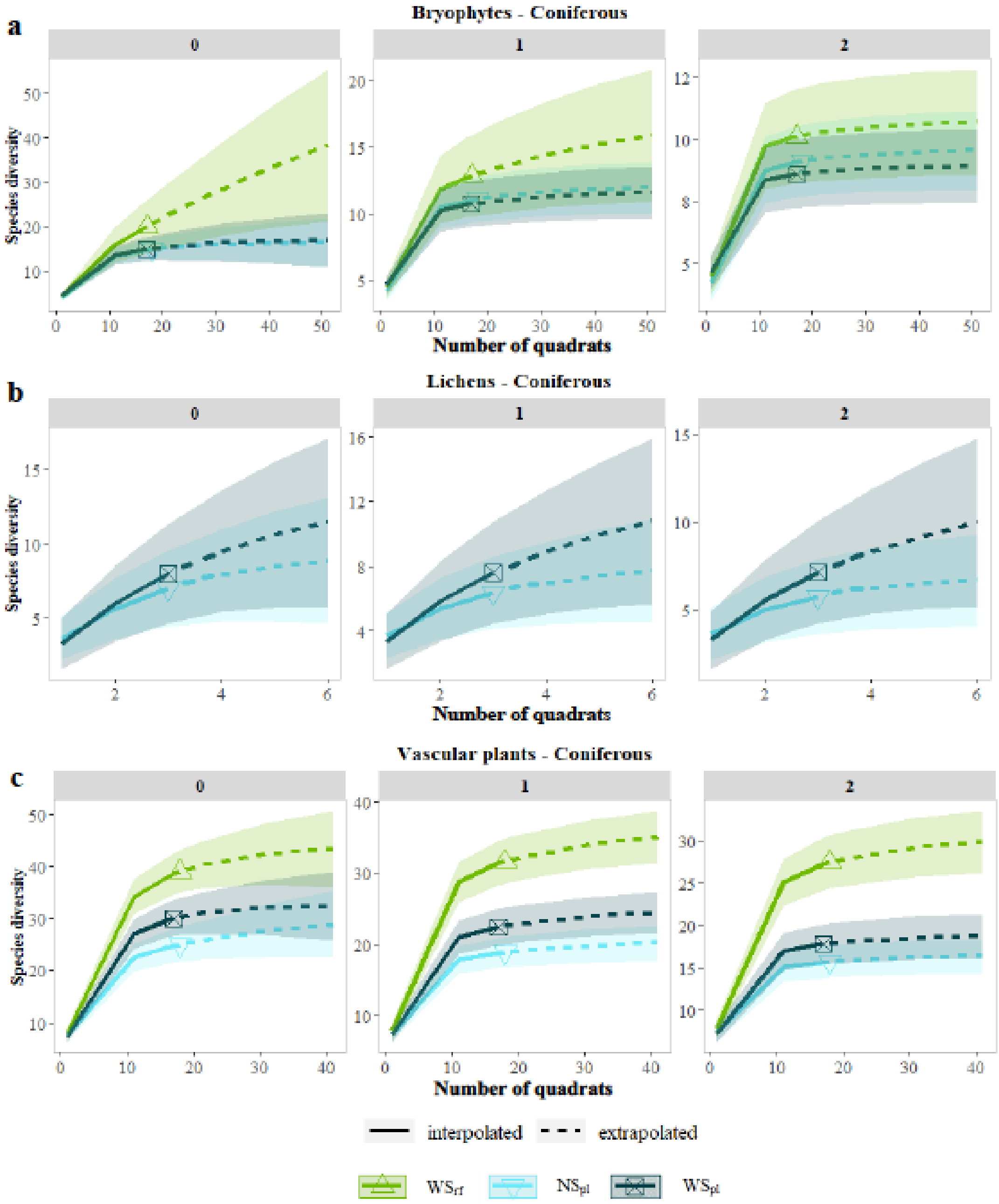

Figure 18

Species diversity including a) bryophytes, b) lichens, and c) vascular plants for Hill numbers (q = 0, 1, 2) for each of coniferous stands (WS_{rf} in green, NS_{pl} in light blue and WS_{pl} in dark blue). Sample-size-based rarefaction and extrapolation are respectively in solid and dashed line curves with 95% confidence intervals for Hill numbers. The symbols indicate the observed Hill numbers (q = 0, 1, 2).

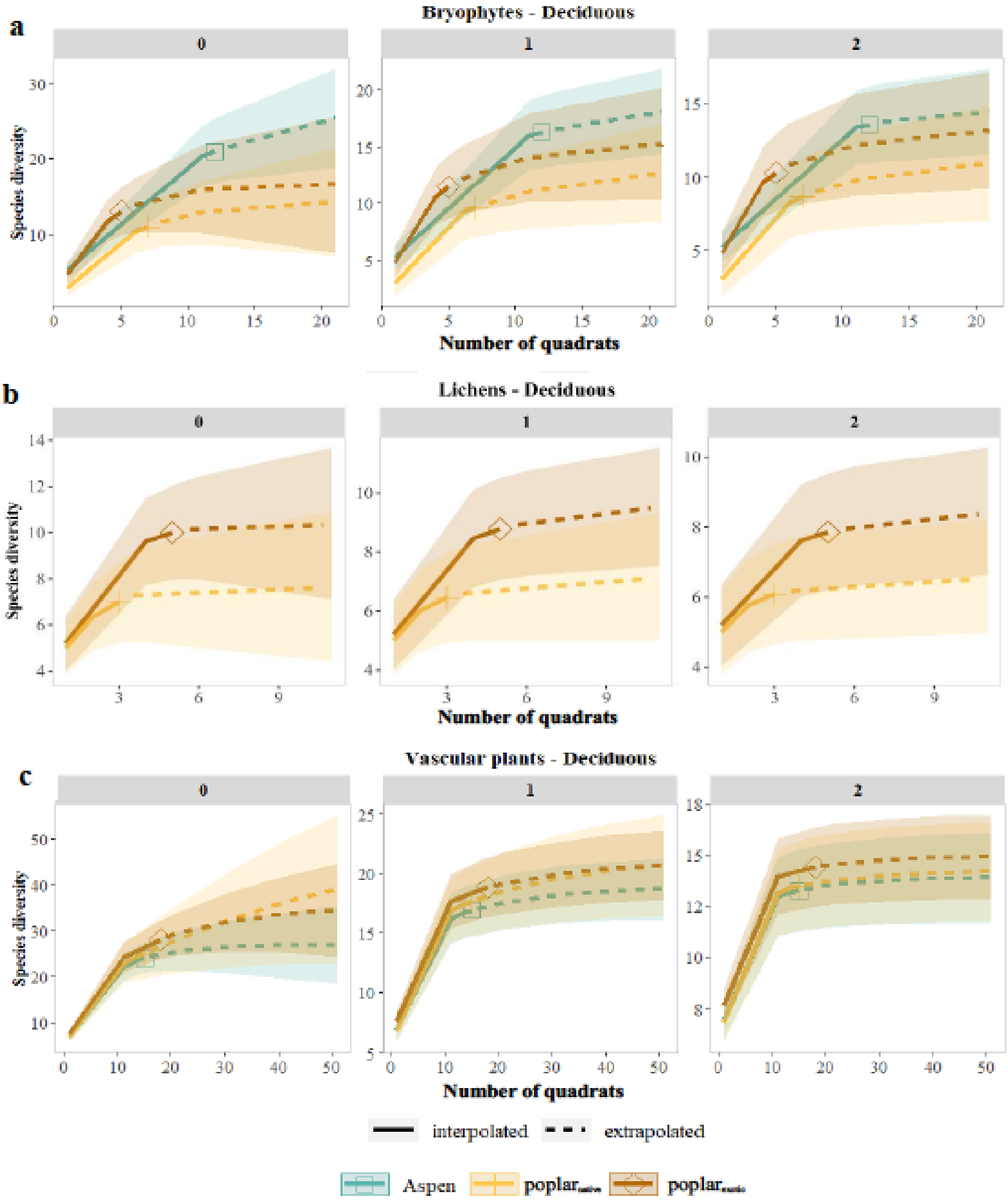

Figure 19

Species diversity including a) bryophytes, b) lichens, and c) vascular plants for Hill numbers (q = 0, 1, 2) for each of deciduous stands (Aspen in blue, poplar$_{native}$ in orange and poplar$_{exotic}$ in brown). Sample-size-based rarefaction and extrapolation are respectively in solid and dashed line curves with 95% confidence intervals for Hill numbers. The symbols indicate the observed Hill numbers (q = 0, 1, 2).

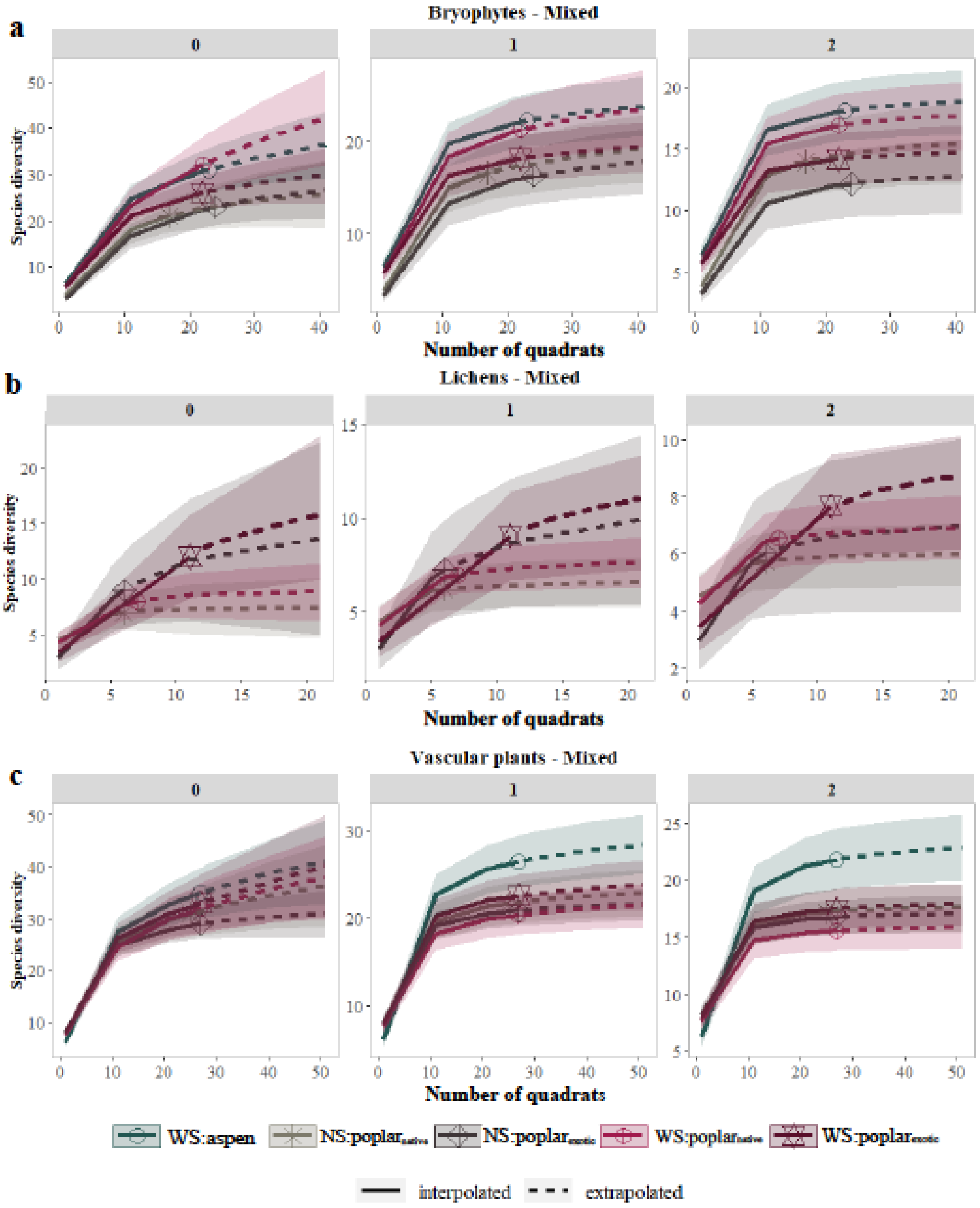

Figure 20
Species diversity including a) bryophytes, b) lichens, and c) vascular plants for Hill numbers (q = 0, 1, 2) for each of mixed stands (WS:aspen in dark blue, NS:poplar$_{\text{native}}$ in light gray, NS:poplar$_{\text{exotic}}$ in dark gray, WS:poplar$_{\text{native}}$ in dark pink and WS:poplar$_{\text{exotic}}$ in dark purple). Sample-size-based rarefaction and extrapolation are respectively in solid and dashed line curves with 95% confidence intervals for Hill numbers. The symbols indicate the observed Hill numbers (q = 0, 1, 2).

3.5.2 Influence of the management type on the understory vegetation community composition

Understory vegetation communities varied with management type (PERMANOVA; *p* = 0.001; Tableau 8a). The first axis of the PCoA explained 9.52% of the variance while the variability of species assemblages in reference forests was captured on the second axis (5.33% of variance) with a demarcation between bryophytes and vascular plants (Figure 21). Overall, the first axis showed a gradient from reference forests on the left side of the ordination (Figure 21), in association with plant species typically found in native forests such as *Acer spicatum* (ACESPI), *Alnus incana* (ALNINC), and *Trientalis borealis* (TRIBOR) to plantations on the right of the ordination (Figure 21), in association with light-demanding species such as *Carex* spp. (CARSPP), *Epilobium angustifolium* (EPIANG), *Fragaria virginiana* (FRAVIR), *Hieracium* spp. (HIESPP). Although some species were shared among the two management types, especially bryophyte species (e.g., *Brachythecium falcatum* (BRAFAL), *Campyliadelphus chrysophyllus* (CAMCHR) and *Platygyrium repens* (PLAREP)), forest species found in reference forests (e.g., *Clintonia borealis (*CLIBOR), *Lonicera canadensis* (LONCAN) and *Viburnum nudum* (VIBNUD)) were absent in plantations (Figure 21). Species that are usually sensitive to anthropogenic disturbances such as *Athyrium filix-femina* (ATHFIL) were present in reference forests but absent in plantations.

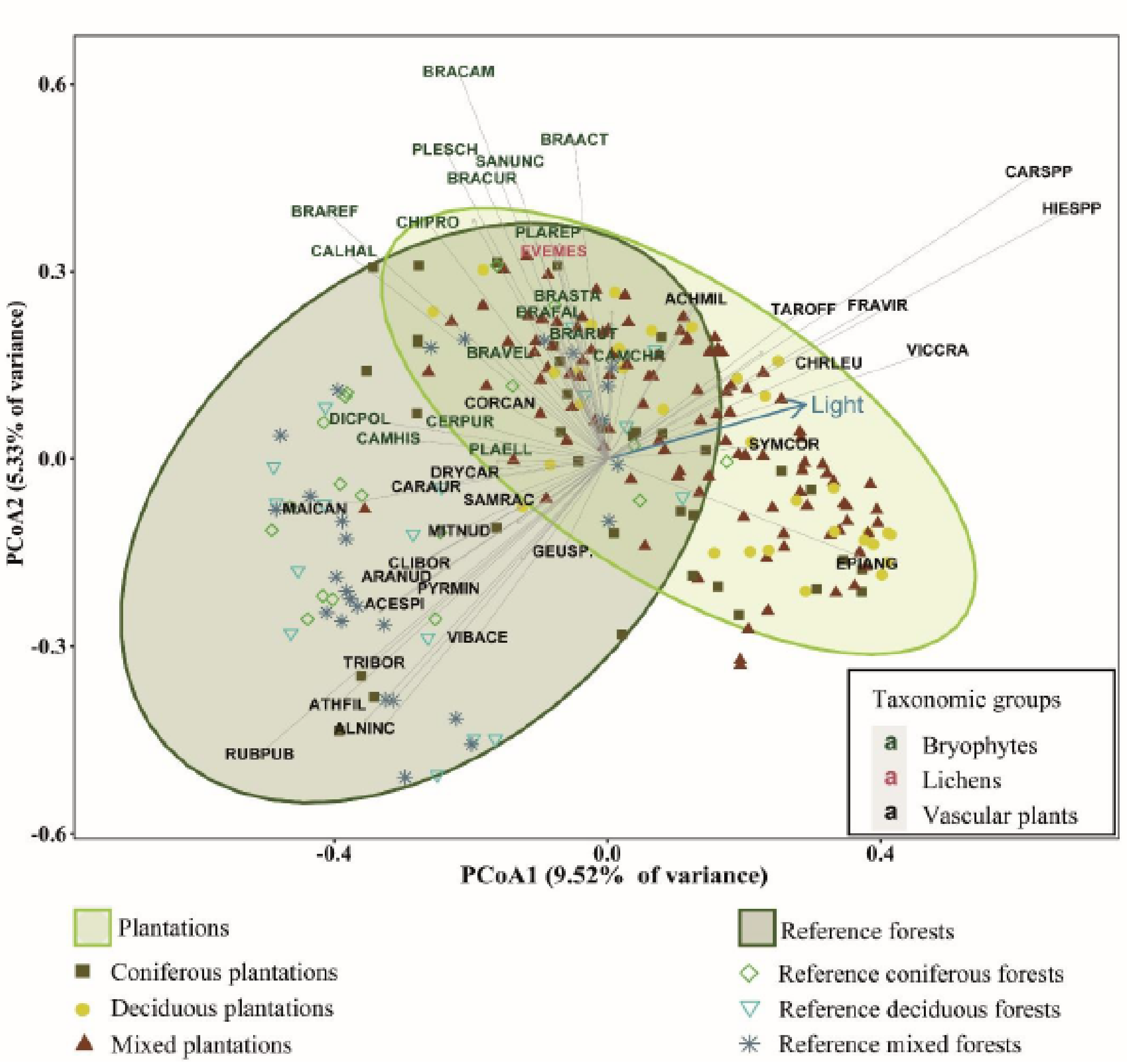

Figure 21

Principal coordinate analysis (PCoA) based on the Bray-Curtis distance on the understory vegetation. The ellipses represent the 95% confidence intervals of the mean positioned according to forest management type: plantations (light green), reference for forests (dark green). The symbols indicate stand types. Text colors indicate taxonomic groups (bryophytes in green, lichens in pink and vascular plants in black). The light blue arrow corresponds to incident light. See supplementary information Tableau S11 for more details on species names.

3.5.3 Effects of overstory species identity of plantations on understory vegetation community composition: patterns in each overstory type

Bryophyte and lichen community composition. The bryophyte and lichen community composition showed significant differences between stand types (PERMANOVA; $p = 0.007$, $p = 0.002$ and $p = 0.001$; Tableaux 2b, 2d and 2f). The first axis of the PCoA on the bryophyte and lichen community for coniferous, deciduous, and mixed overstories respectively explained 11.87%, 20.38% and 9.41% of variance while the second axis respectively explained 10.24%, 14.50% and 7.08% of variance (Figure 22).

The bryophyte composition was generally similar between the three stand types of coniferous overstories (i.e., NS_{pl}, WS_{pl} and WS_{rf}) as the ellipses of stand types overlapped (Figure 6a). There was no evident compositional disparity between exotic spruce (NS_{pl}) and native spruce (WS_{pl}). This indicates that the overstory species identity in coniferous plantations has no effect on the composition of bryophyte and lichen communities in coniferous plantations compared to reference coniferous forest.

Deciduous and mixed plantations were dominated by epiphytic lichen species such as *Evernia mesomorpha* (EVEMES), *Hypogymnia physodes* (HYPPHY) and *Tuckermannopsis americana* (TUCAME) (Figures. 6d and 6f). In contrast, reference deciduous and mixed forests were only composed of bryophytes (e.g., *Brachythecium falcatum* (BRAFAL), *Campyliadelphus chrysophyllus* (CAMCHR) and *Pleurozium sschreberi* (PLESCH)) and did not contain any lichen species (Figures. 6d and 6f). The differences in bryophyte and lichen community composition between plantations and reference forests were consistent regardless of overstory species identity in deciduous and mixed overstories.

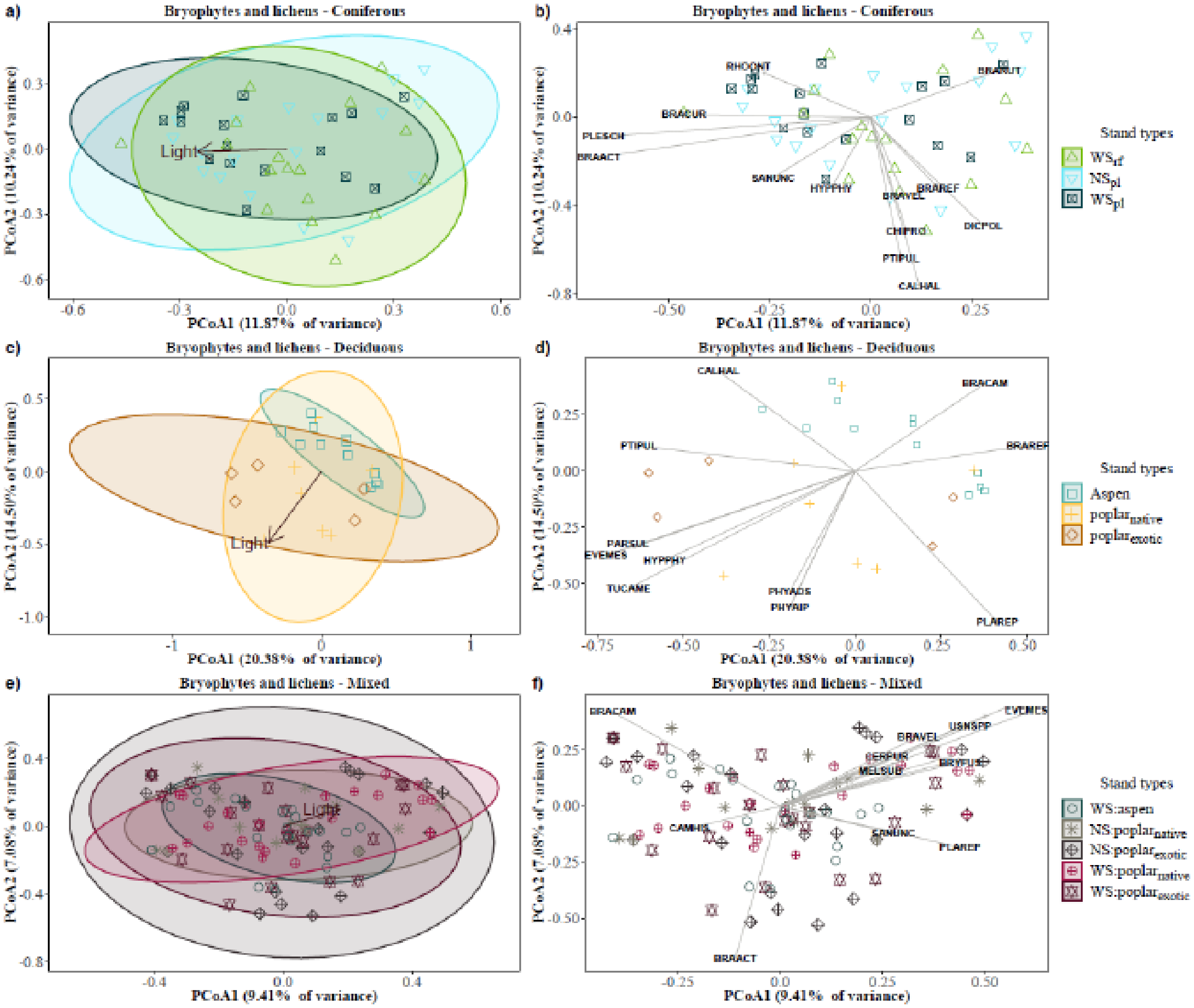

Figure 22
Principal coordinate analysis (PCoA) based on the Bray-Curtis distance on bryophyte and lichen community composition for a) and b) coniferous stands; c) and d) deciduous stands; and e) and f) for mixed stands. The ellipses represent the 95% confidence intervals of the mean positions of stand types. The symbols indicate stand types. Overlay of all species vectors on c), d) and f). See supplementary information Tableau S11 for more details on species names.

Vascular plant community composition. The vascular plant community composition varied with stand type (plantation or reference forest) for the three overstory types (i.e., coniferous, deciduous, and mixed) (PERMANOVA; *p* = 0.001; Tableaux 8c, 8e and 8g). The first axis of the PCoA on the vascular plant community for coniferous, deciduous, and mixed overstories respectively explained 19.77%, 25.70% and 12.10% of variance while the second axes respectively explained 9.22%, 9.64% and 8.70% of variance (Figure 23).

Although many vascular plant species were shared between the three stand types of coniferous overstories (i.e., NS_{pl}, WS_{pl} and WS_{rf}) such as *Achillea millefolium* (ACHMIL), *Symphyotrichum cordifolium* (SYMCOR) and *Fragaria virginiana* (FRAVIR) (on the left side of the ordination (Figure 23b)), many others were only associated with WS_{rf} such as *Elymus caninus* (ELYCAN), *Maianthemum canadense* (MAICAN), *Alnus incana* (ALNINC) and *Acer spicatum* (ACESPI) (on the right side of the ordination (Figure 23b)). The vascular plant communities in exotic spruce (NS_{pl}) and native spruce (WS_{pl}) plantations were composed of ruderal and light-demanding species (e.g., *Carex* spp. (CARSPP) and *Hieracium* spp. (HIESPP) (Figure 23b)) and exhibited a similar composition.

Vascular plant composition generally differed between deciduous plantations and reference deciduous forests as shrub and forest species dominated aspen forests but were absent in $poplar_{exotic}$ and $poplar_{native}$ plantations (Figure 23d). We observed the same pattern in mixed overstories as vascular plant community composition differed between plantations and reference forests regardless of mixture and overstory species identity. Generally, grass species such as *Carex* spp. and ruderal herbaceous species such as *Hieracium* spp. (HIESPP) and *Solidago rugosa* (SOLRUG) dominated deciduous and mixed plantations (Figures. 23d and 23f). In contrast, deciduous and mixed reference forests were associated with shrub species such as *Alnus incana* (ALNINC), *Acer spicatum* (ACESPI) and *Rubus idaeus* (RUBIDA) and forest species such as *Aralia nudicaulis* (ARNUD) and *Maianthemum canadense* (MAICAN) (Figures. 23d and 23f). The second axis of the PCoA on the vascular plant community for mixed overstories reflected the variability of vascular plant assemblages in mixed plantations.

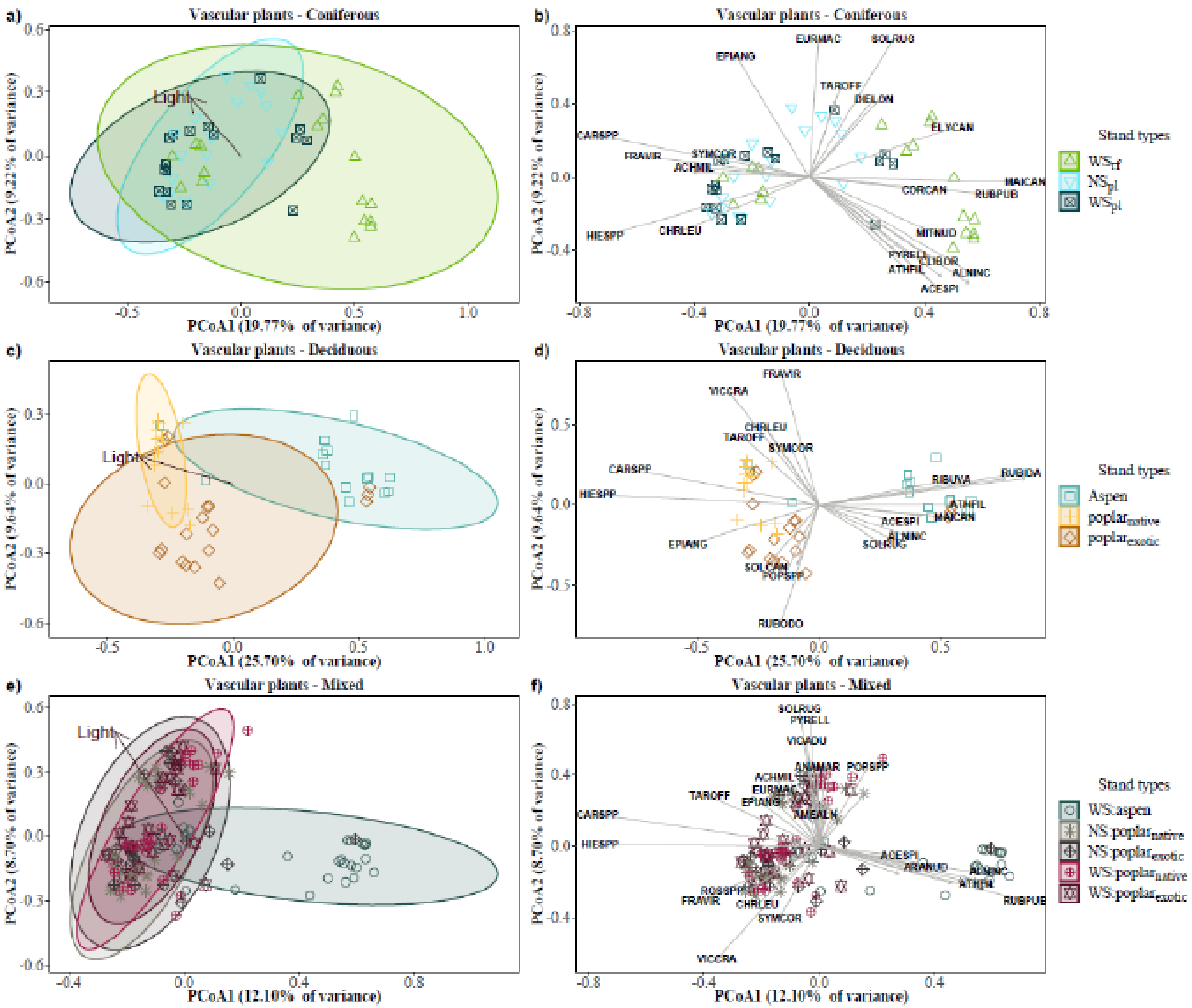

Figure 23
Principal coordinate analysis (PCoA) based on the Bray-Curtis distance on vascular plant community composition for a) and b) coniferous stands; c) and d) deciduous stands; and e) and f) for mixed stands. The ellipses represent the 95% confidence intervals of the mean positions of stand types. The symbols indicate stand types. Overlay of all species vectors on c), d) and f). See supplementary information Tableau S11 for more details on species names.

Tableau 8
Effect of management type (all overstory types combined) on the composition of a) all vegetation and effect of stand type by overstory type on the composition of b), d), f) bryophytes and lichens, and c), e), g) vascular plants using the permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis transformed community data.

Communities	**Variable**	**Df**	**Sum of squares**	**F statistic**	**R^2**	***p value***
All overstory type						
a) All vegetation	Management type	1	7.36	27.93	0.11	**0.001*****
	Residuals	236	62.22			
Coniferous						
b) Bryophytes and lichens	Stand type	2	0.98	2.01	0.07	**0.007****
	Residuals	49	12.03			
c) Vascular plants only	Stand type	2	2.73	5.29	0.17	**0.001*****
	Residuals	50	12.91			
Deciduous						
d) Bryophytes and lichens	Stand type	2	1.43	2.52	0.19	**0.002****
	Residuals	21	5.97			
e) Vascular plants only	Stand type	2	3.82	9.19	0.29	**0.001*****
	Residuals	45	9.35			
Mixed						
f) Bryophytes and lichens	Stand type	4	3.67	2.86	0.09	**0.001*****
	Residuals	105	33.69			
g) Vascular plants only	Stand type	4	6.76	8.00	0.20	**0.001*****
	Residuals	128	27.03			

(*) indicates the levels of significance: ns: nonsignificant. $p > 0.05$; *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$0.0001 < p < 0.001$.

3.6 Discussion

3.6.1 Plantations are not biological deserts

Our findings contradict the notion that plantations are biological deserts and provide evidence that they can harbor levels of biodiversity similar to that of reference forests, which is inconsistent with our first hypothesis. Bryophyte diversity and composition were similar between plantations and reference forests in all overstory types. The similarity in bryophyte diversity between plantations and reference forests is probably due to the dominance of generalist moss species, as bryophyte communities of plantations and reference forests were both mainly composed of *Brachythecium falcatum* (BRAFAL) and *Campyliadelphus chrysophyllus* (CAMCHR). These mosses can rapidly colonize and disperse in young stands (Boudreault *et al.*, 2018), which may explain their presence in the relatively young plantations and reference forests. However, as bryophyte establishment depends on the availability of substrates and microhabitats (e.g., deadwood and wood debris) (Király & Ódor, 2010; Boudreault *et al.*, 2018), we expect that as reference forests age, they will increasingly provide more diverse microhabitats than plantations. Thus, reference forests could eventually harbor specialized species such as liverworts and epixylic bryophytes (Söderström, 1988; Noualhaguet *et al.*, 2023). This could therefore lead to a disparity in bryophyte composition between reference forests and plantations at later developmental stages.

Deciduous and mixed plantations contained a similar vascular plant diversity as reference deciduous and mixed forests. Deciduous trees generally produce nutrient-rich broadleaf litter and create conditions of high light availability and soil temperatures, which can stimulate organic matter decomposition and favor the establishment of vascular plants (Laganière *et al.*, 2010; Cavard *et al.*, 2011a; Augusto *et al.*, 2015). Thus, the similarity in litter type within deciduous overstories may have led to similar vascular plant diversity between deciduous plantations and reference deciduous forests. Tree diversity in mixed plantations may have generated more diverse microhabitats favoring the growth and occurrence of different understory species (Ampoorter *et al.*, 2020; Messier *et al.*, 2022). We showed that plantations could harbor levels of biodiversity similar to reference forests, although mechanical site preparation was carried out prior to planting, as reported by Guillemette &

DesRochers (2008) and Benomar *et al.* (2013). Our results concur with a meta-analysis that revealed that vascular plant species richness tended to be higher in managed forests such as plantations, due to disturbances (e.g., canopy openings, litter removal, and soil disturbance) that favored shade-intolerant, ruderal and competitive plant species (Paillet *et al.*, 2010).

A greater vascular plant diversity in reference forests compared to plantations was only observed in coniferous overstories for vascular plant species. Our reference coniferous forests (WS$_{rf}$) were established after clear-cutting followed by reforestation with white spruce. Thus, it is possible to link the greater vascular plant diversity in reference coniferous forests to the presence of seed banks from the previous forest, combined with the introduction of new pioneer species (e.g., *Achillea millefolium* (ACHMIL), *Symphyotrichum cordifolium* (SYMCOR) and *Fragaria virginiana* (FRAVIR)) after canopy openings (De Grandpre & Bergeron, 1997; Fahey & Puettmann, 2007; Caners *et al.*, 2009).

Epiphytic lichen species were only present in plantations and were particularly associated with the presence of hybrid poplars (whether exotic or native) in the overstory. This result is inconsistent with other studies that showed that plantations altered species composition and reduced the occurrence of lichens (Humphrey *et al.*, 2002; Paillet *et al.*, 2010). The presence of epiphytic lichens is associated with non-acidic barks and nutrient-rich substrates (Jüriado *et al.*, 2003; Hämäläinen *et al.*, 2023). Hybrid poplar plantations might have provided suitable habitats and bark for lichen communities, contributing to support biodiversity in plantations (Randriamananjara *et al.*, 2023). Lichens generally thrive in well-lit environments (Humphrey *et al.*, 2002; Jüriado *et al.*, 2009; Boudreault *et al.*, 2013). Plantations, especially hybrid poplar plantations (Tableau S10), exhibited greater understory light levels than reference forests, which could also explain the presence of lichen species in plantations. The presence of shrub species in reference forests may compete for resources such as sunlight creating conditions that are less favorable for lichens (terricolous and epiphytic) to establish and thrive (Gilbert, 1993; Will-Wolf *et al.*, 2004; Randlane *et al.*, 2017).

3.6.2 Patterns of the understory community composition

Twenty years after the establishment of our plantations, the vascular plant community composition differed from our reference forests. As hypothesized, we found that plantations were composed of plant species that can rapidly colonize the available space, while forest species were associated with reference forests. Species composition could also reflect the environment prior to stand establishment and be influenced by the proximity to seed sources (Bellemare *et al.*, 2002; Felton *et al.*, 2010; Brudvig & Damschen, 2011). Thus, the presence of ruderal species (e.g., *Carex* spp. (CARSPP) and *Hieracium* spp. (HIESPP)) in plantations had probably been influenced by the previous agricultural environment for the Amos and Rivière-Héva sites. In contrast, the presence of shrub species such as *Alnus incana* (ALNINC) and *Acer spicatum* (ACESPI) and forest species such as *Aralia nudicaulis* (ARNUD) and *Maianthemum canadense* (MAICAN) in reference forests may be due to the regrowth of their rhizomes or seed banks from the pre-existing forests (Holl & Aide, 2011). Although some plantations were established on a previously forested site (Nédelec), vascular plant composition always differed between reference forests and plantations. This suggests that silvicultural practices prior to the establishment of plantations had probably eliminated forest species seedbanks (Battles *et al.*, 2001; Brudvig & Damschen, 2011; Kutnar *et al.*, 2023), as soil preparation was carried out on plantation sites to remove pre-existing vegetation and tree stumps (Guillemette & DesRochers, 2008; Benomar *et al.*, 2013). Thus, the intensive site preparation in plantations had probably generated new habitats that were available for colonization and thus favored ruderal species (e.g., *Carex* spp (CARSPP), *Hieracium* spp (HIESPP), *Solidago rugosa* (SOLRUG)) (Haeussler *et al.*, 2002; Soo *et al.*, 2009). Our results also showed that species sensitive to anthropogenic disturbances such as *Athyrium filix-femina* was absent from plantations. This finding is consistent with the fact that silvicultural interventions prior to the plantation establishment may have influenced the vascular plant community composition (Buscardo *et al.*, 2008).

3.6.3 Effects of overstory species identity on the understory vegetation

Overstory species identity of plantations is a key determinant of the effects of plantations on understory vegetation diversity compared to reference forests. The presence of native spruce (white spruce) in mixed plantations led to similar levels of bryophyte diversity in mixed plantations and reference mixed forests, while in contrast exotic poplar species harbored more diverse vascular plant communities than native poplar species in mixed plantations. These results partially support our hypothesis since we expected native species to consistently harbor more diverse understory vegetation communities than exotic species. Aboveground biomass was higher in white spruce and hybrid poplar mixture plantations compared to Norway spruce and hybrid polar mixtures (Benomar *et al.*, 2013). Thus, the presence of white spruce in mixed plantations had probably limited moisture evaporation from the soil because of the higher aboveground biomass (Millar, 1974; Facelli & Pickett, 1991). This might have created microclimate conditions similar to those in reference forests that were favorable to the establishment of bryophytes.

Tree species have different morphological, phenological, chemical and physical traits that can differently influence the understory vegetation (Barbier *et al.*, 2008; Laganière *et al.*, 2010). In our study, poplar$_{\text{exotic}}$ (*Populus maximowiczii* x *P. balsamifera* L.) had more sylleptic branches (i.e., branches close to the trunk) than poplar$_{\text{native}}$ (*Populus trichocarpa* Torrey & A. Gray x *P. balsamifera* L.) (Benomar *et al.*, 2012). This has probably affected understory vegetation by changing abiotic environments such as incident light during the whole growing season (Porté *et al.*, 2004). Hybrid poplar clones also have seasonal variations in the canopy associated with leaf budding and defoliation (Elferjani *et al.*, 2016). In the case of our studied hybrid poplar clones, poplar$_{\text{exotic}}$ leaf out earlier, have a later onset of dormancy and a longer growing season duration than poplar$_{\text{native}}$ (Elferjani *et al.*, 2016). Thus, poplar$_{\text{exotic}}$ plantations had a longer canopy closure period and created a forest environment earlier in the growing season than poplar$_{\text{native}}$ plantations, generating a similar closed-canopy forest environment as reference mixed forests. This could explain why the presence of exotic poplar in mixtures favored similar vascular plant diversity in mixed plantations and reference mixed forests.

3.7 Conclusion

We showed that the understory vegetation in plantations could be as diverse as in reference forests, although the vascular community composition differed between plantations and reference forests. Our results highlight the presence of lichen species in plantations and their absence in reference forests providing evidence that plantations contribute to enhancing biodiversity.

We showed that ruderal species dominated plantations whereas forest species were more representative of reference forests. As the source of seeds are often difficult to determine, we were unable to include this factor in our analyses. However, we emphasize the importance of the effects of proximity to seed sources from surrounding stands on differences in species composition between plantations and reference forests.

According to our results, the overstory species identity of the plantation is an important driver to consider in reforestation to maintain understory diversity. We recommend that WS:poplar$_{exotic}$ should be favored over the other mixtures in order to increase bryophyte, vascular plant and lichen diversity.

3.8 Acknowledgments

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CONCLUSION GÉNÉRALE

Cette thèse a permis de mettre en évidence l'impact des plantations à croissance rapide utilisant des peupliers hybrides sur la biodiversité de la végétation de sous-bois incluant trois groupes taxonomiques (plantes vasculaires, bryophytes et lichens). Elle a également permis de démontrer l'effet des plantations sur la biodiversité de la végétation de sous-bois selon leur type et composition. Cette thèse a permis de faire des recommandations en matière de gestion des plantations forestières dans le but de favoriser la biodiversité de la végétation de sous-bois. Nous avons également fourni des réponses en ce qui a trait au choix des espèces à utiliser dans les plantations pour améliorer la biodiversité de la végétation de sous-bois.

Effet de la mixité des espèces/clones sur la biodiversité de la végétation de sous-bois. Les résultats du Chapitre 1 montrent que les plantations mixtes abritaient un plus grand nombre d'espèces de bryophytes par rapport aux monocultures de peupliers hybrides, alors qu'il n'y avait pas d'impact sur les plantes vasculaires. La présence de l'épinette dans les plantations mixtes a favorisé l'établissement des bryophytes se trouvant sur le sol tandis que les peupliers hybrides ont favorisé l'établissement des lichens se trouvant sur les troncs d'arbres. En termes de composition spécifique des communautés de sous-bois, les plantations mixtes étaient composées d'espèces communes aux monocultures de peupliers hybrides et d'épinettes. La présence de plusieurs espèces d'arbres dans les plantations mixtes peut donc offrir une plus grande disponibilité en ressources et en habitats par rapport aux monocultures, favorisant la coexistence de diverses espèces (Carnus *et al.*, 2006; Jonsson *et al.*, 2019; Feng *et al.*, 2022). Dans un contexte de reboisement et d'afforestation, il serait alors recommandé de favoriser les plantations mixtes en mélangeant le peuplier hybride avec de l'épinette afin d'améliorer la biodiversité de la végétation de sous-bois.

Notre étude est l'une des premières à évaluer l'effet du mélange de clones de peupliers hybrides sur les trois groupes taxonomiques (plantes vasculaires, bryophytes et lichens) de la végétation de sous-bois dans la forêt boréale du Québec

(Chapitre 2). Conformément à notre hypothèse, les plantations polyclonales avaient une plus grande diversité fonctionnelle de plantes vasculaires par rapport aux plantations monoclonales. L'effet positif du mélange clonal peut être expliqué par la différenciation des niches écologiques des clones qui se diffèrent par leurs traits morphologiques, foliaires et phénologiques (Benomar *et al.*, 2012; Elferjani *et al.*, 2016; Rabearison *et al.*, 2023). Cela peut améliorer la disponibilité des ressources (par exemple la lumière) et des nutriments et influencer positivement la diversité fonctionnelle de la végétation de sous-bois. Les effets positifs du mélange de clones sur la diversité fonctionnelle étaient plus évidents dans les sites se trouvant plus au nord où les conditions environnementales sont plus sévères (Villebois). En revanche, la disparité de la composition fonctionnelle entre les plantations monoclonales et polyclonales était plus évidente sur le site le plus au sud et le plus productif (c'est-à-dire Duhamel). La divergence des communautés végétales tendait à être plus marquée dans les milieux riches en ressources que dans les milieux pauvres (Royer-Tardif *et al.*, 2017). Notre étude suggère que les plantations polyclonales sont une option prometteuse pour améliorer la biodiversité de la végétation de sous-bois dans les sites où les ressources sont limitées.

Les plantes vasculaires étant généralement associées aux canopées feuillues, nous avons sélectionné des traits fonctionnels de plantes vasculaires dans les plantations monoclonales et polyclonales (Chapitre 2). Les futures études pourront intégrer les traits fonctionnels des bryophytes et des lichens. Il serait également pertinent d'évaluer l'effet d'autres types de mélange d'espèces/clones comme le mélange d'espèces de conifères sur la biodiversité de la végétation de sous-bois étant donné que la canopée de feuillus et de conifères influence différemment la végétation de sous-bois.

La mixité des espèces peut influencer les propriétés physicochimiques du sol (par exemple, la concentration en éléments chimiques, le pH, l'humidité et la température du sol), influençant par conséquent l'établissement de la végétation de sous-bois. Évaluer l'effet du type de plantation sur ces variables et les considérer comme facteurs potentiels pour expliquer la biodiversité de la végétation de sous-bois serait une piste à explorer dans les futures études. La végétation de sous-bois peut influencer le cycle des nutriments et la décomposition de la matière organique (Fenton & Bergeron, 2006; Grau-Andres *et al.*, 2022), ce qui peut ensuite avoir un impact sur le sol et la productivité des plantations. Il serait alors pertinent d'évaluer la productivité des plantations et le stockage du carbone dans le sol en lien avec la diversité végétale du sous-bois et la mixité des espèces/clones de la canopée.

Impact des plantations sur la biodiversité et influence des pratiques de préparation du sol, de l'historique d'utilisation des terres et du gradient latitudinal. Bien que la composition de la communauté vasculaire différait entre les plantations et les forêts de référence, les plantations étaient aussi diverses que les forêts de références, démontrant ainsi que l'on ne devrait pas nécessairement qualifier les plantations des déserts de biodiversité (Chapitre 3). Nos résultats montrent que les lichens étaient présents dans les plantations, mais absents dans les forêts de référence confirmant le potentiel des plantations à maintenir la biodiversité dans un paysage de forêt aménagée. Toutefois, compte tenu de la complexité et de l'hétérogénéité des forêts gérées de manière extensive par rapport aux plantations (Ehbrecht *et al.*, 2017; Ehbrecht *et al.*, 2021), l'absence de lichens dans les forêts de référence peut s'expliquer par leur jeune âge. En effet, de nombreux micro-habitats à l'échelle de l'arbre se développent avec le vieillissement (Hämäläinen *et al.*, 2023), les forêts de références que nous avons étudiées n'ont probablement pas fourni les micro-habitats nécessaires pour favoriser la diversité des espèces de lichens observées dans des forêts plus anciennes.

Notre étude montre que la préparation du sol effectuée avant et pendant l'établissement des plantations a probablement influencé la composition des communautés des plantes vasculaires (Chapitre 3). Bien que le site de Nédelec soit un ancien site forestier, la composition en plantes vasculaires dans les plantations était différente de celle des forêts de références. Cette différence confirme que la méthode et l'intensité de préparation du site avant l'établissement des plantations peuvent détruire ou éliminer la végétation forestière préexistante (Nagai & Yoshida, 2006; Newmaster *et al.*, 2007). Nos résultats mettent également en évidence l'impact des pratiques d'utilisation et de gestion des terres avant l'établissement des plantations sur la composition des plantes vasculaires. Les plantations sur les friches agricoles étaient composées de plantes vasculaires rudérales, tandis que les plantations sur des anciens sites forestiers étaient composées d'espèces typiques des forêts (Chapitres 1, 2 et 3). Dans un contexte de reboisement et d'afforestation, il serait donc important de considérer l'historique d'utilisation des terres et le paysage environnant.

Nos résultats montrent que le gradient latitudinal a influencé l'assemblage des traits fonctionnels chez les plantes vasculaires de sous-bois. Les plantes vasculaires de sous-bois avaient généralement tendance à présenter des traits conservateurs dans le nord, alors que celles du sud avaient tendance à présenter des traits acquisitifs, suggérant les effets des facteurs climatiques et des conditions environnementales.

Importance de l'identité de l'espèce. La variation de la composition fonctionnelle de la communauté associée à chaque plantation monoclonale a montré l'effet de l'identité du clone sur les traits fonctionnels (Chapitre 2). Nous avons montré que les espèces de plantes vasculaires pouvaient présenter des stratégies différentes pour survivre, se disperser et acquérir des ressources dans chaque plantation monoclonale, d'un site à l'autre. La composition fonctionnelle de la communauté de plantes vasculaires différait entre toutes les plantations monoclonales, à l'exception des Clones 2 et 3, sur le site de Duhamel (Chapitre 2). L'effet de l'identité des espèces sur la biodiversité est particulièrement prononcé dans les environnements riches en ressources (Loreau & Hector, 2001; Cavard *et al.*, 2011b). Dans ce contexte, la similarité fonctionnelle entre les communautés végétales des Clones 2 et 3 peut s'expliquer par la similitude génétique de leurs croisements génétiques (*P. balsamifera* x *maximowiczii* Henry). L'effet des plantations sur la diversité des espèces de sous-bois, par rapport aux forêts de référence, était aussi lié à l'identité des espèces dans les plantations où la présence d'épinette blanche et du peuplier hybride exotique (*P. maximowiczii* Henry x *balsamifera* L.) dans les plantations mixtes a augmenté le nombre d'espèces de bryophytes et de plantes vasculaires respectivement (Chapitre 3). Nos résultats mettent donc en évidence l'effet de l'identité de l'espèce sur la diversité taxonomique et fonctionnelle de la végétation de sous-bois. Nous recommandons de privilégier le mélange épinette blanche et peuplier hybride exotique (*P. maximowiczii* Henry x *balsamifera* L.) par rapport aux autres mélanges afin d'augmenter la diversité des bryophytes, des plantes vasculaires et des lichens. Nous recommandons également de mélanger des clones de peuplier ayant des traits phénologiques, chimiques et morphologiques différents afin de favoriser la diversité fonctionnelle des plantes de sous-bois.

Retombées de la thèse. L'acceptation sociale des plantations à croissance rapide est nécessaire pour leur installation sur des terrains privés et leur inclusion dans les plans de gestion forestière. L'importance de ces plantations augmentera dans le futur, à mesure que leurs avantages sur la productivité et la biodiversité sont démontrés. À travers notre étude, nous avons démontré que les plantations à croissance rapide pouvaient abriter une diversité végétale significative et servir d'habitats pour les lichens et que l'établissement des plantations mixtes constitue un atout pour maintenir la diversité végétale du sous-bois. Pour tirer profit des plantations à croissance rapide, il est important de sélectionner des espèces qui sont bénéfiques pour la biodiversité de la végétation de sous-bois. Notre étude a permis de montrer que les plantations combinant des espèces exotiques avec de l'épinette blanche pouvaient améliorer la biodiversité de la végétation de sous-bois. Cela démontre que les espèces exotiques ne sont pas nécessairement néfastes pour la biodiversité. Il est toutefois important d'éviter une préparation intensive du sol pour préserver la végétation herbacée et les débris ligneux qui sont essentiels pour de nombreuses espèces forestières.

Notre étude a également montré que les plantations à croissance rapide qui sont établies sur des terres agricoles abandonnées peuvent offrir des opportunités pour maintenir la biodiversité (par exemple, la diversité des lichens) sur ce type de terres (Carnus *et al.*, 2006; Brockerhoff *et al.*, 2008). En outre, compte tenu de la demande croissante en bois, les plantations à croissance rapide à proximité représentent une source alternative de production ligneuse, jouant ainsi un rôle de refuge dans un contexte où la majorité des forêts publiques sont allouées à l'exploitation forestière.

L’intégration de tous les groupes taxonomiques de la végétation de sous-bois constitue un point important de notre étude, car en séparant les espèces en trois groupes taxonomiques (plantes vasculaires, bryophytes et lichens), nous avons apporté un niveau d’analyse plus précis que des études qui se limitent à une mesure globale de la biodiversité. Cette approche a permis de montrer de manière détaillée les réponses de la végétation de sous-bois à son environnement. Notre approche a également permis d’évaluer l’importance des peupliers hybrides en tant qu’habitats pour les lichens épiphytes. Ces arbres, par leur structure et leur écorce, ont offert des micro-habitats propices à la colonisation des lichens, soulignant ainsi leur rôle crucial dans le maintien de la diversité biologique au sein du sous-bois. En favorisant la présence de lichens, les peupliers hybrides contribuent non seulement à l’enrichissement de la biodiversité, mais aussi à la création de conditions écologiques favorables à d’autres espèces.

ANNEXE A – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 1

Tableau S1
Results of the Generalized Linear Mixed Model (GLMM) on the total (all taxonomic groups), vascular plant, bryophyte, and lichen species richness as a function of plantation type (in alphabetical order). Results of ANOVA are reported after each result of GLMM.

Plantation types	estimate	se	z value	p value
Total (all taxonomic groups)				
Intercept (NS)	2.65	0.17	15.36	**< 0.001*****
NS:poplar1	-0.37	0.16	-2.26	**< 0.05***
NS:poplar2	-0.19	0.16	-1.17	0.24
poplar1	-0.62	0.18	-3.54	**< 0.001*****
poplar2	-0.33	0.17	-1.95	0.05
WS	0.03	0.17	0.20	0.84
WS:poplar1	-0.06	0.16	-0.39	0.70
WS:poplar2	0.01	0.16	0.05	0.96
ANOVA				
Source of variation	**Chisq**	**p value**		
Plantation type	25.90	**< 0.001*****		
Vascular plant				
Intercept (NS)	1.98	0.14	13.80	**< 0.001*****
NS:poplar1	0.00	0.12	-0.03	0.98
NS:poplar2	0.10	0.12	0.87	0.39
poplar1	-0.26	0.14	-1.85	0.06
poplar2	0.03	0.13	0.25	0.80
WS	-0.06	0.13	-0.41	0.68
WS:poplar1	0.04	0.12	0.31	0.76
WS:poplar2	0.07	0.12	0.57	0.57
ANOVA				
Source of variation	**Chisq**	**p value**		
Plantation type	9.45	0.22		

Tableau S1 (suite)

		Bryophyte		
Intercept (NS)	1.83	0.31	5.83	**< 0.001*****
NS:poplar1	-1.03	0.35	-2.95	**< 0.01****
NS:poplar2	-0.76	0.34	-2.23	**< 0.05***
poplar1	-1.77	0.41	-4.34	**< 0.001*****
poplar2	-1.56	0.40	-3.89	**< 0.001*****
WS	0.13	0.35	0.39	0.70
WS:poplar1	-0.34	0.34	-1.02	0.31
WS:poplar2	-0.18	0.33	-0.55	0.58
ANOVA				
Source of variation	**Chisq**	**p value**		
Plantation type	44.36	**< 0.001*****		
		Lichen		
Intercept (NS)	-0.89	1.34	-0.67	0.51
NS:poplar1	-0.66	0.77	-0.86	0.39
NS:poplar2	-0.75	0.79	-0.95	0.34
poplar1	-0.82	0.84	-0.97	0.33
poplar2	0.14	0.78	0.18	0.86
WS	-0.88	0.85	-1.04	0.30
WS:poplar1	-0.37	0.75	-0.49	0.62
WS:poplar2	0.16	0.72	0.22	0.83
ANOVA				
Source of variation	**Chisq**	**p value**		
Plantation type	4.78	0.68		

(*) indicates the levels of significance: ns: nonsignificant. $p > 0.05$; *$0.01 < p < 0.05$; **$0.001 < p < 0.01$; ***$0.0001 < p < 0.001$.

Tableau S2

Results of linear mixed models (LMM) on the effect of plantation types on incident light. Results of ANOVA are reported after the results of LMM.

Plantation types	**estimate**	**se**	**df**	**t value**	***p value***
Intercept (NS)	1.74	0.43	22.10	4.047	< **0.001*****
NS:poplar1	0.66	0.44	105	1.486	0.14
NS:poplar2	0.79	0.44	105	1.789	0.07
poplar1	1.89	0.51	105	3.697	< **0.001*****
poplar2	1.64	0.51	105	3.225	**< 0.01****
WS	-0.19	0.51	105	-0.381	0.70
WS:poplar1	0.39	0.44	105	0.892	0.37
WS:poplar2	0.59	0.44	105	1.34	0.18
ANOVA					
Source of variation	**F**	**p value**			
Plantation type	4.19	**< 0.001*****			

(*) indicates the levels of significance: ns: nonsignificant. p > 0.05; *0.01 < p < 0.05; **0.001 < p < 0.01; ***0.001 < p < 0.0001.

Tableau S3
Species list in all sampled quadrats. a) Vascular plants; b) Bryophytes, c) Lichens.

ID	Species	Abbreviation	Taxonomic group
	a) Vascular plants		
1	*Carex* spp.	CARSPP	Vascular plant
2	*Abies balsamea*	ABIBAL	Vascular plant
3	*Achillea millefolium*	ACHMIL	Vascular plant
4	*Alnus incana*	ALNINC	Vascular plant
5	*Amelanchier alnifolia*	AMEALN	Vascular plant
6	*Anaphalis margaritacea*	ANAMAR	Vascular plant
7	*Apocynum androsaemifolium*	APOAND	Vascular plant
8	*Botrychium matricariifolium*	BOTMAT	Vascular plant
9	*Chrysanthemum leucanthemum*	CHRLEU	Vascular plant
10	*Clintonia borealis*	CLIBOR	Vascular plant
11	*Cornus canadensis*	CORCAN	Vascular plant
12	*Diervilla lonicera*	DIELON	Vascular plant
13	*Epilobium angustifolium*	EPIANG	Vascular plant
14	*Equisetum sylvaticum*	EQUSYL	Vascular plant
15	*Erigeron canadensis*	ERICAN	Vascular plant
16	*Eurybia macrophylla*	EURMAC	Vascular plant
17	*Fragaria americana*	FRAAME	Vascular plant
18	*Fragaria virginiana*	FRAVIR	Vascular plant
19	*Fraxinus nigra*	FRANIG	Vascular plant
20	*Galeopsis tetrahit*	GALTET	Vascular plant
21	*Galium triflorum*	GALTRI	Vascular plant
22	*Gaultheria procumbens*	GAUPRO	Vascular plant
23	*Hieracium* spp.	HIESPP	Vascular plant
24	*Huperzia lucidula*	HUPLUC	Vascular plant
25	*Hydrophilum canadense*	HYDCAN	Vascular plant
26	*Lycopodium complanatum*	LYCCOM	Vascular plant

Tableau S3 (suite)

27	*Lycopodium obscurum*	LYCOBS	Vascular plant
28	*Maianthemum canadense*	MAICAN	Vascular plant
29	*Picea abies*	PICABI	Vascular plant
30	*Picea glauca*	PICGLA	Vascular plant
31	*Populus* spp.	POPSPP	Vascular plant
32	*Prunus* spp.	PRUSPP	Vascular plant
33	*Pteridium aquilinum*	PTEAQU	Vascular plant
34	*Pyrola elliptica*	PYRELL	Vascular plant
35	*Ranunculus acris*	RANACR	Vascular plant
36	*Ribes rubrum*	RIBRUB	Vascular plant
37	*Rosa* spp.	ROSSPP	Vascular plant
38	*Rubus odoratus*	RUBODO	Vascular plant
39	*Rubus pubescens*	RUBPUB	Vascular plant
40	*Rumex acetosa*	RUMACE	Vascular plant
41	*Salix bebbiana*	SALBEB	Vascular plant
42	*Salix* spp.	SALSPP	Vascular plant
43	*Solidago canadensis*	SOLCAN	Vascular plant
44	*Solidago rugosa*	SOLRUG	Vascular plant
45	*Symphyotrichum cordifolium*	SYMCOR	Vascular plant
46	*Taraxacum officinale*	TAROFF	Vascular plant
47	*Trifolium pratense*	TRIPRA	Vascular plant
48	*Vaccinium angustifolium*	VACANG	Vascular plant
49	*Vicia cracca*	VICCRA	Vascular plant
50	*Viola adunca*	VIOADU	Vascular plant
	b) Bryophytes		
1	*Abietinella abietina*	ABIABI	Bryophyte
2	*Amblystegium serpens*	AMBSER	Bryophyte
3	*Brachythecium acutum*	BRAACT	Bryophyte
4	*Brachythecium campestre*	BRACAM	Bryophyte
5	*Brachythecium curtum*	BRACUR	Bryophyte

Tableau S3 (suite)

6	*Brachythecium falcatum*	BRAFAL	Bryophyte
7	*Brachythecium reflexum*	BRAREF	Bryophyte
8	*Brachythecium rutabulum*	BRARUT	Bryophyte
9	*Brachythecium* spp.	BRASPP	Bryophyte
10	*Brachythecium starkei*	BRASTA	Bryophyte
11	*Brachythecium velutinum*	BRAVEL	Bryophyte
12	*Bryum archangelicum*	BRYARC	Bryophyte
13	*Bryum creberrimum*	BRYCRE	Bryophyte
14	*Callicladium haldanianum*	CALHAL	Bryophyte
15	*Campyliadelphus chrysophyllus*	CAMCHR	Bryophyte
16	*Campylophyllum hispidulum*	CAMHIS	Bryophyte
17	*Ceratodon purpureus*	CERPUR	Bryophyte
18	*Chiloscyphus coadunatus*	CHICOA	Bryophyte
19	*Chiloscyphus profundus*	CHIPRO	Bryophyte
20	*Dicranum flagellare*	DICFLA	Bryophyte
21	*Dicranum ontariense*	DICONT	Bryophyte
22	*Dicranum polysetum*	DICPOL	Bryophyte
23	*Dicranum scoparium*	DICSCO	Bryophyte
24	*Haplocladium microphyllum*	HAPMIC	Bryophyte
25	*Hypnum curvifolium*	HYPCUR	Bryophyte
26	*Hypnum imponens*	HYPIMP	Bryophyte
27	*Hypnum plicatulum*	HYPPLI	Bryophyte
28	*Oncophorus wahlenbergii*	ONCWAH	Bryophyte
29	*Orthotrichum obtusifolium*	ORTOBT	Bryophyte
30	*Orthotrichum speciosum*	ORTSPE	Bryophyte
31	*Orthotrichum stellatum*	ORTSTE	Bryophyte
32	*Plagiomnium cuspidatum*	PLACUS	Bryophyte
33	*Plagiomnium ellipticum*	PLAELL	Bryophyte
34	*Plagiomnium medium*	PLAMED	Bryophyte
35	*Plagiothecium denticulatum*	PLADEN	Bryophyte

Tableau S3 (suite)

36	*Platygyrium repens*	PLAREP	Bryophyte
37	*Pleurozium schreberi*	PLESCH	Bryophyte
38	*Pohlia nutans*	POHNUT	Bryophyte
39	*Polytrichum commune*	POLCOM	Bryophyte
40	*Ptilidium pulcherrimum*	PTIPUL	Bryophyte
41	*Ptilium crista-castrensis*	PTICRI	Bryophyte
42	*Rhodobryum ontariense*	RHOONT	Bryophyte
43	*Rhytidiadelphus triquetrus*	RHYTRI	Bryophyte
44	*Sanionia uncinata*	SANUNC	Bryophyte
45	*Thuidium delicatulum*	THUDEL	Bryophyte
46	*Ulota crispa*	ULOCRI	Bryophyte
	c) Lichens		
1	*Bryoria fuscescens*	BRYFUS	Lichen
2	*Cladonia coniocraea*	CLACON	Lichen
3	*Cladonia cristatella*	CLACRI	Lichen
4	*Cladonia gracilis spp. turbinata*	CLATUR	Lichen
5	*Cladonia rangiferina*	CLARAN	Lichen
6	*Cladonia* spp.	CLASPP	Lichen
7	*Evernia mesomorpha*	EVEMES	Lichen
8	*Hypogymnia physodes*	HYPPHY	Lichen
9	*Melanelia subaurifera*	MELSUB	Lichen
10	*Melanohalea septentrionalis*	MELSEP	Lichen
11	*Parmelia squarrosa*	PARSQU	Lichen
12	*Parmelia sulcata*	PARSUL	Lichen
13	*Phaeophyscia* spp.	PHASPP	Lichen
14	*Physcia adscendens*	PHYADS	Lichen
15	*Physcia aipolia*	PHYAIP	Lichen
16	*Tuckermannopsis americana*	TUCAME	Lichen
17	*Usnea* spp.	USNSPP	Lichen
18	*Vulpicida pinastri*	VULPIN	Lichen

Tableau S3 (suite)

19	*Xanthomendoza hasseana*	XANHAS	Lichen

ANNEXE B – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 2

Tableau S4
PERMANOVA post hoc pair-wise comparisons of plantation types at each site on vascular plant, and bryophyte and lichen composition of total bryophytes based on 999 permutation.

		Vascular plants		Bryophytes and lichens	
Site	Pairs	R^2	p.adjusted	R^2	p.adjusted
Villebois	Clone2 *vs* Clone4	0.10	0.07	0.23	**0.01***
	Clone2 *vs* Clone1	0.05	0.28	0.19	0.06
	Clone2 *vs* Clone3	0.07	0.15	0.20	0.10
	Clone2 vs Polyclonal	0.10	**0.003***	0.04	0.32
	Clone4 *vs* Clone1	0.11	0.02	0.09	0.25
	Clone4 *vs* Clone3	0.12	0.02	0.15	0.17
	Clone4 *vs* Polyclonal	0.09	**0.003***	0.06	0.06
	Clone1 *vs* Clone3	0.02	0.84	0.10	0.59
	Clone1 *vs* Polyclonal	0.13	**0.003***	0.05	0.17
	Clone3 *vs* Polyclonal	0.12	**0.003***	0.05	0.23
Duparquet	Clone2 *vs* Clone4	0.10	**0.01***	0.07	0.27
	Clone2 *vs* Clone1	0.08	0.04	0.07	0.27
	Clone2 *vs* Clone3	0.07	0.07	0.08	0.26
	Clone2 vs Polyclonal	0.09	**0.003***	0.04	0.19
	Clone4 *vs* Clone1	0.12	**0.01***	0.07	0.26
	Clone4 *vs* Clone3	0.04	0.60	0.04	0.63
	Clone4 *vs* Polyclonal	0.09	**0.003***	0.02	0.87
	Clone1 *vs* Clone3	0.08	0.04	0.08	0.19
	Clone1 *vs* Polyclonal	0.08	**0.003***	0.06	0.02
	Clone3 *vs* Polyclonal	0.06	**0.01***	0.02	0.64
Duhamel	Clone2 *vs* Clone4	0.09	**0.004***	0.10	0.30
	Clone2 *vs* Clone1	0.09	**0.01***	0.12	0.11
	Clone2 *vs* Clone3	0.03	0.84	0.14	0.30

Tableau S4 (suite)

Clone2 *vs* Polyclonal	0.06	**0.001***	0.09	0.07
Clone4 *vs* Clone1	0.13	**0.001***	0.04	0.49
Clone4 *vs* Clone3	0.11	**0.001***	0.07	0.30
Clone4 *vs* Polyclonal	0.08	**0.001***	0.05	0.20
Clone1 *vs* Clone3	0.13	**0.001***	0.12	0.11
Clone1 *vs* Polyclonal	0.13	**0.001***	0.09	0.04
Clone3 *vs* Polyclonal	0.07	**0.001***	0.04	0.30

Tableau S5
PERMANOVA post hoc pair-wise comparisons of sites on vascular plant, and bryophyte and lichen composition of total bryophytes based on 999 permutation.

Pairs	Vascular plants		Bryophytes and lichens	
	R^2	p.adjusted	R^2	p.adjusted
Site				
Duhamel *vs* Duparquet	0.13	**0.001****	0.16	**0.001****
Duhamel *vs* Villebois	0.15	**0.001****	0.04	**0.001****
Duparquet *vs* Villebois	0.23	**0.001****	0.17	**0.001****

Tableau S6
PERMANOVA post hoc pair-wise comparisons of sites on community functional composition based on 999 permutation

Pairs	Functional composition	
	R^2	p.adjusted
Site		
Duhamel *vs* Duparquet	0.21	**0.001****
Duhamel *vs* Villebois	0.16	**0.001****
Duparquet *vs* Villebois	0.33	**0.001****

Tableau S7
Results of the best model for community functional composition (presented as species scores on the first and second axes of PCA) tested with lmer.

Variable	**Model name**	**k**	**AICc**	**ΔAICc**
PCA1 (first axis)	Site	5	665.12	0.00
PCA2 (second axis)	Temperature + Precipitation + Site	6	766.00	0.00

Tableau S8
Species list in all sampled quadrats. a) Vascular plants; b) Lichens, c) Bryophytes.

Species	Abbreviation	Taxonomic group
	a) VASCULAR PLANTS	
Abies balsamea	ABIBAL	Vascular plant
Achillea millefolium	ACHMIL	Vascular plant
Alnus incana	ALNINC	Vascular plant
Amelanchier alnifolia	AMEALN	Vascular plant
Anemonoides quinquefolia	ANEQUI	Vascular plant
Aralia nudicaulis	ARLNUD	Vascular plant
Athyrium filix-femina	ATHFIL	Vascular plant
Botrychium matricariifolium	BOTMAT	Vascular plant
Carex aurea	CARAUR	Vascular plant
Cerastium fontanum	CERFON	Vascular plant
Chrysanthemum leucanthemum	CHRLEU	Vascular plant
Cornus stolonifera	CORSTO	Vascular plant
Elymus repens	ELYREP	Vascular plant
Epilobium angustifolium	EPIANG	Vascular plant
Epipactis helleborine	EPIHEL	Vascular plant
Equisetum arvense	EQUARV	Vascular plant
Equisetum sylvaticum	EQUSYL	Vascular plant
Erigeron strigosus	ERISTR	Vascular plant
Eurybia macrophylla	EURMAC	Vascular plant
Fragaria virginiana	FRAVIR	Vascular plant
Galium triflorum	GALTRI	Vascular plant
Gnaphalium uliginosum	GNAULI	Vascular plant
Hieracium spp.	HIESPP	Vascular plant
Linnaea borealis	LINBOR	Vascular plant
Maianthemum canadense	MAICAN	Vascular plant
Pastinaca sativa	PASSAT	Vascular plant

Tableau S8 (suite)

Petasites frigidus	PETFRI	Vascular plant
Picea glauca	PICGLA	Vascular plant
Pinus strobus	PINSTR	Vascular plant
Plantago rugelii	PLARUG	Vascular plant
Populus spp.	POPSPP	Vascular plant
Prunella vulgaris	PRUVUL	Vascular plant
Prunus pensylvanica	PRUPEN	Vascular plant
Prunus virginiana	PRUVIR	Vascular plant
Pyrola elliptica	PYRELL	Vascular plant
Pyrola minor	PYRMIN	Vascular plant
Ranunculus acris	RANACR	Vascular plant
Rhinanthus minor	RHIMIN	Vascular plant
Rosa sp.	ROSSP.	Vascular plant
Rubus idaeus	RUBIDA	Vascular plant
Rubus pubescens	RUBPUB	Vascular plant
Rubus spectabilis	RUBSPE	Vascular plant
Salix sp.	SALSP.	Vascular plant
Sambucus nigra	SAMNIG	Vascular plant
Solidago canadensis	SOLCAN	Vascular plant
Solidago rugosa	SOLRUG	Vascular plant
Sorbus americana	SORAME	Vascular plant
Symphyotrichum cordifolium	SYMCOR	Vascular plant
Taraxacum officinale	TAROFF	Vascular plant
Trientalis borealis	TRIBOR	Vascular plant
Trifolium pratense	TRIPRA	Vascular plant
Vaccinium angustifolium	VACANG	Vascular plant
Veronica persica	VERPER	Vascular plant
Vicia cracca	VICCRA	Vascular plant
Viola adunca	VIOADU	Vascular plant

Tableau S8 (suite)

b) LICHENS		
Cladonia chlorophaea	CLACHL	Lichen
Cladonia coniocraea	CLACON	Lichen
Cladonia crispata	CLACRI	Lichen
Cladonia cristatella	CLACRI	Lichen
Cladonia fimbriata	CLAFIM	Lichen
Cladonia gracilis spp. turbinata	CLATUR	Lichen
Cladonia rangiferina	CLARAN	Lichen
Cladonia spp.	CLASPP	Lichen
Cladonia verticillata	CLAVER	Lichen
Peltigera sp.	PELSP.	Lichen
Xanthomendoza hasseana	XANHAS	Lichen
c) BRYOPHYTES		
Amblystegium serpens	AMBSER	Bryophyte
Brachythecium acuminatum	BRAACU	Bryophyte
Brachythecium acutum	BRAACT	Bryophyte
Brachythecium campestre	BRACAM	Bryophyte
Brachythecium curtum	BRACUR	Bryophyte
Brachythecium erythrorrhizon	BRAERY	Bryophyte
Brachythecium reflexum	BRAREF	Bryophyte
Brachythecium rutabulum	BRARUT	Bryophyte
Brachythecium spp.	BRASP.	Bryophyte
Brachythecium starkei	BRASTA	Bryophyte
Brachythecium velutinum	BRAVEL	Bryophyte
Bryum archangelicum	BRYARC	Bryophyte
Callicladium haldanianum	CALHAL	Bryophyte
Campyliadelphus chrysophyllus	CAMCHR	Bryophyte
Campylophyllum hispidulum	CAMHIS	Bryophyte
Ceratodon purpureus	CERPUR	Bryophyte
Chiloscyphus profundus	CHIPRO	Bryophyte

Tableau S8 (suite)

Dicranella heteromalla	DICHET	Bryophyte
Dicranum ontariense	DICONT	Bryophyte
Dicranum polysetum	DICPOL	Bryophyte
Eurhynchiastrum pulchellum	EURPUL	Bryophyte
Fissidens bryoides	FISBRY	Bryophyte
Fissidens osmundoides	FISOSM	Bryophyte
Hypnum curvifolium	HYPCUR	Bryophyte
Hypnum plicatulum	HYPPLI	Bryophyte
Oncophorus wahlenbergii	ONCWAH	Bryophyte
Orthotrichum obtusifolium	ORTOBT	Bryophyte
Plagiomnium cuspidatum	PLACUS	Bryophyte
Platydictya subtilis	PLASUB	Bryophyte
Platygyrium repens	PLAREP	Bryophyte
Pleurozium schreberi	PLESCH	Bryophyte
Polytrichum commune	POLCOM	Bryophyte
Ptilidium pulcherrimum	PTIPUL	Bryophyte
Ptilium crista-castrensis	PTICRI	Bryophyte
Sanionia uncinata	SANUNC	Bryophyte
Thuidium delicatulum	THUDEL	Bryophyte

ANNEXE C – MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 3

Tableau S9
Overstory type and management type of each studied stand type including size and replicates of each stand type.

Overstory type	Stand type	Management type	Size	Number of replicates
Coniferous	NS_{pl}	Plantation	15x15 m	3
	WS_{pl}	Plantation	15x15 m	3
	WS_{rf}	Reference forest	15x15 m	3
Deciduous	$poplar_{native}$	Plantation	15x15 m	3
	$poplar_{exotic}$	Plantation	15x15 m	3
	Aspen	Reference forest	15x15 m	3
Mixed	NS: $poplar_{native}$	Plantation	15x15 m	3
	NS:$poplar_{exotic}$	Plantation	15x15 m	3
	WS: $poplar_{native}$	Plantation	15x15 m	3
	WS:$poplar_{exotic}$	Plantation	15x15 m	3
	WS:aspen	Reference forest	15x15 m	3

Tableau S10
Mean (±SEM) incident light for each stand type (in ascending order). Results of ANOVA are reported after the result of mean values. Significant differences ($p \leq 0.05$) between stand types are indicated by different letters. Reference forests are in italics.

Stand type	Light (%)
WS$_{rf}$	2.74 (±1.65) ^{a}
WS$_{pl}$	3.47 (±1.94) ^{a}
Aspen	4.07 (±1.78) ^{a}
NSpl	4.22 (±2.35) ^{a}
WS:poplar$_{native}$	6.26 (±3.16) ^{ab}
WS:poplar$_{exotic}$	7.63 (±3.85) ^{ab}
WS:aspen	8.42 (±4.30) ^{ab}
NS:poplar$_{exotic}$	9.30 (±4.70) ^{ab}
NS:poplar$_{native}$	9.97 (±5.13) ^{ab}
poplar$_{exotic}$	21.86 (±12.21) ^{b}
poplar$_{native}$	26.04 (±14.85) ^{b}

ANOVA

Source of variation	**p value**
Stand type	**< 0.001*****

Tableau S11
Species list in all sampled quadrats. a) Vascular plants; b) Bryophytes, c) Lichens.

Species	Abbreviation	Taxonomic group
a) Vascular plants		
Abies balsamea	ABIBAL	Vascular plant
Acer spicatum	ACESPI	Vascular plant
Achillea millefolium	ACHMIL	Vascular plant
Actaea rubra	ACTRUB	Vascular plant
Alnus incana	ALNINC	Vascular plant
Amelanchier alnifolia	AMEALN	Vascular plant
Aralia nudicaulis	ARANUD	Vascular plant
Anaphalis margaritacea	ANAMAR	Vascular plant
Apocynum androsaemifolium	APOAND	Vascular plant
Athyrium filix-femina	ATHFIL	Vascular plant
Botrychium matricariifolium	BOTMAT	Vascular plant
Carex aurea	CARAUR	Vascular plant
Carex spp.	CARSPP	Vascular plant
Cerastium fontanum	CERFON	Vascular plant
Chrysanthemum leucanthemum	CHRLEU	Vascular plant
Clintonia borealis	CLIBOR	Vascular plant
Cornus canadensis	CORCAN	Vascular plant
Diervilla lonicera	DIELON	Vascular plant
Dryopteris carthusiana	DRYCAR	Vascular plant
Elymus caninus	ELYCAN	Vascular plant
Epilobium angustifolium	EPIANG	Vascular plant
Equisetum sylvaticum	EQUSYL	Vascular plant
Erigeron canadensis	ERICAN	Vascular plant
Eurybia macrophylla	EURMAC	Vascular plant
Fragaria americana	FRAAME	Vascular plant
Fragaria virginiana	FRAVIR	Vascular plant

Tableau S11 (suite)

Fraxinus nigra	FRANIG	Vascular plant
Galeopsis tetrahit	GALTET	Vascular plant
Galium triflorum	GALTRI	Vascular plant
Gaultheria procumbens	GAUPRO	Vascular plant
Geum sp.	GEUSP.	Vascular plant
Hieracium spp.	HIESPP	Vascular plant
Huperzia lucidula	HUPLUC	Vascular plant
Hydrophilum canadense	HYDCAN	Vascular plant
Impatiens capensis	IMPCAP	Vascular plant
Kalmia angustifolia	KALANG	Vascular plant
Lonicera canadensis	LONCAN	Vascular plant
Lycopodium complanatum	LYCCOM	Vascular plant
Lycopodium obscurum	LYCOBS	Vascular plant
Maianthemum canadense	MAICAN	Vascular plant
Mitella nuda	MITNUD	Vascular plant
Picea abies	PICABI	Vascular plant
Picea glauca	PICGLA	Vascular plant
Populus spp.	POPSPP	Vascular plant
Prunus pensylvanica	PRUPEN	Vascular plant
Prunus spp.	PRUSPP	Vascular plant
Pteridium aquilinum	PTEAQU	Vascular plant
Pyrola elliptica	PYRELL	Vascular plant
Ranunculus acris	RANACR	Vascular plant
Rhamnus sp.	RHASP.	Vascular plant
Ribes rubrum	RIBRUB	Vascular plant
Ribes uva-crispa	RIBUVA	Vascular plant
Rosa spp.	ROSSPP	Vascular plant
Rubus idaeus	RUBIDA	Vascular plant
Rubus odoratus	RUBODO	Vascular plant
Rubus pubescens	RUBPUB	Vascular plant

Tableau S11 (suite)

Rumex acetosa	RUMACE	Vascular plant
Salix bebbiana	SALBEB	Vascular plant
Salix spp.	SALSPP	Vascular plant
Sambucus racemosa	SAMRAC	Vascular plant
Solidago canadensis	SOLCAN	Vascular plant
Solidago rugosa	SOLRUG	Vascular plant
Symphyotrichum cordifolium	SYMCOR	Vascular plant
Taraxacum officinale	TAROFF	Vascular plant
Trientalis borealis	TRIBOR	Vascular plant
Trifolium pratense	TRIPRA	Vascular plant
Vaccinium angustifolium	VACANG	Vascular plant
Viburnum acerifolium	VIBACE	Vascular plant
Viburnum nudum	VIBNUD	Vascular plant
Vicia cracca	VICCRA	Vascular plant
Viola adunca	VIOADU	Vascular plant
b) Bryophytes		
Abietinella abietina	ABIABI	Bryophyte
Amblystegium serpens	AMBSER	Bryophyte
Brachythecium acutum	BRAACT	Bryophyte
Brachythecium campestre	BRACAM	Bryophyte
Brachythecium curtum	BRACUR	Bryophyte
Brachythecium erythrorrhizon	BRAERY	Bryophyte
Brachythecium falcatum	BRAFAL	Bryophyte
Brachythecium reflexum	BRAREF	Bryophyte
Brachythecium rutabulum	BRARUT	Bryophyte
Brachythecium spp.	BRASPP	Bryophyte
Brachythecium starkei	BRASTA	Bryophyte
Brachythecium velutinum	BRAVEL	Bryophyte
Brynhia novae-angliae	BRYNOV	Bryophyte
Bryoria fuscescens	BRYNOV	Bryophyte

Tableau S11 (suite)

Bryum archangelicum	BRYARC	Bryophyte
Bryum creberrimum	BRYCRE	Bryophyte
Callicladium haldanianum	CALHAL	Bryophyte
Campyliadelphus chrysophyllus	CAMCHR	Bryophyte
Campylophyllum hispidulum	CAMHIS	Bryophyte
Ceratodon purpureus	CERPUR	Bryophyte
Chiloscyphus coadunatus	CHICOA	Bryophyte
Chiloscyphus profundus	CHIPRO	Bryophyte
Dicranum flagellare	DICFLA	Bryophyte
Dicranum ontariense	DICONT	Bryophyte
Dicranum polysetum	DICPOL	Bryophyte
Dicranum scoparium	DICSCO	Bryophyte
Haplocladium microphyllum	HAPMIC	Bryophyte
Hypnum curvifolium	HYPCUR	Bryophyte
Hypnum imponens	HYPIMP	Bryophyte
Hypnum plicatulum	HYPPLI	Bryophyte
Oncophorus wahlenbergii	ONCWAH	Bryophyte
Orthotrichum obtusifolium	ORTOBT	Bryophyte
Orthotrichum speciosum	ORTSPE	Bryophyte
Orthotrichum stellatum	ORTSTE	Bryophyte
Plagiomnium cuspidatum	PLACUS	Bryophyte
Plagiomnium ellipticum	PLAELL	Bryophyte
Plagiomnium medium	PLAMED	Bryophyte
Plagiothecium denticulatum	PLADEN	Bryophyte
Platygyrium repens	PLAREP	Bryophyte
Pleurozium schreberi	PLESCH	Bryophyte
Pohlia nutans	POHNUT	Bryophyte
Polytrichum commune	POLCOM	Bryophyte
Ptilidium ciliare	PTICIL	Bryophyte
Ptilidium pulcherrimum	PTIPUL	Bryophyte

Tableau S11 (suite)

Ptilium crista-castrensis	PTICRI	Bryophyte
Rhodobryum ontariense	RHOONT	Bryophyte
Rhododendron groenlandicum	RHOGRO	Bryophyte
Rhytidiadelphus triquetrus	RHYTRI	Bryophyte
Sanionia uncinata	SANUNC	Bryophyte
Thuidium delicatulum	THUDEL	Bryophyte
Ulota crispa	ULOCRI	Bryophyte
c) Lichens		
Bryoria fuscescens	BRYFUS	Lichen
Cladonia coniocraea	CLACON	Lichen
Cladonia cristatella	CLACRI	Lichen
Cladonia fimbriata	CLAFIM	Lichen
Cladonia gracilis spp. turbinata	CLATUR	Lichen
Cladonia rangiferina	CLARAN	Lichen
Cladonia spp.	CLASPP	Lichen
Evernia mesomorpha	EVEMES	Lichen
Hypogymnia physodes	HYPPHY	Lichen
Melanelia subaurifera	MELSUB	Lichen
Melanohalea septentrionalis	MELSEP	Lichen
Parmelia squarrosa	PARSQU	Lichen
Parmelia sulcata	PARSUL	Lichen
Phaeophyscia spp.	PHASPP	Lichen
Physcia adscendens	PHYADS	Lichen
Physcia aipolia	PHYAIP	Lichen
Tuckermannopsis americana	TUCAME	Lichen
Usnea spp.	USNSPP	Lichen
Vulpicida pinastri	VULPIN	Lichen
Xanthomendoza hasseana	XANHAS	Lichen

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