Université du Québec en Abitibi-Témiscamingue

EN QUOI LE SITE D'ORIGINE DES PLANTATIONS INFLUENCE-T-IL LES COMMUNAUTÉS VÉGÉTALES, LES STOCKS DE CARBONE ET LE MICROBIOME ?

Thèse
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Par
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Seize sites d'études dispersés sur un territoire de 57 000 km². Sept cent cinquante-quatre m² de végétation inventoriés et identifiés, 408 kg de sol prélevé et transporté, 1715 peupliers hybrides mesurés, les travaux de terrain furent longs et exigeants. Tout cela n'aurait pas pu être mené à bien sans l'aide et le travail d'Abigail Leavens et de Camille Lamothe. D'autres personnes sont venues prêter main forte durant l'été 2022 et je tiens également à les remercier pour leur soutien. Merci à Karelle Rheault, Aro Randriamananjara et Jeri Rabearison. Au laboratoire, j'ai pu compter sur l'aide de Julie Arsenault pour son aide lors de l'identification des bryophytes ainsi que Martine Hardy et Julie Rannou pour avoir guidé mes manipulations respectivement dans les laboratoires d'Amos et de Notre-Dame-du-Nord. Je profite de ce paragraphe pour remercier également Hélène Lavoie et Dany Charron grâce à qui j'ai pu bénéficier d'un environnement serein et propice aux études au campus de l'UQAT à Amos.

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RÉSUMÉ

Au Québec, l'aménagement écosystémique vise à apporter des solutions pour une gestion durable de la ressource forestière tout en protégeant les attributs et les fonctions des forêts naturelles. Pourtant, les coupes procédant à la récolte intégrale des arbres commerciaux restent majoritaires et rendent une image négative de la foresterie auprès du grand public. La sylviculture intensive fait partie de ces pratiques disposant d'une faible acceptabilité au sein de la société notamment pour des raisons esthétiques liées à la nature majoritairement monospécifique des plantations, à leur homogénéité structurale et à leur sous-bois peu végétalisé. Néanmoins, cette dernière présente des avantages lui permettant d'être envisagée comme pratique dans le cadre d'un aménagement écosystémique, car les plantations à croissance rapide et à haut rendement permettraient de diminuer la pression de récolte qui pèse sur les forêts naturelles matures en concentrant la production sur de plus petites surfaces et en fournissant une part des services rendus par les écosystèmes forestiers.

Les anciens sites de coupes mal régénérés et les terres agricoles abandonnées représentent une opportunité pour l'implantation d'essences à croissance rapide comme le peuplier hybride (PEH). Cependant, les opérations de préparation de terrain précédant l'établissement d'une telle plantation, les entretiens de la végétation compétitive ainsi que le changement brusque de couvert végétal sont susceptibles de modifier profondément les fonctions de l'écosystème. L'influence du reboisement est également étroitement liée au site d'origine de la plantation et peu de connaissances sont disponibles sur l'effet du site d'origine sur le reboisement avec des PEH. Cette thèse avait pour but d'évaluer l'impact de l'origine du site et du reboisement sur la diversité végétale, la diversité microbienne et l'état des stocks de carbone dans les plantations de peupliers hybrides afin d'aider à la prise de décision concernant la sélection des sites pour l'implantation de PEH. Nous avons étudié des plantations de PEH établies sur des terres agricoles abandonnées arborant une végétation herbacée ou arbustive, et sur d'anciens sites de coupes forestières que nous avons comparé à des zones adjacentes non reboisées.

Nos résultats ont montré que le reboisement d'anciens sites forestiers a engendré une diminution des stocks de carbone organique dans le sol, une perte de diversité fongique et une perte de diversité des plantes vasculaires dans les plantations, comparativement à leurs équivalents non reboisés. Les plantations établies sur des friches herbacées et arbustives ont, au contraire, conservé des caractéristiques proches de leurs équivalents non reboisés. De plus, nos résultats tendent à montrer que le reboisement de friches herbacées aboutit à une hausse de la diversité végétale à l'échelle du paysage et à une hausse de l'abondance relative des ectomycorhizes au sein des communautés microbiennes. Nous concluons cette thèse en recommandant de cibler les friches agricoles, herbacées de préférence, plutôt que les sites forestiers afin de profiter du haut rendement des PEH tout en préservant les diversités végétale et microbienne, ainsi que les stocks de carbone organique du sol.

Mots clés : Peuplier hybride, Friche agricole, Plantation, Diversité végétale, Bryophyte, Microbiome, Carbone organique du sol

Keywords: Hybrid poplar, Abandoned agricultural land, Plantation, Plant diversity, Bryophyte, Microbiome, Soil organic carbon

AVANT-PROPOS

Cette thèse présente le travail de quatre années de recherche réalisées dans le cadre du programme de doctorat sur mesure en écologie forestière de l'Université du Québec en Abitibi-Témiscamingue et se compose de 3 chapitres. L'introduction générale développe le contexte qui a amené à déterminer la problématique, les hypothèses et les objectifs de cette étude. Les chapitres 1, 2 et 3 sont le cœur du manuscrit, ce sont trois articles scientifiques rédigés en anglais dévoilant les résultats des trois principaux objectifs de cette thèse.

Le chapitre 1, “Impact of the origin of sites planted with hybrid poplar on plant community composition and diversity”, aborde les effets du reboisement par du peuplier hybride sur la diversité et la composition des communautés de plantes vasculaires et non vasculaires en fonction de l'origine du site de la plantation. Cet article a été publié dans la Revue “New Forests” en début d'année 2025.

Zanin, G., DesRochers, A., & Fenton, N. J. (2025). Impact of the origin of sites planted with hybrid poplar on plant community composition and diversity. New Forests, 56(1), 12. https://doi.org/10.1007/s11056-024-10080-8.

Le chapitre 2, “How does site origin affect the diversity and composition of the soil microbiome afforested with fast growing hybrid poplar? “, explore les conséquences de l'établissement d'une plantation de peuplier hybride sur la diversité et la composition les communautés bactériennes et fongiques du sol. Existe-t-il un lien avec l'origine du site sur lequel la plantation est établie ? L'article fut soumis pour publication à la revue “Ecosphere” en Octobre 2025.

Le chapitre 3, “Converting abandoned agricultural lands to plantations: Effect on soil organic carbon stocks”, traite de l'impact des plantations de peuplier hybride sur les stocks de carbone du sol organique et minéral. Dans ce chapitre nous avons cherché à savoir si les terres agricoles abandonnées sont de bons candidats pour l'établissement de plantations si l'on prend en considération les stocks de carbone organique. Cet article a été publié dans la Revue “Soil use and management” en fin d’année 2025.

Zanin, G., Fenton, N. J., Poirier, V., & DesRochers, A. (2025). Converting Abandoned Agricultural Lands to Intensive Hybrid Poplar Plantations : Effects on Soil Organic Carbon Stocks. Soil Use and Management, 41(4), e70136. https://doi.org/10.1111/sum.70136.

Enfin, la conclusion générale achève cette thèse en faisant la synthèse des résultats obtenus et amène des perspectives de recherche. Elle propose également des recommandations quant aux choix possibles de site pour l’implantation de peuplier hybride.

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Texte en Français :

C : Carbone

dhp : Diamètre à hauteur de poitrine

GES : Gaz à effet de serre

N : Azote

NQ : Nord-du-Québec

ON : Ontario

OSB : Panneau de lamelles minces, longues et orientées

P. : Populus

PEH : Peuplier hybride

PIB : Produit intérieur brut

QC : Québec

spp : Espèce (pl)

Text in English:

AAL: Abandoned agricultural land

Aff.: Afforestation

AIC: Akaike information criterion

ANOVA: Analysis of variance

ASV: Amplicon sequence variant

C: Carbon

C_{tot}: Total carbon

CO_2: Carbon dioxide

DBH: Diameter at breast height

DNA: Deoxyribonucleic acid

ECM: Ectomycorrhiza

F: Fermentation

H: Humus

H.AAL: Herbaceous abandoned agricultural land

Int.: Interaction

ITS: Internal transcribed spacer

L: Litter

LIC: Light intercepted by canopy

N: Nitrogen

NF: Non-afforested

NQ: Northern Quebec

ns: Not significant

N-S: North-South

N_{tot}: Total nitrogen

OC: Organic carbon

ON: Ontario

Ori.: Origin

P: Precipitation

PCA: Principal component analysis

PCoA: Principal coordinate analysis

PCR: Polymerase chain reaction

PEH: Hybrid poplar

permANOVA: Permutational analysis of variance

Pr/p: Probability

Q: Quebec

rRNA: Ribosomal ribonucleic acid

S.AAL: Shrubby abandoned agricultural land

SCC: Soil Clay Content

SOC: Soil Organic Carbon

spp: Species (pl)

sq: Square

SWC: Soil water content

T: Temperature

W-E: West-East

LISTE DES SYMBOLES ET DES UNITÉS

% : Pourcentage/Percentage

µm : Micromètre/Micrometer

µmol.s^{-1}.m^{-2} : Micromole par seconde par mètre carré/Micromole per second per square metre

°C : Degrés Celsius/Degrees Celcius

cm : Centimètre/Centimeter

cm : Centimètre carré/Square centimeter

g : Gramme/Gram

g.kg^{-1} : Gramme par kilogramme/Gram per kilogram

km^2 : Kilomètre carré/Square kilometer

m^3 : Mètre cube/Cubic meter

mm : Millimètre/Millimetre

nm : Nanomètre/Nanometer

m^3.ha^{-1}.year^{-1} : Mètre cube par hectare par année/Cubic meter per hectare per yea

Mg.ha^{-1} : Mégagramme par hectare/Megagram per hectare

S : Svedberg

INTRODUCTION GÉNÉRALE

Silviculture. En 2018, la production mondiale de bois a atteint pour la première fois 4 milliards de mètres cubes et devrait continuer de croitre pour atteindre les 6 milliards à l'horizon 2050 (Barua et al., 2014; FAO, 2024). Le nouvel essor des économies de la Chine, de l'Inde ou du Brésil au cours des dernières décennies a considérablement accru la demande en matériaux de construction, pâte à papier et produits manufacturés issus de la filière du bois (Hurmekoski & Hetemäki, 2013; McEwan et al., 2020). À cela s'ajoute le caractère renouvelable du bois qui, associé à la nécessité de réduire notre dépendance vis-à-vis des énergies fossiles, fait de cette ressource un bien recherché pour le développement de bioénergies et de nouveaux biomatériaux (González-García et al., 2011; B. Talbot & Ackerman, 2009). Néanmoins, la récolte intensive conventionnelle de bois sur de courtes rotations aboutit à la création de forêts équiennes relativement jeune et à la disparition progressive de vieilles forêts et de leurs services associés (Bergeron et al., 2017; Jobidon et al., 2015; Peura et al., 2018). Plusieurs approches ont été développées pour limiter l'impact des pratiques sylvicoles sur les écosystèmes comme la foresterie de rétention en Suède ou l'aménagement écosystémique au Québec (Bergeron et al., 2007; Simonsson et al., 2015). L'aménagement écosystémique québécois a pour objectif d'émuler les perturbations naturelles lors d'opérations forestières afin de permettre à l'écosystème de se régénérer plus facilement après une coupe, de garantir sa durabilité et de réduire les écarts entre forêt naturelle et forêt aménagée (Bergeron et al., 2007). Malgré le développement d'outils afin de limiter l'impact des pratiques sylvicoles sur les écosystèmes, il est fréquent que l'intégralité des arbres marchands soient coupés lors des opérations de récoltes. De plus, les arbres issus des forêts naturelles ou faiblement aménagées ne suffiront probablement pas à combler la demande en bois dans les années futures (Warman, 2014).

Les plantations intensivement aménagées sont susceptibles de fournir dans un futur proche la majorité de la demande de l'industrie forestière permettant ainsi de substituer une partie du bois issu des forêts naturelles par celui des plantations et donc de limiter les perturbations liées à sa récolte au sein des écosystèmes forestiers tout en rendant une partie des services écosystémiques des forêts naturelles (McEwan et al., 2020). Néanmoins, malgré de hauts rendements sur des surfaces modestes, établir des plantations demande de la surface disponible. Or la sylviculture doit faire face à la concurrence des terres dédiées à la production de denrées agricoles et à l'expansion de l'urbanisation et des zones naturelles protégées. De plus, il n'est généralement pas souhaitable de substituer un milieu naturel comme une forêt ou un milieu humide par une plantation. Dans le monde, de nombreux territoires ruraux sont sujets à une importante déprise agricole laissant de grandes surfaces de terres à l'abandon. Ces friches agricoles apparaissent alors comme une possible opportunité d'extension pour la sylviculture intensive et l'établissement de plantations à croissance rapide et à haut rendement.

Les terres agricoles abandonnées. Une terre agricole abandonnée est une ancienne parcelle dédiée à la culture ou à l'élevage qui fut progressivement abandonnée par ses exploitants et où la végétation évolue avec peu ou sans intervention humaine (Alix-Garcia et al., 2012; T. Shi et al., 2018; Sroka et al., 2019). Ce processus est principalement observé dans les pays développés avec un haut PIB par habitant (Figure 1) et ses causes sont multifactorielles en incluant des problématiques liées à l'économie, la politique, le social ou encore l'écologie (Queiroz et al., 2014; Subedi et al., 2022). Par exemple, les zones rurales marginalisées montagneuses souffrent souvent de ce phénomène en raison de terrain accidenté limitant l'usage de machines agricoles, d'une faible densité de population réduisant la main-d'œuvre disponible ou encore de sols peu fertiles affectant la productivité de l'exploitation (S. Li et al., 2018; Lieskovský et al., 2015; Murua et al., 2013). À l'échelle mondiale, la mise en concurrence d'exploitation de différents pays pousse les exploitants les moins performants à s'adapter ou à changer d'activité comme ce fut le cas lors de la chute de l'URSS, les agriculteurs soviétiques n'étaient plus compétitifs lorsque l'économie de leur pays s'est ouverte (Lieskovský et al., 2015). Plus localement, dans la région québécoise de l'Abitibi-Témiscamingue, de nombreuses terres agricoles ont été défrichées au cours du XX^{e} siècle lors de différentes vagues de colonisation encouragées par le gouvernement québécois. Aujourd'hui, les friches agricoles représentent dans la région une superficie d’environ 388 km² selon les données écoforestières (Ministère des ressources naturelles et des forêts, 2017). Bien que fertiles, les sols argileux de la région sont difficiles à travailler. Les épisodes de sécheresse les rendent durs et cassants tandis que les propriétés imperméables de l’argile favorisent la formation de cuvettes d’eau dans les dépressions des champs lors des précipitations. De plus, le climat rigoureux réduit la saison de croissance. Enfin, d’importantes opportunités économiques dans les secteurs des mines ou de la foresterie ont fini de convaincre beaucoup d’exploitants de délaisser leurs terres pour des emplois mieux rémunérés.

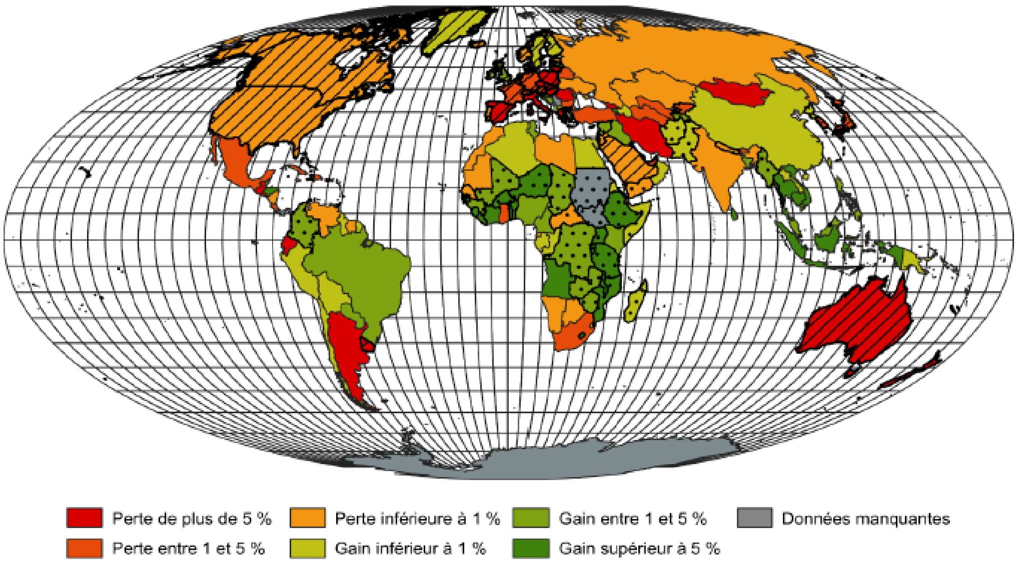

Figure 1
Gains et pertes de surfaces agricoles par pays en pourcentage de leur superficie totale. Les hachures correspondent à un PIB par habitant supérieur à 15 000 $ et les points à un PIB par habitant inférieur à 1 500 $.

Source : FAOSTAT 2022.

Les opportunités d’aménagement et de restauration offertes par les terres agricoles sont beaucoup discutées dans la littérature. Certaines publications proposent dans certains cas de miser sur un retour de la production agricole sur les parcelles délaissées. De nombreux paysages ruraux sont façonnés par une agriculture extensive traditionnelle et sont appréciés par les populations pour leur valeur esthétique et historique (Fischer et al., 2012; Mitchell & Buggey, 2000). Ce patrimoine permet à des régions rurales de bénéficier d'un attrait touristique et donc d'un apport financier non négligeable, d'autant que ces territoires sont souvent isolés, marginalisés et en première ligne face à la déprise agricole (Fischer et al., 2012; Mitchell & Buggey, 2000). Outre les bénéfices économiques et sociaux apportés par les systèmes agraires traditionnels, de nombreux services écosystémiques leur sont associés. On peut citer la conservation de la biodiversité spécifique à ces paysages ouverts, la protection des sols face à l'érosion ou encore la prévention des feux de broussailles (Barrett & Mitchell, 2016; Rey Benayas et al., 2007; Stanchi et al., 2012). Néanmoins, il n'est pas toujours envisageable de rétablir une activité agricole sur ces terres, les contraintes qui ont conduit dans un premier temps à leur abandon peuvent demeurer trop importantes pour envisager cette possibilité (Meyfroidt et al., 2016). D'autres études proposent de favoriser une restauration passive de l'écosystème après l'abandon (Navarro & Pereira, 2012; Rey-Benayas et al., 2010). Lorsqu'une terre agricole est abandonnée, une succession secondaire s'établit et la friche évolue progressivement d'une végétation herbacée vers une végétation arbustive pour finir par la restauration d'un écosystème forestier et des services qui lui sont associés (Chazdon et al., 2020; Ustaoglu & Collier, 2018). Cependant, cette restauration passive peut se heurter à différentes problématiques. Les perturbations induites par l'activité agricole peuvent mener à la création de barrières écologiques ralentissant ou stoppant la succession secondaire comme l'invasion par des espèces exotiques ou la dégradation trop importante des sols (Parrotta et al., 1997). De plus, le bon déroulement de cette succession dépend de nombreux facteurs comme le climat, le sol ou bien la distance séparant la succession des réserves de graines et de propagules (Cruz-Alonso et al., 2019). Le reboisement des friches agricoles se présente comme une troisième alternative à leur aménagement. Il peut permettre de répondre aux objectifs de production de bois tout en permettant d'abolir les barrières qui pèsent sur la succession secondaire. Si de nombreuses essences d'arbres peuvent être utilisées dans le cadre de campagne de reboisement, l'une des essences caducifoliées fréquemment utilisées au Québec pour le reboisement de friche agricole est le peuplier hybride (Vouligny & Gariépy, s. d., Figure 2).

Le peuplier hybride. Le genre Populus regroupe des espèces d’arbres caducifoliés, rarement sempervirents, rencontrés dans une large variété d’habitats au sein de l’hémisphère nord (Isebrands & Richardson, 2013). Grâce à leur croissance rapide et à leur facilité de propagation par bouturage, les peupliers et leurs hybrides sont souvent utilisés à l’échelle mondiale pour la production de bois, de papier et de bioénergies (Thakur et al., 2021). Ils sont également employés dans le but de restaurer des services écosystémiques comme la préservation des sols, la séquestration du carbone et la protection des ressources en eau (Ball et al., 2005; DeGryze et al., 2004). En effet, ils possèdent la capacité de pouvoir se développer sur des sols pauvres en nutriments, hypersalins ou chargés de polluants (Chen & Polle, 2010; Nogues et al., 2019). Enfin, le peuplier est une plante modèle abondamment utilisée en laboratoire en raison de sa facilité de culture, son court cycle de vie et la bonne connaissance de son génome de petite taille (Taylor, 2002) dont le séquençage fut publié par Tuskan et al. (2006).

Figure 2
Plantation de peuplier hybride (clone 915 319) à Saint-Dominique-du-Rosaire, QC, Canada.

On doit l'apparition des premières cultures d'hybrides en Europe à l'arrivée des essences venues d'Amérique du Nord dans les années 1750. Le premier croisement contrôlé de parents sélectionnés est réalisé par A. Henry en 1912 aux jardins Kew de Londres (*Populus deltoides [W. Bartram ex Marshall] x Populus trichocarpa [Torr. & A.Gray ex Hook.]*). Du côté du Canada, les premiers individus hybrides sont utilisés comme brise-vent dans la région des Prairies en 1903. Puis c'est en 1952 que l'on voit les premiers essais au Québec, principalement conduit par des compagnies comme la Compagnie internationale du papier (Dickmann, 2006; Ménétrier, 2008). Les peupliers hybrides sont dotés d'un rendement important sur de brèves rotations. En 20 à 30 ans, les peupliers hybrides produisent en moyennes 11,6 m3.ha^{-1}.an^{-1} (Ménétrier, 2008). Dans des conditions de cultures optimales, le peuplier peut produire

1 à 2,5 fois plus de bois sur une période 3 fois plus courte comparée à d'autres espèces comme l'épinette (Ménétrier, 2008). Même si l'épinette, et plus généralement les résineux, reste préférée par l'industrie du bois d'œuvre par rapport au peuplier (Isebrands & Richardson, 2013), celui-ci possède de nombreux débouchés pour la construction notamment via la fabrication de panneaux OSB (Oriented Strand Board) ou du contreplaqué. De nos jours, de nouveaux cultivars de peupliers hybrides sont développés à l'aide du génie génétique afin de réduire l'impact de perturbations biotiques (ravageurs, insectes) et abiotiques (sécheresse) sur les peuplements (Thakur et al., 2021).

Comme de nombreuses autres plantations industrielles, la populiculture est souvent perçue négativement par le grand public en raison d'une faible diversité apparente dans le sous-bois des plantations (Buijs & Lawrence, 2013). Bien que ces écosystèmes soient en effet généralement moins riches et diversifiés que des forêts naturelles, ces derniers peuvent toutefois abriter une certaine diversité végétale, et fournir certains services comme la séquestration du carbone (Boothroyd-Roberts et al., 2013; Winans et al., 2015).

Diversité végétale. Plusieurs notions permettent de décrire la biodiversité. On parle de richesse spécifique pour évoquer le nombre d'espèces présentes dans un habitat donné. La diversité spécifique, quant à elle, ajoute une autre dimension à la notion de richesse en incluant dans son calcul le nombre d'individus par espèces. Il existe différents indices calculant la diversité spécifique comme l'indice de Shannon (Shannon, 1948), l'indice de Simpson (Simpson, 1949) ou encore l'indice de Berger-Parker (Berger & Parker, 1970). Enfin, l'équitabilité (ou evenness en anglais) mesure l'homogénéité de la répartition du nombre d'individus par espèces (Pielou, 1969). Par exemple, une communauté composée de 20 individus de l'espèce A et 300 de l'espèce B sera moins équitable (even) qu'une communauté avec 102 individus de l'espèce A et 95 de l'espèce B (Purvis & Hector, 2000; Spellerberg & Fedor, 2003; Xu et al., 2020).

En 1972, Whittaker proposait 4 indicateurs, toujours utilisés de nos jours, offrant la possibilité d'évaluer la variabilité spatiale des espèces présentes : la diversité ponctuelle qui réfère à la diversité d'un point ou d'un micro-habitat spécifique de l'espace, la diversité alpha (α) qui sert à désigner la diversité à une échelle locale, la diversité gamma (γ) qui permet de la décrire à l'échelle du paysage et la diversité bêta (β) qui permet de dépeindre la variabilité entre deux habitats ou le long d'un gradient (Xu et al., 2020). Néanmoins, la méthode de calcul et ce que représentent ces indicateurs restent débattus dans la littérature. Par exemple, selon Jurasinski et al. (2009), la diversité β peut être divisée en deux groupes en fonction de ce qui est mesuré : variation de la richesse spécifique vs variation dans la composition spécifique. Les diversités α et γ peuvent être quant-à-elles regroupées sous le terme d'inventaire de la diversité. En revanche pour Moreno & Rodríguez (2010), les termes α et γ devraient être gardés séparés, car la diversité α s'intéresse à un niveau local et homogène tandis que la diversité γ s'intéresse à un niveau plus large et hétérogène.

Au début des années 90, la biodiversité était vue comme un simple paramètre de l'écosystème pouvant affecter ses fonctions (van der Plas, 2019). Mais à la fin de cette décennie, la perception de la biodiversité a changé ; elle est désormais considérée comme l'un des moteurs assurant le bon fonctionnement de l'écosystème (Tilman et al., 1996). Par la suite, plusieurs auteurs ont montré qu'une perte de biodiversité pouvait altérer les fonctions et les processus des écosystèmes (Hooper et al., 2005; Loreau et al., 2001) affectant en conséquence les services rendus à la société par les écosystèmes tels que la production de nourriture, la gestion de l'eau, le contrôle des nuisibles, la pollinisation, la régulation du climat par la séquestration du carbone ou encore les aspects récréatifs (Aerts & Honnay, 2011; Mori et al., 2017).

Les plantes vasculaires sont abondamment étudiées dans la littérature sur la biodiversité à l'inverse des espèces non vasculaires que sont les bryophytes (Figure 3). Pourtant à de hautes latitudes comme dans les biomes boréaux, les écosystèmes sont caractérisés par une importante communauté de bryophytes et en général l'abondance des mousses augmente tandis que celle des plantes vasculaires diminue au fur et à mesure que l'on progresse le long du gradient latitudinal (Turetsky et al., 2012). En outre, elles remplissent de nombreuses fonctions au sein des forêts boréales avec des rôles dans le cycle des nutriments, la productivité primaire, la rétention d'eau et l'accumulation de carbone (Chapin et al., 2010; Turetsky et al., 2012). Les bryophytes peuvent être divisées en deux catégories en fonction de leur affinité avec des micro-habitats spécifiques : les espèces spécialistes avec de fortes exigences écologiques et une faible capacité de dispersion ; les espèces généralistes avec de faibles exigences écologiques et une forte capacité de dispersion (Barbé et al., 2020).

Figure 3
Un exemple de bryophyte abondante en forêts boréales, la Pleurozie dorée (Pleurozium schreberi).

Le couvert végétal et le microbiome entretiennent des relations étroites en raison des associations symbiotiques liant ces deux grands règnes du vivant. Les ectomycorhizes, les mycorhizes arbusculaires et les nodosités racinaires des fabacées sont des exemples parmi d'autres d'association plantes-microorganismes jouant des rôles essentiels dans de nombreuses fonctions et services écosystémiques (Smith & Read, 2008; Soyano et al., 2021).

Microbiome. Du fait d'une grande diversité au sein du monde microbien, les microorganismes sont les êtres vivants les plus largement répandus à la surface du globe, présents dans tout type de milieux et capables de survivre dans des environnements extrêmes, des eaux hypersalines de la mer Morte jusqu'aux glaces de l'Antarctique (Goordial et al., 2016; Thombre et al., 2016). Dans les écosystèmes terrestres, les microorganismes jouent un rôle clé dans la décomposition de la matière organique, les cycles de nutriments et la santé des plantes (Cavicchioli et al., 2019). En forêt, les microorganismes sont localisés dans de nombreux habitats comme le feuillage des arbres, le bois mort ou encore les surfaces minérales. Chacun de ces compartiments possède ses propres caractéristiques influençant l'abondance et la composition microbienne (Baldrian, 2017). Mais l'habitat renfermant la plus grande quantité de microorganismes au sein d'une forêt reste le sol, où la composition et l'activité de la communauté microbienne sont principalement déterminées par les différentes propriétés édaphiques comme la teneur en matière organique, le pH ou la texture du sol (Lauber et al., 2008; Rousk et al., 2010), ainsi que par la composition végétale (Tedersoo et al., 2016).

Les ectomycorhizes et les mycorhizes arbusculaires présentent généralement des préférences pour certaines plantes hôtes (Lang et al., 2011). Cette spécificité s'observe aussi dans les taxons non symbiotiques en raison du prolongement du mycélium des mycorhizes hôtes spécifiques en dehors de la rhizosphère et de leur interaction avec le reste de la communauté microbienne (Urbanová et al., 2015). De même, il est à noter que, dans les forêts boréales, les ectomycorhizes représentent près du tiers de la biomasse microbienne (Högberg & Högberg, 2002). En forêt, la litière du sol abrite également une part non négligeable du microbiome où il est constitué majoritairement de taxa saprotrophiques pouvant métaboliser des composés récalcitrants faits de structures polyphénoliques comme la lignine (Lindahl et al., 2007). La communauté bactérienne de la litière diffère de celle du sol, l'abondance relative de *Proteobacteria* et de *Bacteroidetes* y est plus importante

(López-Mondéjar et al., 2015). Tout comme le microbiome du sol, celui de la litière est influencé par la végétation. Les microorganismes présents dans la litière semblent adaptés à décomposer les débris végétaux spécifiques du milieu dans lequel ils évoluent (Chomel et al., 2016; Prescott & Grayston, 2013).

Un changement d'utilisation des sols vers une forêt plantée entraine des modifications importantes au sein de la communauté microbienne du sol. D'anciennes terres agricoles, reboisées avec des robinier faux-acacia (*Robinia pseudoacacia* [L.]), ont montré une biomasse microbienne et des diversités α et β plus importantes comparativement à des terres agricoles non reboisées (Ren et al., 2016). D'autres études de reboisement de sols cultivés par du peuplier hybride montrent que la communauté bactérienne perd en abondance après une afforestation, tandis que la communauté fongique voit son abondance et sa diversité augmenter (Yannikos et al., 2014; Zheng et al., 2017). Les auteurs expliquent cette différence de réponse des communautés fongiques et bactériennes par la capacité des champignons à métaboliser la cellulose et la lignine, ces composés étant plus abondants dans les plantations par rapport aux sols cultivés par des plantes herbacées. A contrario, l'afforestation de prairies naturelles par du pin rouge de Chine (*Pinus tabuliformis [Carrièrel]*) sur le plateau de Loess en Chine a conduit à une baisse de l'abondance et de la diversité fongique tandis que la communauté bactérienne s'est révélée peu affectée (K. Wang et al., 2019). Les auteurs expliquent ce résultat par la capacité de la communauté bactérienne à métaboliser une grande variété de composés la rendant plus résistante et résiliente face à une perturbation. Toujours concernant des prairies naturelles, Chen et al. (2021) ont observé une transition dans la communauté bactérienne où elle est dominée par les *Acitnobacteria* oligotrophes en prairie, puis dominée par les *Alphaproteobacteria* copiotrophes en plantations. Selon les auteurs, ce changement peut être attribué à l'augmentation de substrats carbonés et azotés dans les sols des plantations. Enfin, l'étude de Vitali et al. (2016) nous apprend que l'afforestation d'une forêt naturelle influence la communauté microbienne en diminuant la diversité α et en modifiant la composition des communautés.

Les microorganismes présents dans le sol sont intimement liés aux cycles des nutriments (Figure 4). Le microbiome intervient dans la minéralisation, la stabilisation et le turn-over de la matière organique et leurs résidus et exsudats contribuent à hauteur de 80 % au C de la matière organique du sol. Cela nous indique que les microorganismes du sol sont des acteurs clés de la séquestration du C (Liang et al. 2017 ; Wiesmeier et al. 2019).

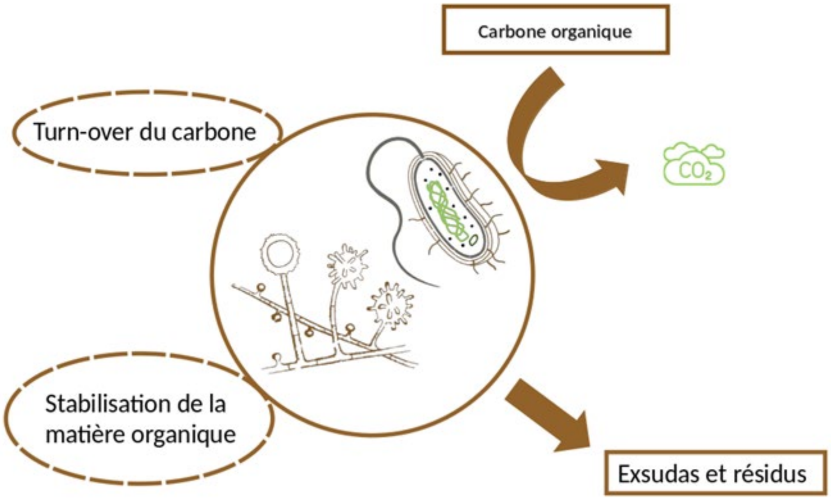

Figure 4
Schématisation des interactions entre le microbiome et le carbone organique présent dans le sol. Les cercles en pointillés montrent des exemples du rôle des microorganismes dans le cycle du carbone et les flèches, les flux de carbone.

Il en va de même pour le couvert végétal. La diversité et la composition des communautés qui le compose influencent considérablement les flux de carbone au sein des écosystèmes (Figure 5). En effet, le carbone du sol provient principalement de la décomposition des tissus végétaux, ainsi l'apport de carbone au sol dépend des caractéristiques de la végétation comme de sa rapidité de croissance, de la concentration de carbone dans ses tissus ou bien des caractéristiques physico-chimiques des feuilles influençant la vitesse de décomposition de la litière (De Deyn et al., 2008). De plus, l'apport en C au sol des exsudats racinaires compte pour 5 à 33 % de la photo-assimilation journalière, et peuvent affecter la décomposition du carbone en stimulant l'activité microbienne (Bardgett et al., 2014). Les traits de la végétation influencent également les stocks de carbone en structurant la distribution verticale du carbone dans le sol via différents profils d'allocation (Jobbágy & Jackson, 2000).

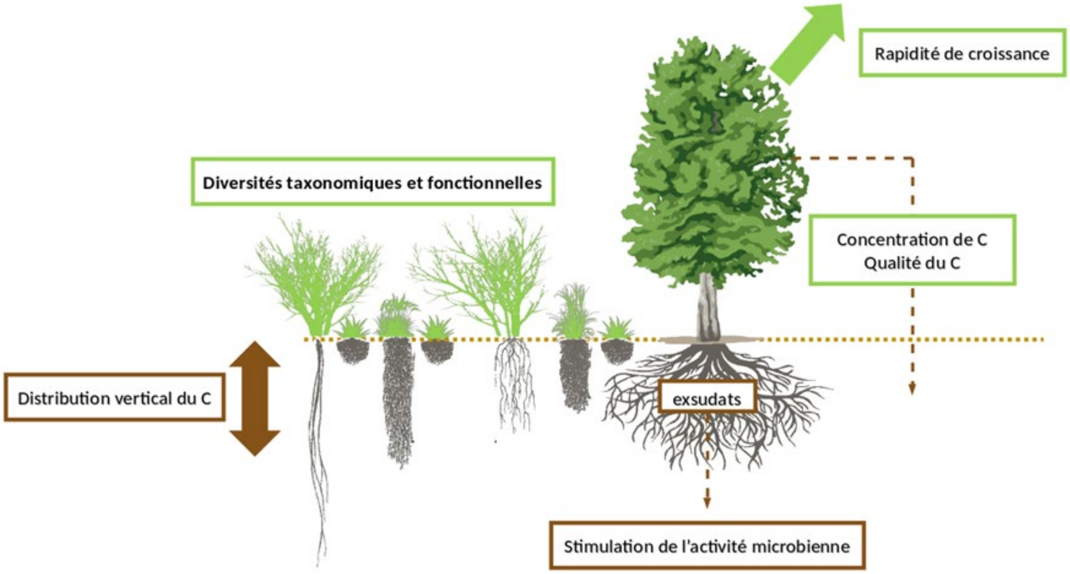

Figure 5
Les différentes influences schématisées de la végétation sur le cycle du carbone.

Carbone. Le relargage par les activités humaines d'une grande quantité de gaz à effet de serre (GES) depuis le début de la révolution industrielle provoque une modification profonde du climat qui verra les températures moyennes grimper de presque 3 °C d'ici la fin du siècle si les émissions de GES demeurent inchangées (IPCC, 2021). La reforestation de zones agricoles abandonnées est une stratégie envisagée pour atténuer les changements climatiques en cours et à venir (Raihan et al., 2019). En effet, la majorité des stocks de carbone des biomes terrestres sont emmagasinés dans le sol des milieux forestiers (Jackson et al., 2017). Des pratiques sylvicoles visant à améliorer la séquestration du carbone ou bien le reboisement de zones déboisées représentent donc un fort potentiel d'accumulation du carbone (Mayer et al., 2020). Cette capacité de stockage est le résultat de la différence entre le carbone acquis par la photosynthèse et le carbone perdu par la respiration cellulaire des organismes de l'écosystème, le lessivage et l'érosion des sols (Paterson et al., 2009).

Le carbone du sol est présent sous forme de composés organiques issus de la décomposition par la faune et les microorganismes de tissus organiques provenant de la biomasse végétale (feuille, tige et racine) et animale (fèces et corps) (Mayer et al., 2020). Les exsudats des racines et leurs microbiotes associés fournissent également des molécules organiques riches en carbone et exercent une grande influence sur les communautés microbiennes du sol (Paterson et al., 2007). Le carbone organique peut persister ainsi dans le sol pendant plusieurs siècles (Schmidt et al., 2011). Cette persistance peut s'expliquer par 3 principaux mécanismes de protection limitant l'accès des microorganismes et des enzymes extracellulaires aux composés organiques (Figure 6) : (I) La formation de micro et macro-agrégats constitués de cellules microbiennes, d'exsudats racinaires et de mucus (Lal et al., 2015) ; (II) L'association de la matière organique à la matrice minérale du sol (Dungait et al., 2012; Hemingway et al., 2019) et (III) la récalcitrance de différents composés (Lützow et al., 2006). En ce qui concerne le carbone, le sol ne peut pas être considéré comme un compartiment homogène. En effet, le carbone organique est distribué de manière inégale le long d'un gradient de profondeur où l'on observe une baisse constante des concentrations de carbone au fur et à mesure que l'on progresse vers les strates inférieures (Jobbágy & Jackson, 2000). De plus, les différentes perturbations pouvant affecter les stocks de carbone ont un impact variable en fonction de la profondeur (Jobbágy & Jackson, 2000; Laganière et al., 2010). La conversion de terres cultivées vers une plantation engendre une hausse des stocks de carbone organique dans les 10 premiers cm du sol minéral et reste non significative au-delà (Bárcena et al., 2014; S. Shi et al., 2016). Cependant, d'autres résultats indiquent que les couches profondes peuvent accumuler du carbone sur le plus long terme, 50 ans après la plantation (Zak et al., 1990). Les mécanismes pouvant expliquer la lente accumulation de carbone dans les couches profondes sont : l'incorporation de carbone provenant des compartiments supérieurs vers ceux inférieurs par la faune et le lessivage du carbone dissous en plus de l'apport par les exsudats racinaires (Bárcena et al., 2014).

La capacité des sols à séquestrer du carbone dépend de plusieurs facteurs comme le climat, les propriétés physico-chimiques du sol et l'utilisation des terres (Wiesmeier et al., 2019). Les variables climatiques tels que les précipitations, l'humidité et les températures jouent sur la séquestration grâce à leur rôle respectif dans la production primaire nette, la stabilisation du carbone et l'activité de décomposition du microbiome (Chaplot et al., 2010; Conant et al., 2011; Doetterl et al., 2015). En ce qui concerne les caractéristiques du sol, on peut noter que la proportion d'argile dans le sol est fortement corrélée aux stocks de carbone organique (Wiesmeier et al., 2019). De plus, la composition minéralogique du sol conditionne l'association du C avec les surfaces minérales actives favorisant sa séquestration (Hobley et al., 2015; Percival et al., 2000).

L'utilisation des terres et leurs pratiques associées peuvent favoriser ou non la capacité de séquestration des sols. Les labours répétés des terres agraires rendent accessible le carbone organique aux décomposeurs accélérant sa minéralisation (Del Galdo et al., 2003). Au contraire, dans les biomes boréaux et tempérés, la végétation pérenne des forêts et prairies favorise l'accumulation de carbone (Guo & Gifford, 2002; Laganière et al., 2010). Néanmoins, ces écosystèmes n'accumulent pas le carbone de la même façon. Comparativement, les forêts l'accumulent plus dans les organes des végétaux et la couche organique du sol tandis que les prairies stockent le carbone préférentiellement dans le sol (Schulze, 2000; Vesterdal et al., 2002; White et al., 2000). En prairie, le carbone organique du sol est séquestré principalement par association à la matière minérale alors qu'en forêt on observe une séquestration relativement plus importante par les composés récalcitrants (Peichl et al., 2012).

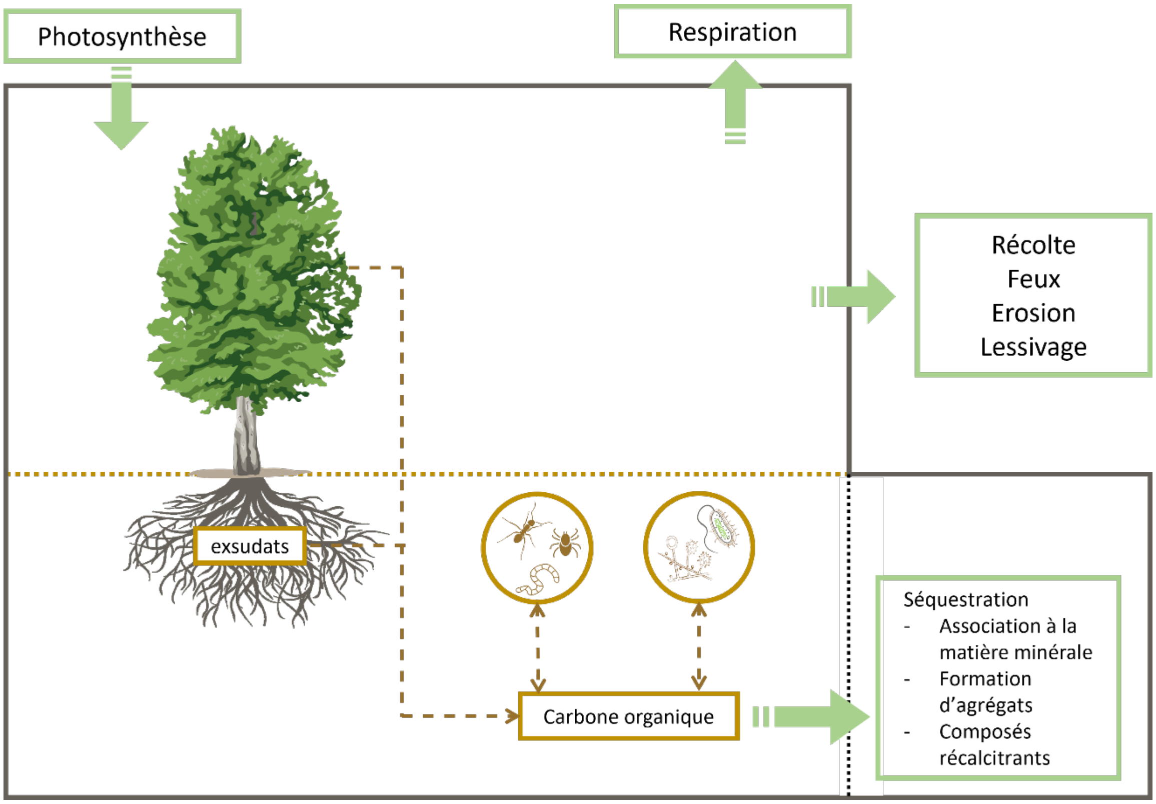

Figure 6
Schéma simplifié des mécanismes de séquestration du carbone dans les sols, les flèches représentent des flux de carbone.

Des facteurs spécifiques aux plantations sont aussi impliqués dans la capacité des sols à séquestrer le carbone. Les différentes techniques existantes de préparation mécanique du sol comme la scarification, le buttage et le hersage (Löf et al., 2012) sont susceptibles d'engendrer, à court et moyen terme, des pertes de carbone en raison de l'accélération du taux de décomposition de la matière organique (Ameray et al., 2021; Mayer et al., 2020). En outre, plus les perturbations associées à la préparation des sols sont élevées, plus la perte de carbone sera importante (Laganière et al., 2010). Néanmoins, la préparation du sol avant reboisement a pour but de favoriser la croissance, la survie et le développement des racines des jeunes arbres. Ce qui, à long terme, a pour conséquence de favoriser la production de biomasse et de composer les pertes de carbone liées à la préparation du terrain (Jandl et al., 2007).

Les liens étroits existant entre le couvert végétal, le cycle du carbone et les microorganismes nous amènent à prendre en compte ces trois éléments pour développer la problématique de cette présente thèse.

Problématique. Le reboisement de terres agricoles dans un court laps de temps après la cessation de leur exploitation est généralement perçu comme une transition positive pour la diversité ou la capacité à séquestrer du carbone. Bien que la mise en œuvre de certaines pratiques favorise la séquestration de carbone dans les sols des terres cultivées (Tiefenbacher et al., 2021), elles présentent généralement une déplétion de carbone plus important comparé aux prairies permanentes, temporaires et aux forêts (Pellerin et al., 2021). Cela s'explique principalement par l'exportation de matières organiques lors de la récolte, l'utilisation de fertilisants azotés, le travail du sol et par l'érosion (Drewniak et al., 2015; Lal, 2018). Le reboisement d'une terre cultivée permet d'augmenter la quantité de carbone dans le sol en éliminant les perturbations liées à l'activité agricole, mais aussi en accentuant les apports de litière et en favorisant la formation des agrégats par les organismes du sol (Guo & Gifford, 2002; Jégou et al., 2000; Laganière et al., 2010). Il en va de même pour la biodiversité malgré la place plus importante donnée aux agrosystèmes durables (Isbell et al., 2017). En effet, les champs cultivés sont des milieux où la biodiversité est souvent faible du fait de la prévalence de monocultures et de l'application de traitements contrôlant la compétition. Cependant, il est fréquent que les efforts de reboisement ciblent également des terres agricoles où la fin de leur exploitation remonte à plusieurs années, voire à plusieurs décennies (Fayet et al., 2022; Subedi et al., 2022).

L'abandon de terres agricoles entraine la mise en place d'une succession secondaire où la végétation peut évoluer progressivement vers la reconstitution d'un écosystème forestier. Plusieurs études montrent un effet positif de la restauration passive avec peu ou sans intervention humaine sur les fonctions de l'écosystème comme la biodiversité (Chazdon et al., 2020; Plieninger et al., 2014; Wilson et al., 2017) et la séquestration de carbone (Bell et al., 2021; Kämpf et al., 2016; Wertebach et al., 2017). Les communautés microbiennes du sol sont également sensibles à l'abandon des terres agricoles même si la nature des changements observés au sein de ses communautés ne fait pas consensus (Balami et al., 2021; G. Wang et al., 2021; Zhang et al., 2016). Or le reboisement, en raison des pratiques sylvicoles qui lui sont associées, est source de nombreuses perturbations pour les écosystèmes. Les opérations liées à l'établissement de la plantation comme la préparation du site, le discage ou la scarification sont susceptibles de perturber de nombreux micro-habitats ainsi que la banque de graine limitant donc la diversité végétale au sein de la plantation (Löf et al., 2012). Il semble légitime de se questionner sur le bienfondé d'une substitution d'une friche agricole par une plantation de peuplier hybride en ce qui concerne la diversité végétale, la séquestration du carbone et la composition des communautés microbiennes.

Un autre facteur à prendre en compte dans les conséquences d'un reboisement sur un écosystème est l'effet de l'historique des sols. En effet, les communautés végétales gardent en mémoire l'utilisation des sols précédant l'établissement d'une plantation (Bellemare et al., 2002; Gachet et al., 2007; Soo et al., 2009). Ainsi, l'impact du reboisement sur la composition et la diversité des communautés végétales peut varier en fonction du site sur lequel la plantation est établie. Gachet et al. (2007) ont montré que la végétation de sous-bois d'une plantation établie dans un environnement forestier convergeait plus rapidement vers celle d'une forêt naturelle par rapport à celle d'une plantation établie sur d'anciens sites agricoles en raison de la présence de matériel reproductif comme des graines ou des propagules. L'afforestation de terres en pâturage disposant d'une végétation herbacée pérenne mène à la persistance d'espèces adaptées aux milieux ouverts comme le Dactyle aggloméré (*Dactylis glomerata* [L.]) et le reboisement de sites cultivés aboutit à une plus grande proportion d'espèces rudérales dans la plantation (Soo et al., 2009). Les stocks de carbone présents dans le sol sont influencés par de nombreux facteurs et la capacité de séquestration des plantations est donc susceptible d'être dépendante de la nature du site d'origine. Plusieurs études indiquent que les plantations établies sur des terres cultivées ont une plus grande capacité de séquestration dans le sol et la biomasse que les plantations installées sur des prairies (Laganière et al., 2010; Lutter et al., 2016). S. Shi et al. (2016) ainsi que Guo et al. (2021) introduisent dans leurs métaanalyses des plantations sur friches en comparaison de celles effectuées sur des prairies et des cultures. Cependant, ces analyses reposaient principalement sur des études n'incluant qu'un seul type de site et étaient d'origines géographiques variées. Or, la structure des friches diffère grandement entre les biomes et dans le temps. Peu d'études comparent donc directement les effets de l'utilisation précédente des sols sur la séquestration du carbone en incluant à leur analyse des terres abandonnées aujourd'hui à l'état de friches.

Les communautés microbiennes sont également sensibles à un changement d'utilisation des sols. Lors d'un reboisement sur d'anciennes terres cultivées, l'augmentation des apports organiques de la litière et des racines, la modification de composition végétale ainsi que la diminution du pH et de la température du sol entrainent un accroissement de la biomasse microbienne ainsi qu'une hausse de la diversité des communautés bactériennes (Ren et al., 2016; Soleimani et al., 2019). Cependant, Zheng et al. (2017) ont observé une perte d'abondance au sein de la communauté bactérienne après une afforestation par du peuplier hybride, ils expliquent leur résultat par la baisse de carbone organique dissous et de NH_4^+. Dans cette même étude, l'abondance et la richesse de la communauté fongique se sont avérées stimulées par le reboisement des terres agricoles notamment à cause de la capacité des champignons à décomposer la lignine et la cellulose. L'afforestation d'une prairie influence également le microbiome du sol. Chen et al. (2021) ont montré une augmentation de la richesse et de la diversité des communautés bactériennes après le reboisement d'une prairie. Mais cette conclusion diffère de celle de la publication de Wang et al. (2019) où la diversité microbienne n'a pas évolué positivement lors du reboisement d'une prairie et où la diversité fongique avait diminué. La variété de réponses observées dans la littérature concernant le comportement de la communauté microbienne lors d'un reboisement ne permet pas de dégager des tendances claires quant à l'impact de l'utilisation précédente des sols sur le microbiome.

En résumé (Figure 7): le reboisement de terres agricoles est généralement positif en terme de biodiversité et de carbone séquestré mais il est également source de perturbations importantes. Est-il donc judicieux de reboiser des terres agricoles abandonnées depuis plusieurs années en raison de l'avancée d'une succession secondaire qui permet de restaurer certaines fonctions de l'écosystème ? Les possibilités d'établissements de plantations intensives de peuplier hybrides dans notre région d'études sont variées, est-il préférable de cibler des sites provenant d'anciennes coupes forestières et donc influencés par un environnement forestier ? Ou bien est-il plutôt souhaitable de reboiser prioritairement les friches agricoles, nombreuses en Abitibi-Témiscamingue ? En effet, l'impact d'un reboisement sur la diversité végétale, les stocks de carbone et les communautés microbiennes dépend grandement de l'historique des terres reboisées. Enfin, les friches agricoles existent à différents stades de végétations, on peut se demander quelles seraient les différences d'impact entre le reboisement d'une friche arborant une végétation herbacée et une friche arborant une végétation plus avancée composée principalement d'une végétation arbustive.

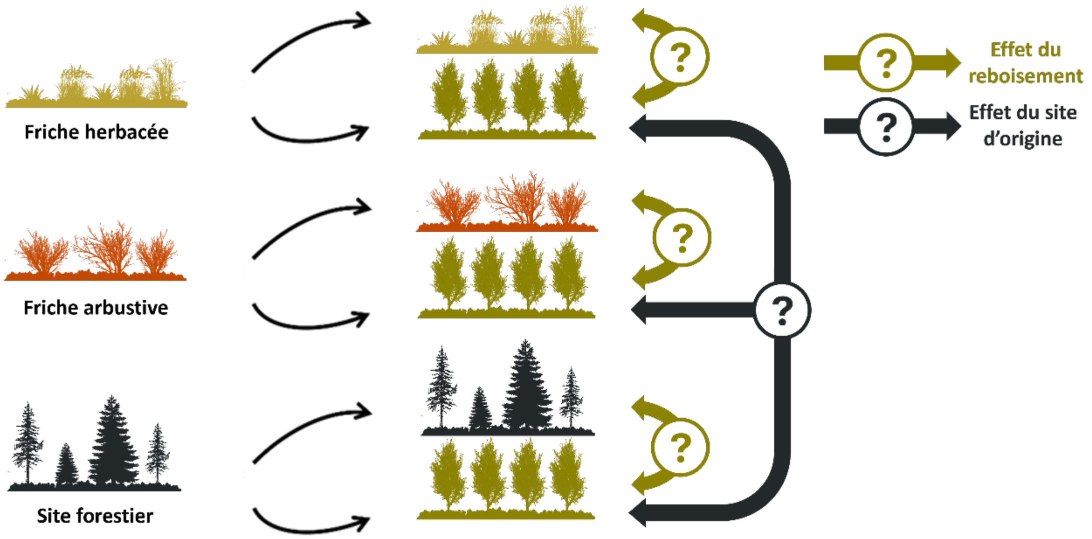

Figure 7
Résumé des problématiques étudiées dans le présent manuscrit.

Objectifs et hypothèses. Dans le premier chapitre, nous tenterons de déterminer l'influence du site d'origine sur la diversité et la composition des communautés végétales lorsque l'on établit une plantation intensive de peuplier hybride sur des friches agricoles à différents stades de végétation et dans un environnement forestier. Nous avons comparé les plantations avec des zones adjacentes non reboisées en prenant en compte l'état de la végétation au moment de la plantation.

En général, les sols forestiers contiennent une plus grande proportion de matériaux reproductifs issus d'espèces forestières adaptées aux environnements ombragés (Gachet et al., 2007; Hébert et al., 2016; Jacob et al., 2017). Notre première hypothèse suppose que l'établissement d'une plantation de peuplier hybride sur des sites forestiers va permettre une plus grande diversité végétale que sur une friche agricole en raison de la présence de matériaux reproductifs d'espèces forestières. Notre seconde hypothèse est que les plantations sur les friches agricoles avec une végétation arbustive contiendront une plus grande diversité végétale que celles sur les friches agricoles avec une végétation herbacée, mais plus faible que les plantations établies sur des sites forestiers en raison de l'établissement progressif d'espèces forestières au cours de la succession secondaire. Enfin, puisque les perturbations liées aux activités agricoles sont profitables à de nombreuses espèces intolérantes à l'ombre avec une importante capacité de dispersion et une longue durée de persistance dans le sol (Aubin et al., 2014; Gachet et al., 2007; Soo et al., 2009), nous pensons que les plantations établies sur des friches herbacées auront une plus grande proportion d'espèces rudérales intolérantes à l'ombre, tandis que les plantations établies sur des sites forestiers contiendront une plus grande proportion d'espèces forestières tolérantes à l'ombre.

Dans le second chapitre, notre objectif était d'évaluer les conséquences d'un reboisement par du peuplier hybride sur les communautés fongiques et bactériennes du sol. Nous cherchons à comprendre les effets du reboisement en fonction de l'origine du site ciblé par l'établissement d'une plantation.

Bien que certains microorganismes soient spécifiques de leurs hôtes ou bien influencés par les espèces végétales de l’écosystème (Balami et al., 2021; Lang et al., 2011), l’assemblage du microbiome dépend, dans la plupart des cas, principalement de paramètres édaphiques et de la communauté de microorganismes déjà présents dans le milieu lors du reboisement (Dove et al., 2021). Le microbiome au sein des plantations de peuplier devrait varier en composition et en diversité en fonction de l’origine du site reboisé. En outre, les espèces fongiques sont mieux adaptées à des environnements riches en lignines et cellulose, car elles sont capables de métaboliser ces composés complexes. Tandis que les communautés bactériennes dominent les sols agricoles pauvres en matière organique (Six et al., 2006; Zheng et al., 2017). On peut alors s’attendre à une biodiversité fongique plus importante dans les plantations établies sur des friches arbustives, et à l’inverse une biodiversité de la communauté bactérienne plus importante lorsque les peupliers hybrides sont établis sur des friches agricoles herbacées. Enfin, nous supposons qu’il n’est pas préférable de reboiser des friches arbustives du point de vue de la biodiversité microbienne, car la perturbation engendrée par le reboisement pourrait bouleverser une communauté microbienne ayant commencé à s’acclimater à un environnement « quasi » forestier.

L’objectif du troisième chapitre est d’évaluer l’effet de l’origine du site lors du reboisement par du peuplier hybride d’anciens sites agricoles et forestiers sur les stocks de carbones du sol organique et minéral en les comparant à leur équivalent non reboisé.

Nous pensons que la croissance rapide du peuplier hybride et son apport conséquent à la litière peuvent permettre une meilleure accumulation de carbone dans les sols des plantations que dans leurs équivalents non reboisés, et ce, malgré les perturbations liées aux opérations liées à l’établissement de la plantation. La différence observée sur les stocks de carbone entre des terres reboisées et leurs homologues non plantées devrait être dépendante de l’origine des sites plantés (friche herbacée, friche arbustive et site forestier). En effet, nous devons prendre en compte d’une part les quantités initiales potentielles de carbone des sites reboisés et d’autre part la diminution de carbone engendrée par les pratiques sylvicoles lors du reboisement. Cette perte de C devrait être d'autant plus importante que les stocks initiaux sont élevés et dans les cas extrêmes ne devrait pas justifier le recours à un reboisement actif dans le but de séquestrer du carbone. Nous pensons donc que le gain en carbone sera plus important lorsque les plantations sont établies sur des friches agricoles abandonnées plus récemment et arborant une végétation herbacée tandis que les gains seront plus faibles pour une plantation établie en milieux forestiers. Les plantations implantées sur des friches arbustives devraient être un intermédiaire entre les deux.

Sites. Les données analysées dans cette thèse proviennent de 16 sites localisés dans la région québécoise de l'Abitibi-Témiscamingue à l'exception de deux d'entre eux situés en Ontario et dans la région Nord-du-Québec (Figure 8).

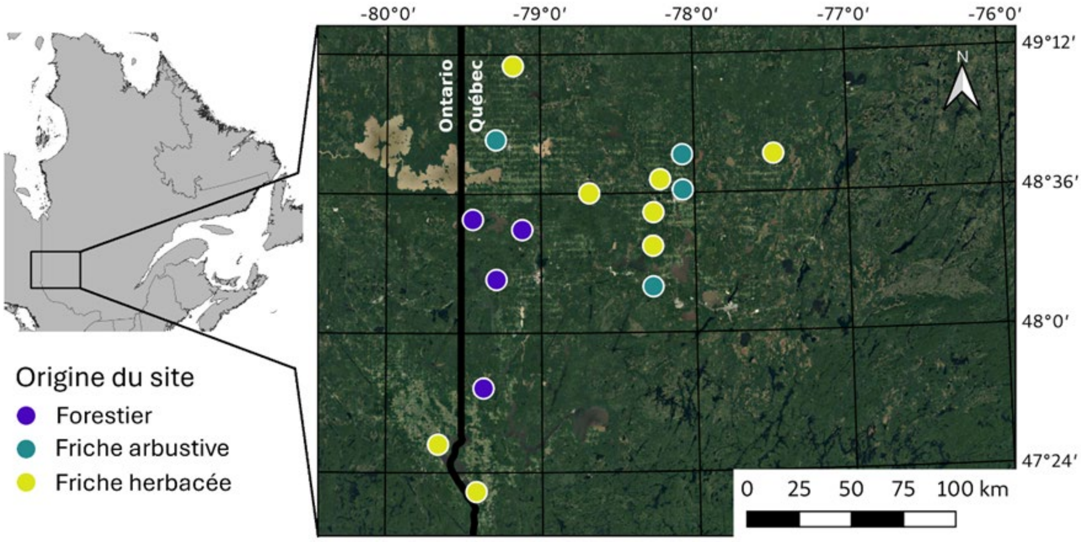

Figure 8 Carte détaillant la localisation de nos 16 sites d'étude ainsi que leur origine.

Source : Google maps 2023

Chaque site se compose d'une plantation de peuplier hybride établie entre 2003 et 2009, et de zones voisines non reboisées. Les zones non-reboisées nous servent de témoin et sont représentative de l'état de la végétation laissée en libre évolution sans intervention de reboisement. En raison des possibles variations liées aux différents clones présents dans les plantations, nous avons limité notre échantillonnage aux zones plantées avec le clone 915 319, un hybride issu d'un croisement entre le peuplier baumier et le peuplier du japon (*Populus balsamifera [L.] x Populus maximowiczii [Henry]*). Pour l'échantillonnage des zones non reboisées, nous avons délimité 3 cercles d'une superficie de 200 m² disposés de manière à être représentatifs de la végétation de la zone (Figure 9). Les plantations furent établies pour 4 d'entre elles sur d'anciens sites de coupes forestières mal régénérés, 4 étaient sur des friches agricoles disposant d'une végétation arbustive et finalement 8 ont été implantées sur des friches herbacées. Des échanges avec les propriétaires, des observations sur le terrain et de précédentes études nous ont permis de connaitre l'état de la végétation avant la plantation. Sur nos sites, les températures moyennes annuelles variaient de 0.1°C à 2.8°C et les précipitations annuelles moyennes de 785,1 mm à 950 mm (Gouvernement du Canada, 2011). Enfin, en raison des dépôts argileux glaciolacustres datant de la dernière glaciation et caractéristique de la ceinture d'argile Quebec-Ontario, les sols de nos sites sont principalement composés d'argile à l'exception du site de Nédelec qui est limoneux. Des informations plus détaillées sur chacun des sites sont disponibles dans le tableau 2.

Figure 9
Vue aérienne de l'un de nos sites localisés à Val-Paradis dans la région du Nord-du-Québec. Les blocs plantés avec le clone 915 319 sont délimités par les lignes orange et les cercles verts représentent les zones non reboisées.

Source : Orthophotographies aériennes de l'inventaire écoforestier du Québec méridional

Travaux de terrain. Dans chaque zone d'échantillonnage, nous avons placé aléatoirement des quadrats d'une surface de 1 m² (Figure 10a et b). Une condition s'applique aux quadrats des plantations : la moitié devaient être disposés entre deux rangs d'arbres et l'autre moitié au pied d'un arbre. Le nombre de quadrats dans les zones non reboisées était de 8 par zone (24 au total) tandis que le nombre de quadrats dans les zones d'échantillonnage de la plantation dépendait du nombre de zones plantées avec le clone 915 319 sur le site : 24 quadrats pour une zone (Site de Rivière-Héva), 4 quadrats pour 5 zones (Sites de Trécesson et Sainte-Gertrude) et 8 quadras pour 3 zones (tous les autres sites). Au sein des quadrats nous avons identifié les espèces de plantes vasculaires présentes ainsi que leur taux de recouvrement (Figure10c et d). Les bryophytes furent récoltées au sol et sur les arbres puis séchées en serre avant leur identification en laboratoire (Figure 10c et e).

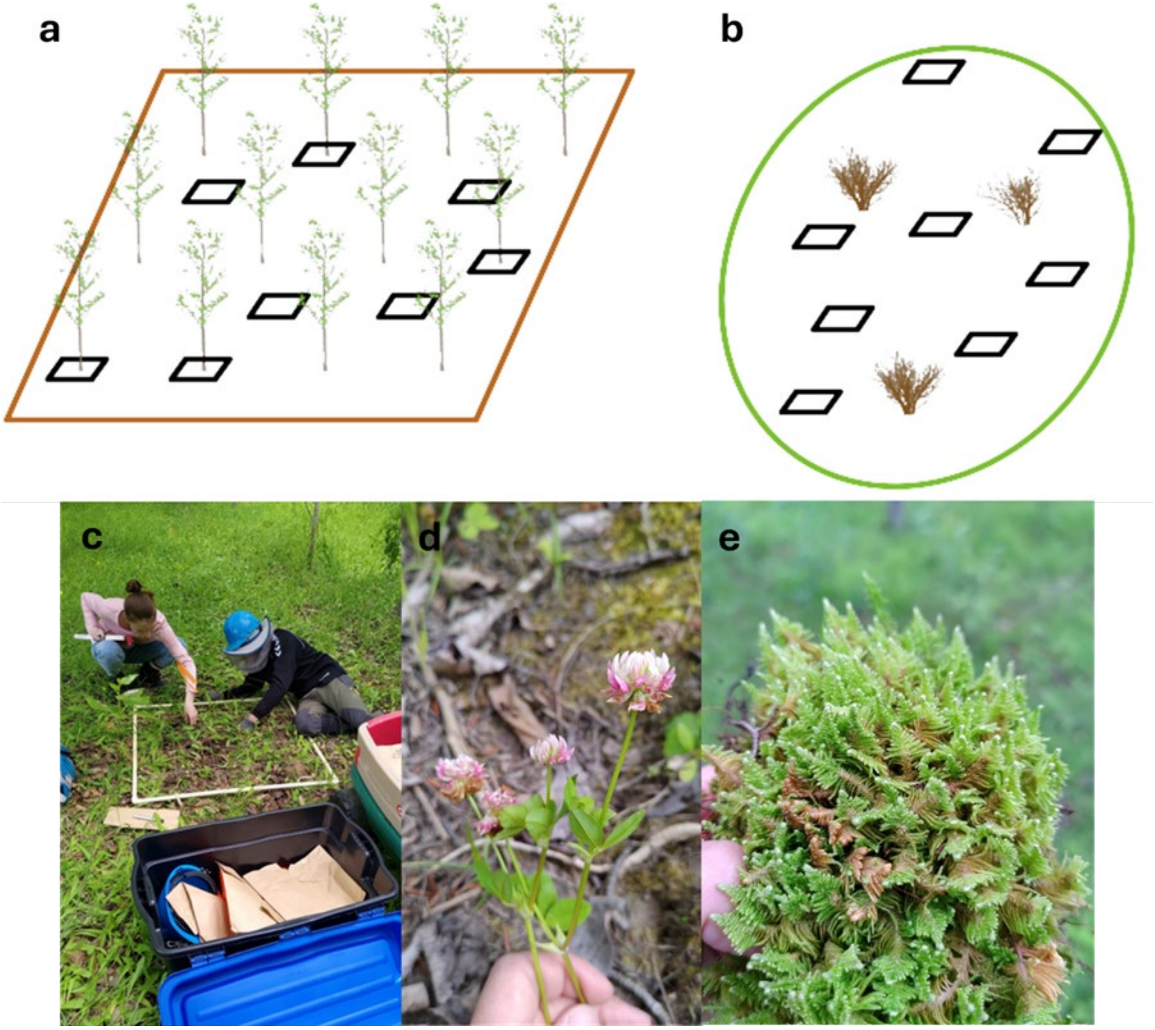

Figure 10
Disposition des quadrats au sein d’une zone plantée avec le clone 915 319 (a) et d’une zone non reboisée (b). Identification et récolte des plantes vasculaires et des bryophytes (c). Une plante vasculaire : *Trifolium sp* (d) et une bryophyte : *Ptilium crista-castrensis [Hedw.]* (e).

Pour les échantillons des chapitres concernant le carbone organique du sol et le microbiome, nous avons sélectionné 12 points d’échantillonnage pour chaque site. Six d’entre eux sont situés au sein de la plantation et 6 autres sont localisés au sein des zones non reboisées (Figure 11a et b). Cette sélection fut réalisée aléatoirement avec toujours une condition pour les plantations, la moitié des points devaient être placés entre deux arbres dans un rang et l’autre moitié entre deux rangs d’arbres. À chaque point d’échantillonnage nous avons prélevé la litière sur une surface de 177cm² contenant des débris végétaux ainsi que les strates L, F et H (Litière, Fermentation et Humus). Puis, avec une tarière hollandaise, nous avons prélevé 3 carottes de sol minéral de 15 cm chacune (0-15 cm, 15-30 cm et 30-45 cm) (Figure 11c et d). Nous avons regroupé nos échantillons dans des sacs plastiques pour former un échantillon composite pour chaque strate de sol, un pour la plantation, l'autre pour la zone non reboisée. Les échantillons ont été placés dans une glacière en attendant la fin de journée de terrain et le retour au laboratoire où ils ont été stockés à -20°C. Avec 16 sites, une plantation et une zone non reboisée par site et 4 strates de sol différent, nous avons collecté un total de 128 échantillons composites. Les échantillons composites de la strate 0-15 cm, issu du sol minéral, ont été utilisés dans les analyses du chapitre microbiome pour l'étude des communautés bactériennes et fongiques (Figure 11c). Enfin, nous avons mesuré au sein des plantations le diamètre à hauteur de poitrine (dhp) des peupliers hybrides pour estimer leur productivité ainsi que les quantités de carbone et d'azote contenu dans leurs tissus.

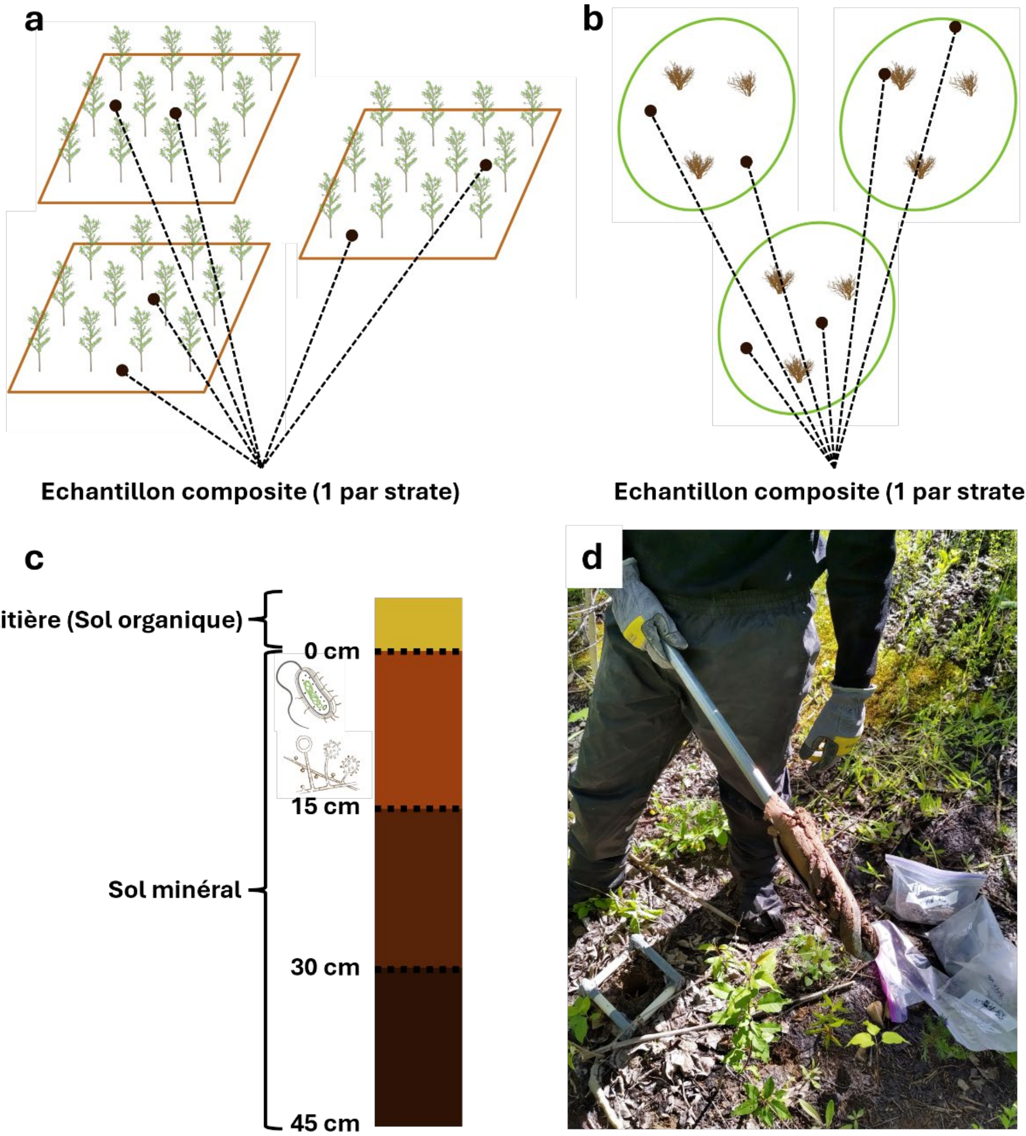

Figure 11
Localisation des points d’échantillonnages du sol au sein des plantations (a) et des zones non reboisées (b). Schéma des différentes strates prélevées (c) et prélèvement in situ à l’aide d’une tarière hollandaise (d).

1. IMPACT OF THE ORIGIN OF SITES PLANTED WITH HYBRID POPLAR ON PLANT COMMUNITY COMPOSITION AND DIVERSITY

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Résumé

L'utilisation d'espèces à croissance rapide dans le cadre d'une sylviculture intensive peut altérer la diversité végétale, mais nous avons que peu de connaissances sur la manière dont elle est affectée par l'utilisation des terres précédant la plantation, ou autrement dit, par l'origine du site. Répondre à cette problématique permettrait de mieux orienter le choix du site afin de limiter les pertes de diversité liées à leur établissement. Cette étude vise donc à déterminer l'impact de l'origine du site sur la diversité et la composition végétale au sein des plantations de peupliers hybrides gérées intensivement. Nous avons étudié les communautés végétales vasculaires et non vasculaires dans des plantations de peupliers hybrides à croissance rapide (PEH) établies sur des terres agricoles abandonnées arborant une végétation herbacée ou arbustive, et sur d'anciennes coupes forestières, et nous les avons comparées à des sites environnants non reboisés. Nos résultats montrent qu'après 15 ans, les plantations de PEH établies sur des terres agricoles abandonnées, qu'elles soient herbacées ou arbustives, présentaient une diversité végétale similaire ou supérieure à leur équivalent non reboisé, même si elles ne contenaient aucune espèce forestière. Lorsqu'elles sont établies sur des terres forestières, les plantations de PEH favorisent l'établissement d'espèces rudérales par rapport aux zones adjacentes non plantées. De plus, la diversité et la richesse des plantes ont tendance à diminuer après l'établissement de la plantation. Par conséquent, si l'on choisit un site pour préserver ou accroître la diversité végétale, il semble préférable de cibler les terres agricoles abandonnées plutôt que les sites forestiers pour installer des plantations de peupliers hybrides.

Mots clés : Silviculture, Friche agricole, Plantation, Diversité végétale, Bryophyte

Abstract

Intensively managed fast-growing tree plantations may affect plant diversity, and we have little knowledge on how it is affected by site origin in order to better orientate site selection for their establishment. The aim of this study was thus to determine the impact of site origin on plant diversity in intensively managed hybrid poplar plantations. We investigated vascular and non-vascular plant communities within fast growing hybrid poplar plantations (PEH) established on abandoned agricultural lands (AAL) with herbaceous or shrubby vegetation, and on previously forested lands, and compared them to adjoining non-afforested surrounding sites. Our results show that PEH plantations established on herbaceous and shrubby AALs had similar or higher plant diversity even though they contained no forest species after 15 years. When established on previously forested lands, PEH plantations favored the establishment of ruderal species compared to their non-reforested equivalents, but plant diversity and richness tended to decrease following plantation establishment. Thus, if site selection is made to preserve or increase plant diversity, abandoned agricultural lands should preferentially be chosen rather than previously forested sites to install intensively managed hybrid poplar plantations.

Keywords: Silviculture, Abandoned Agricultural Land, Plantation, Plant diversity, Bryophyte

1.1 Introduction

Global roundwood production reached 4 billion m³ in 2018 for the first time in history (FAO, 2023). This was accompanied by an increase in the area dedicated to plantations, rising from 2 million km² in 1996 to more than 3 million km² in 2019 (FAO, 2024). Industrial fast-growing plantations such as hybrid poplar can provide higher yields of wood per hectare over shorter periods of time than natural forests, while also providing a certain level of ecosystem services (McEwan et al., 2020; Pawson et al., 2013; Rodriguez et al., 2014). However, new lands available to establish fast-growing plantations are becoming increasingly scarce around the world because of the direct competition with agricultural production, urban expansion and protected natural areas (Lambin & Meyfroidt, 2011). Abandoned agricultural lands (AAL) represent a good opportunity for the establishment of hybrid poplar plantations and are therefore targeted in many plantation programs (Fayet et al., 2022; Subedi et al., 2022).

Plant communities retain a certain legacy of the past land use preceding establishment of plantations (Bellemare et al., 2002; Gachet et al., 2007; Soo et al., 2009). As a result, the impact of tree planting on the composition and diversity of plant communities could differ depending on the site of origin of the plantation; Gachet et al. (2007) showed that the understory vegetation of a plantation on a previously forested site converged more rapidly towards that of a natural forest compared to a stand established on former agricultural land, due to the presence of a large quantity of reproductive materials, such as seeds and propagules. On the other hand, afforestation of a pastures led to the persistence of grasslands species such as *Dactilys glomerata* [L.] within the plantation, while former cultivated sites contained a higher proportion of ruderal species (Soo et al., 2009). The meta-analysis by Bremer & Farley (2010) showed a decrease in plant diversity when plantations were established on natural grasslands, shrublands or primary forests. The impact of plantation establishment on plant communities has therefore been studied, but to our knowledge, no publications have compared the effects of establishing plantations on AALs or on previously forested lands. In addition, AALs exist at different vegetation stages as secondary succession evolves from herbaceous vegetation, to shrubland and finally to a forest vegetation (Chazdon et al., 2020; Ustaoglu & Collier, 2018).

Some studies highlighted a negative impact of plantation establishment on plant diversity compared to the different stages of secondary succession (Prangel et al., 2023; Tullus et al., 2022), but we don’t know the impacts of establishing fast growing plantations on AALs at different stages of vegetation and how they compare to plantations established on previously forested sites. Moreover, secondary succession often increases the richness, diversity and evenness of the plant community, while it decreases the abundance of annual plants in favour of perennial plants (Heydari et al., 2020; Szirmai et al., 2022). Silvicultural operations linked to plantation establishment, such as site preparation, disking or harrowing and the use of herbicides are also likely to disturb numerous microhabitats and seedbanks, limiting plant diversity within the plantation (Löf et al., 2012). Additional questions thus arise on the impact of hybrid poplar plantation establishment compared to non-afforested AALs on plant diversity.

The aim of this study was to determine how site origin impacts the diversity and composition of plant communities when establishing plantations of intensively managed hybrid poplar on AALs at different vegetation stages and previously forested sites. We compared the plantations with adjacent non-afforested areas, considering the state of the vegetation at the time of plantation. Forest soils usually contain a higher proportion of reproductive materials from shade-tolerant forest species (Gachet et al., 2007; Hébert et al., 2016; Jacob et al., 2017). Therefore, our first hypothesis was that establishing hybrid poplar plantations on previously forested lands would harbour greater plant diversity than on AALs due to the presence of forest species reproductive materials. Furthermore, we expected that forest species reproductive materials should be also present in the soils of AALs dominated by a shrubby vegetation, due to the progressive establishment of forest species during secondary succession. Our second hypothesis was thus that AALs with a shrub-dominated vegetation would contain a higher plant diversity than herbaceous AALs after plantation establishment, but lower than that of previously forested sites. Since disturbances linked to farming activities are suitable to many shade intolerant ruderal species, with a high capacity for dispersal and long-lasting persistence in the soil seedbank (Aubin et al., 2014; Gachet et al., 2007; Soo et al., 2009), we also hypothesized that a greater proportion of ruderal and shade-intolerant species would be found in plantations established on herbaceous AALs and that a greater proportion of forest and shade-tolerant species would be found in plantations established on previously forested lands, with intermediary community composition for plantations established on shrubby AALs.

1.2 Materials and methods

1.2.1 Study sites

We selected 16 sites (Table 1), 14 of which were scattered across the Abitibi-Témiscamingue region of Quebec (Figure 12a and b). The two remaining sites were located in Ontario and the region of Northern Quebec, two bordering territories. Each site contained a hybrid poplar plantation established between 2003 and 2009, associated with a neighbouring non-afforested area (Figure 12c). Before plantation establishment, four of the sites were poorly regenerated forest cut blocks, eight were abandoned agricultural land (AAL) with herbaceous vegetation and four were AALs with patches of shrubby vegetation. These three types are referred to in this study as previously forested lands, herbaceous AALs and shrubby AALs, respectively. Discussions with the landowners, observations in the field and previous studies allowed us to obtain information on the state of the sites before planting (Table 1). Mean annual temperatures range from 0.1 °C to 2.8 °C and mean annual precipitations from 785 mm to 950 mm (Government of Canada, 2011). The region has a flat topography and is located on the Quebec-Ontario clay belt formed by the glaciolacustrine deposits of lake Barlow-Ojibway (Vincent & Hardy, 1977). Soils at our study sites are mainly clay and heavy clay, except for the Nédelec (ND) site, which is loamy (Chomel et al., 2014).

1.2.2 Experimental design

The plantations were made up of different hybrid poplar clones, but in order to limit variation due to clonal identity, we restricted sampling to the plots planted with clone 915319 (*Populus maximowiczii x Populus balsamifera*) in each study site. We chose this clone because it was the most frequently planted as it is highly productive in most site types. Within the plantations, we defined the number of sampling areas according to the number of plots planted with clone 915319 which varied from 1 to 5. In each sampling area, we randomly placed 1 m² quadrats with the condition that half of the quadrats were placed at the foot of a tree and the other half in the middle of the tree rows (Figure 12d). The number of quadrats per sampling area depended on the total number of sampling areas in the plantation: 24 quadrats for 1 sampling area (RH), 4 quadrats for 5 sampling areas (TR and SG) and 8 quadrats for 3 sampling areas (all other sites). For the non-afforested areas, we delimited 3 circular sampling areas of 150 m², chosen to be representative of the vegetation of the site and we randomly placed 8 - 1 m² quadrats in each of them (Figure 12e).

1.2.3 Vegetation survey

Field work took place in June and July 2022. In each quadrat, we identified all vascular plant species, and their percent cover within the quadrat was assessed by two observers. For bryophyte species, we collected samples from colonies on soil and tree bark within the quadrats for subsequent identification in the laboratory. Names of the different plant species were determined using the nomenclature of vascular plants of Canada (Canadensys, 2024) for vascular plants and “Flore des bryophytes du Québec-Labrador” (Faubert, 2013) for bryophytes.

1.2.4 Environnemental variables

The annual means of temperature and precipitation were taken from the weather stations closest to each site for the period 1971–2000, which is the period with the most weather stations available from Environment Canada (Government of Canada, 2011). Incident light was measured with a Li-cor line quantum sensor (LI-191R) measuring photosynthetically active radiation (PAR) in µmol.s-1.m-2 for a wave band of 400 nm to 700 nm. Two measurements were taken per quadrat, one with the instrument oriented N-S and the other oriented W-E. Before and after measuring incident light within a block, measurements were taken in an open environment to calculate the percentage of light intercepted by the canopy compared to an open environment. Soil pH was determined in composite samples from the top 20 cm of mineral soil by electrometry methods (Government of Quebec, 2023). We collected two composite samples per site, one for the plantation and one for the non-afforested area. Each composite sample was made by regrouping 6 samples from different random sampling areas.

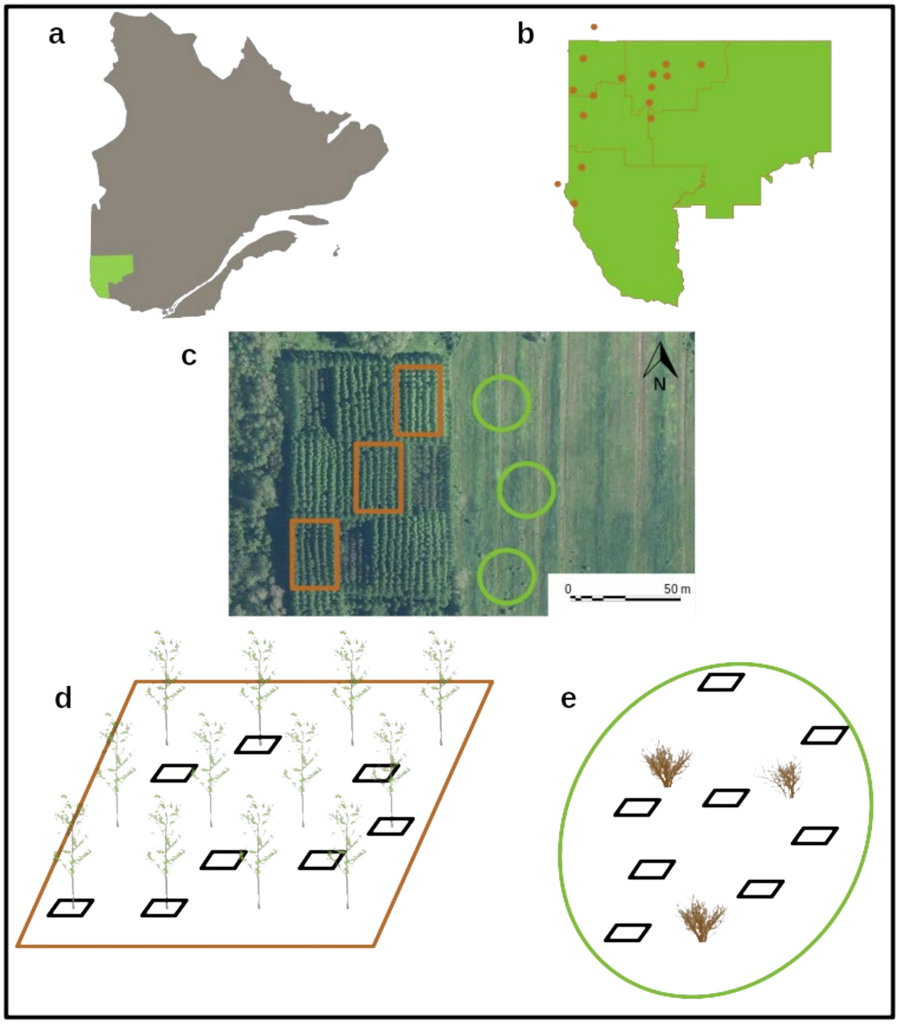

Figure 12
Experimental design. a) Abitibi-Témiscamingue region (green) in the province of Quebec (grey), Canada. b) Location of the sixteen study sites. c) An example of a site (VP) with hybrid poplar plantation sampling areas in orange rectangles and non-afforested sampling areas in green circles. d) and e) show the quadrat layout within respectively a hybrid poplar plantation and a non-afforested area.

Table 1

Detailed information on the study sites, each site is divided into two: the hybrid poplar plantation and the neighbouring non-afforested area. Longitude and latitude are given in the WGS84 coordinate system.

							Hybrid poplar plantation					NF area		
Code	**Municipality**	**Longitude**	**Latitude**	**T (°C)**	**P (mm)**	**Origin of site**	**Year of plantation**	**Soil pH**	**LIC (%)**	**Tree.ha^{-1}**	**Productivity (m^3.ha^{-1}.y^{-1})**	**Soil pH**	**LIC (%)**	**References**
AD	Arntfield	-79.289	48.229	1.7	883	Forest	2005	6.03	47.22	1000	3.11	5.58	94.68	Sigouin, 2008
AM	Amos	-78.076	48.612	1.2	918	S AAL	2003	5.54	75.25	1111	6.80	5.32	51.51	Chomel et al., 2014
DO	Duhamel-Ouest	-79.419	47.317	2.8	819	H AAL	2005	5.82	94.29	833	12.3	5.7	0	Elferjani et al., 2016
DP1	Duparquet	-79.440	48.490	0.7	950	Forest	2005	5.56	59.1	833	3.33	5.37	95.64	Randriamananjara et al., 2023
DP3	Duparquet	-79.120	48.445	0.7	950	Forest	2004	6.04	40.3	1000	0.40	5.43	88.64	Sigouin, 2008
DY	Despinassy	-77.481	48.762	0.5	914	H AAL	2006	5.86	93.88	1000	9.56	6.04	50.97	DesRochers & Tremblay, 2009
LS	La Sarre	-79.290	48.832	0.7	890	S AAL	2006	6.61	83.51	816	6.75	6.41	0	DesRochers & Tremblay, 2009
ND	Nédélec	-79.374	47.763	1.9	916	Forest	2003	5.28	51.31	1111	6.36	5.1	92.25	Chomel et al., 2014
NL	New Liskeard (ON)	-79.664	47.520	2.3	785	H AAL	2007	7.22	93.98	816	16.74	7.34	0	Maurin & DesRochers, 2013
PC	Preissac	-78.273	48.372	1.2	918	H AAL	2004	6.04	85.42	1000	0.53	5.73	50.85	Desrochers & Sigouin, 2014
RH	Rivière-Héva	-78.275	48.197	1.2	914	S AAL	2003	5.26	68.05	1111	12.55	5.13	73	Chomel et al., 2014
SD	St-Dominique-du-Rosaire	-78.076	48.764	0.2	909	S AAL	2006	5.61	93.49	1000	9.18	5.43	89.25	DesRochers & Tremblay, 2009
SG	Sainte-Gertrude	-78.269	48.517	1.2	918	H AAL	2008	5.26	37.23	833	1.72	5.16	0	Larcheveque et al., 2011
TA	Taschereau	-78.684	48.601	0.7	950	H AAL	2007	6.41	91.76	833	13.47	5.74	0	-
TR	Trécesson	-78.222	48.659	1.2	918	H AAL	2009	5.47	39.82	833	1.81	5.5	0	-
VP	Val-Paradis (NQ)	-79.177	49.151	0.1	910	H AAL	2005	5.5	79.44	833	4.57	5.39	0	Elferjani et al., 2016

Notes: ON = Ontario; NQ = Northern Quebec; T =Mean annual temperatures; P = Mean annual precipitations; S = Shrubby; H = Herbaceous, AAL = Abandoned Agricultural Land; LIC = Light Intercepted by Canopy; NF = Non-afforested.

1.2.5 Analysis

Diversity. We used two presence/absence matrices with quadrats as rows instead of sites to calculate three diversity indices for each planted and non-afforested area at each site (α diversity) with the R function “diversity” (vegan, Oksanen et al., 2022). The indices used were species richness, Shannon index and Pielou’s evenness (Pielou, 1969; Shannon, 1948). To test for differences in plant diversity between sites with different origins (previously forested lands vs. shrubby AALs vs. herbaceous AALs) and afforested vs. non-afforested areas at the site level, we completed an analysis of variance (ANOVA) for a fitted mixed model with biodiversity indices as explanatory variables. The site was included as a random effect, while afforestation and site origin were fixed effects. We built the models with the function lmer from the R package lme4 (Bates et al., 2015). Before running the models, we evaluated diagnostic plots to check for the normality of residuals and of the random effects using qqnorm, qqline and ranef functions from “stats” and “lme4” R packages (Bates et al., 2015; R Core Team, 2023). To perform pairwise comparisons, we used the function emmeans from the eponymous R package (Lenth et al., 2024).

To assess the diversity at a regional scale of the plant communities in plantations and non-afforested areas from different origins we used Hill numbers, which represent an intuitive and statistically rigorous alternative to other diversity indices (Hill, 1973; Hsieh et al., 2016) and are calculated using a diversity order q, which determines the sensitivity of the measure to the relative abundance of species. For $q = 0$, the relative abundance of species is not considered and Hill numbers represent species richness. For $q = 1$, Hill numbers are equivalent to the exponential of the Shannon index referred to here as Shannon’s diversity, implying that the emphasis is on frequent species. And finally, for $q = 2$, dominant species are highlighted and the Hill numbers represent the inverse of the Simpson concentration known as Simpson’s diversity (Chao et al., 2014). Rarefaction and extrapolation curves of the Hill’s numbers with a 95% confidence interval allowed us to compare vascular and non-vascular plant biodiversity between our plantations and non-afforested areas according to their origin. Each plotted curve represents an assemblage of communities from different sites, therefore, showing us biodiversity at a regional scale (γ diversity). We used the function “iNEXT” of the eponymous R package (Hsieh et al., 2016) and two presence/absence matrices with sites in rows and species in columns. One matrix was designed for vascular plant communities and the other one for bryophytes communities. Finally, to understand the variations and structure of plant diversity within our study groups, we calculated Sørensen’s beta diversity index and the nestedness and turnover components for each combination of factors studied (afforestation: origin of site) with the R package “betapart” (Baselga & Orme, 2012).

Plant community composition. To carry out analyses of plant community composition, we constructed two community matrices with sites as rows and species as columns. In the vascular plant matrix, we converted percent cover into classes based on a 9-point Braum-Blanquet scale (Braun-Blanquet et al., 1932; Wood et al., 2013). The other matrix was for bryophytes and based on the sum of the species presence in each quadrat for plantations and non-afforested areas at each site. To visualize the composition of plant communities, we used principal coordinate analysis (PCoA; Legendre & Legendre, 2012) using the functions in the R packages "vegan" and “ape” (Oksanen et al., 2022; Paradis & Schliep, 2019). Firstly, we standardized the data in our abundance table using the Decostand function with the Hellinger method (Legendre & Gallagher, 2001), we then created a distance matrix using the vegdist function with the Bray-Curtis distance (Bray & Curtis, 1957). The PCoA on the distance matrix was done with the “pcoa” function and the Cailliez correction to rectify negative eigenvalues (Cailliez, 1983). Environmental variables were added to our ordination with the envfit function, such as incident light intercepted by the canopy, soil pH, mean annual precipitation and temperature. We also added species to the ordination by calculating their weighted average scores with the function wascores from “vegan”. To select the names of species shown in the ordination, we used the function multipatt from the “indicspecies” R package (Legendre & De Cáceres, 2013). This function gives indicator species for different groups represented by each combination of our factors (afforested vs. non-afforested and site origin) with a p-value <0.05. We tested if our studied factors affected the composition of plant communities by performing a multivariate analysis of variance with permutations (PermANOVA;

McArdle & Anderson, 2001) with the adonis2 function (10,000 permutations) on the distance matrix obtained during ordination with the variable site set as strata. We used the same procedure to assess the impact of environmental variables on plant community composition.

Growth rate of hybrid poplar. We measured diameter at breast height (DBH; 1.3 m height) of planted hybrid poplars to estimate their growth rate. We used the allometric equation [1] from Truax et al. (2014) to estimate stem volume of each tree where Y is the stem volume in dm^3 and x the DBH in cm.

$$Y = 0.0939x^{2.61} \qquad \text{(Eq. 1)}$$

We then multiplied Y by the number of trees planted per hectare then by the number of years since plantation establishment and by a factor of 0.001 to obtain the growth rate expressed in $m^3ha^{-1}year^{-1}$. We tested the impact of site origin on growth rate by completing an ANOVA for a fitted linear model with the functions “anova” and “lm” from R. Linearity and homoscedasticity were checked with diagnostic plots using R function “plot”.

All the analyses presented in this study were carried out using R 4.3.1 (R Core Team, 2023) and visual representations using the R packages ggplot2 and cowplot (Wickham, 2016; Wilke, 2024)

1.3 Results

1.3.1 Local diversity

On a local scale (α diversity), species richness of vascular plant communities depended on the origin of the afforested site and interacted with afforestation (Table 2), showing that richness was lower in plantations established on previously forested lands compared to non-afforested areas, whereas richness was similar between non afforested AALs and afforested AALs (Figure 13). The Shannon diversity index was similar among our plantations and non-afforested areas, except for the non-afforested areas originating from previously forested lands that showed the highest diversity and non-afforested shrubby AALs that showed the lowest diversity (Figure 13). The evenness index was similar within and outside plantations and did not vary with site origin.

Table 2
ANOVA summary showing the effect of afforestation and site origin on Richness, Shannon’s index and Pielou’s evenness index for vascular plants and bryophytes. * Indicate significant effect at p<0.05.

	Richness				Shannon’s index				Evenness			
	Sum sq	**Mean sq**	**F**	**Pr(<F)**	**Sum sq**	**Mean sq**	**F**	**Pr(<F)**	**Sum sq**	**Mean sq**	**F**	**Pr(<F)**
Vascular plants												
Afforestation	30.01	30.01	1.21	0.2912	0.024	0.024	0.75	0.40089	0.00039	0.00039	0.76	0.39985
Site origin	180.41	180.41	7.28	0.0076*	0.26	0.13	4.16	0.04011*	0.0030	0.0015	2.91	0.09003
Afforestation: Site origin	196.69	98.34	3.97	0.042*	0.19	0.095	2.95	0.08802	0.00069	0.00034	0.67	0.52851
Bryophytes												
Afforestation	1.513	1.513	0.091	0.768	0.088	0.087	1.24	0.2854	0.0016	0.016	8.60	0.013*
Site origin	176.06	88.030	5.28	0.02095*	0.29	0.15	2.06	0.1677	0.0014	0.00071	0.38	0.69393
Afforestation: Site origin	49.03	24.52	1.47	0.26557	0.56	0.28	3.96	0.0454*	0.0085	0.0042	2.25	0.14815

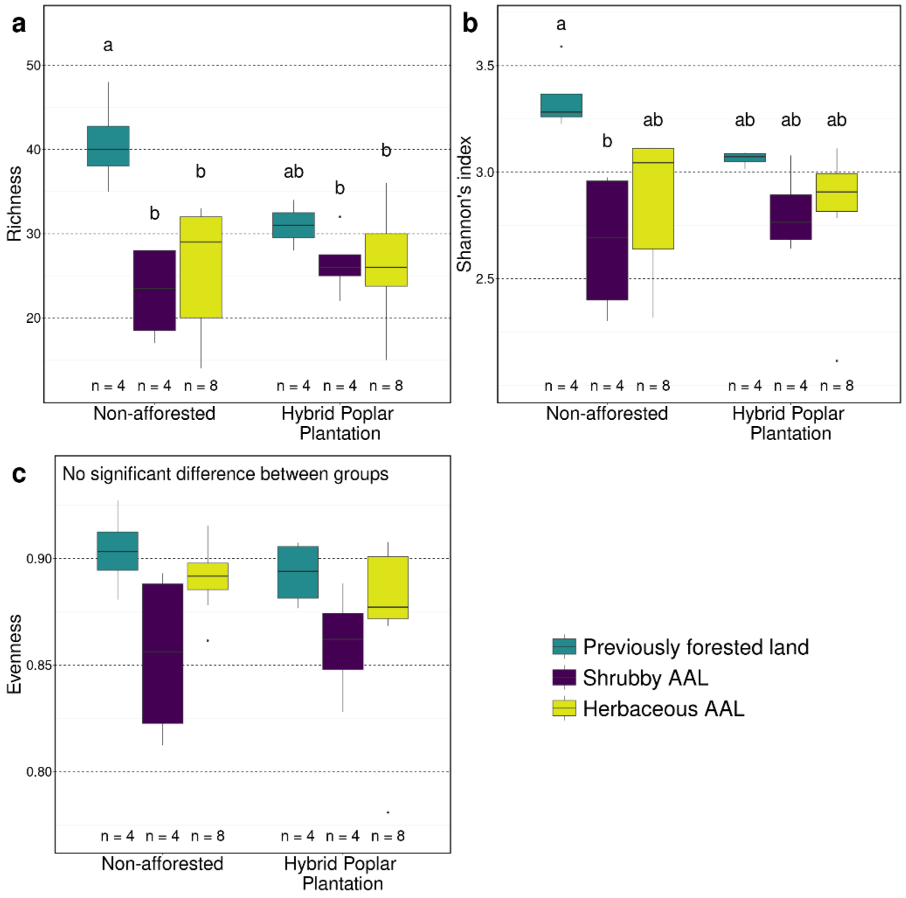

Figure 13
Box-plot statistics of richness (a), Shannon's index (b) and evenness (c) for vascular plants at the local scale (α) for hybrid poplar plantations and non-afforested areas by site origin. Solid lines indicate the median, hinges indicate 1st and 3rd quartiles and whiskers indicate inter quartile ranges multiplied by 1.5. Outlying values are shown as black dots. From left to right: Richness, Shannon's index and Pielou's evenness index. Different lower-case letters above box plots indicate significant differences at $p<0.05$. AAL = Abandoned Agricultural Land.

Richness of the bryophyte communities was highest in non-afforested areas from previously forested lands while non afforested herbaceous AALs had the lowest richness (Table 2, Figure 14). Shannon diversity tended to be higher in plantations on herbaceous AALs compared with adjacent non-afforested areas, whereas there was a slight decrease in diversity in plantations established on shrubby AALs and previously forested lands (Figure 14), giving a significant interaction between site origin and afforestation (Table 2). The evenness index of bryophyte communities was similar between the different site origins but slightly decreased with afforestation (Table 2, Figure 14).

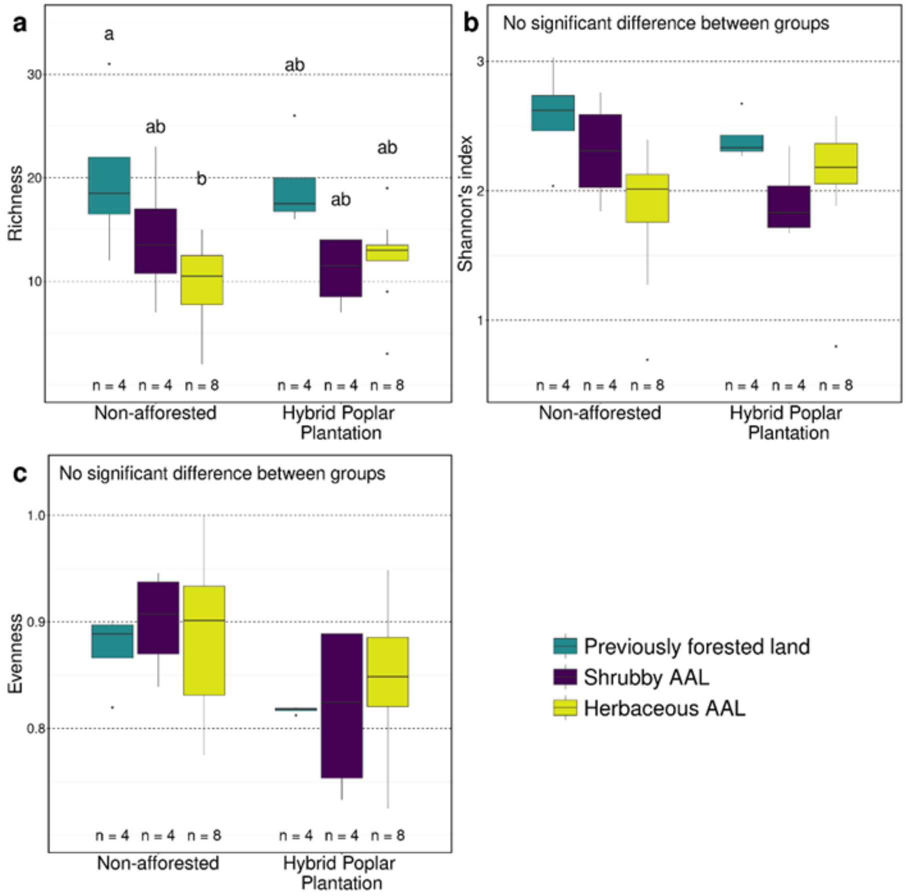

Figure 14
Box-plot statistic of richness, Shannon's index and evenness for bryophytes at the local scale (α) for hybrid poplar plantations and non-afforested areas by site origin. Solid lines indicate the median, hinges indicate 1st and 3rd quartiles and whiskers indicate inter quartile ranges multiplied by 1.5. Outlying values are shown as black dots. From left to right: Richness, Shannon's index and Pielou's evenness index. Different lower-case letters above the box plot indicate significant differences at $p<0.05$. AAL = Abandoned Agricultural Land.

In addition, growth rates of clone 915319 within our study sites varied widely but were similar for all site origins (Table 1).

1.3.2 Regional diversity

The vascular plant community of non-afforested forested lands showed the greatest observed plant diversity for all orders of diversity compared to the other site types and origins. Afforestation of previously forested lands led to a decrease in biodiversity for q=0, 1 and 2 compared with non-afforested areas (Figure 15). Afforested shrubby AALs and their neighbouring non afforested areas harboured similar plant diversity, but in comparison to all other site types, showed the lowest. Afforested herbaceous AALs were richer (q=0) than their non-afforested counterparts but were less diverse for q=2. For q=1, afforested and non-afforested herbaceous AALs had similar plant diversity (Figure 15).

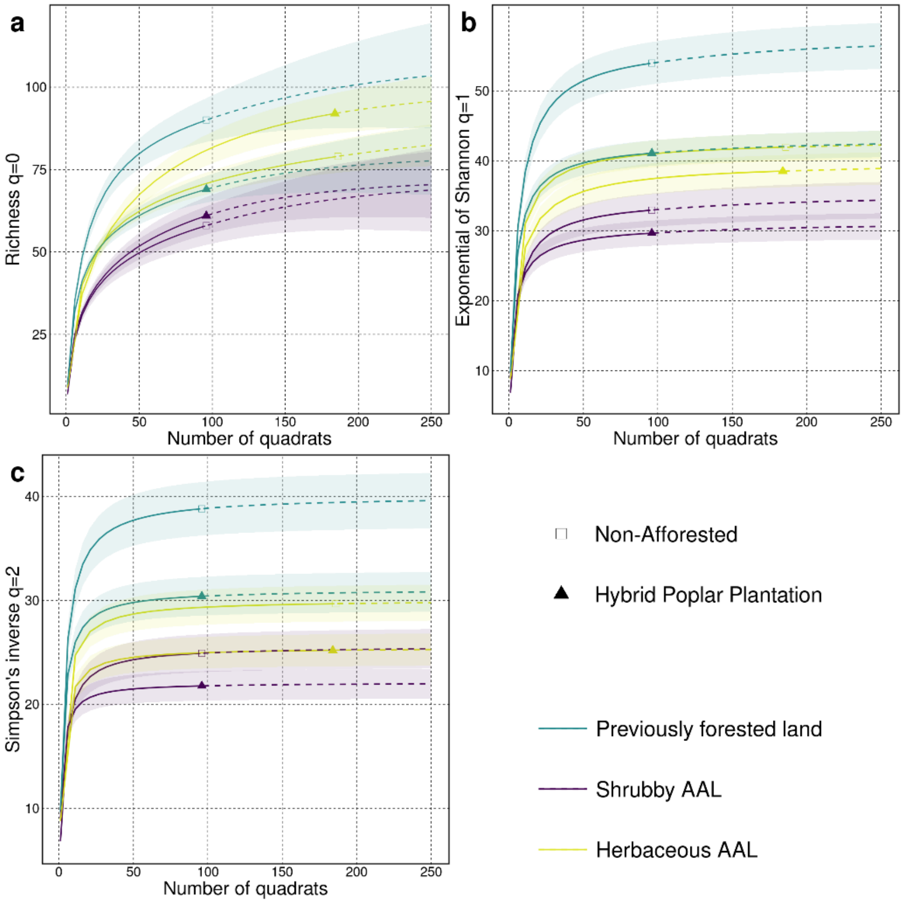

Figure 15
Regional scale species diversity (γ) for vascular plants based on sample size using Hill numbers of species richness q=0 (a), exponential of Shannon q=1 (b) and Simpson's inverse q=2 (c). Solid lines show rarefaction/interpolation and dotted lines show extrapolation with 95% interval confidence (shaded area). Symbols indicate the observed Hill numbers in hybrid poplar plantations or non-afforested areas and colours indicate different site origins. AAL = Abandoned Agricultural Land.

Observed bryophytes richness (q=0) for assembled communities was not affected by afforestation regardless of the site origin. Nevertheless, we observed a higher richness in sites originating from forested lands compared to sites originating from AALs without distinction between herbaceous and shrubby AALs (Figure 16). Afforestation of previously forested lands and shrubby AALs led to a decrease in Shannon and Simpson diversity indices (respectively q=1 and q=2) compared to non-afforested areas of same origins. On the contrary, for both diversity orders, diversity increased in afforested herbaceous AALs compared to their non-afforested counterparts (Figure 16).

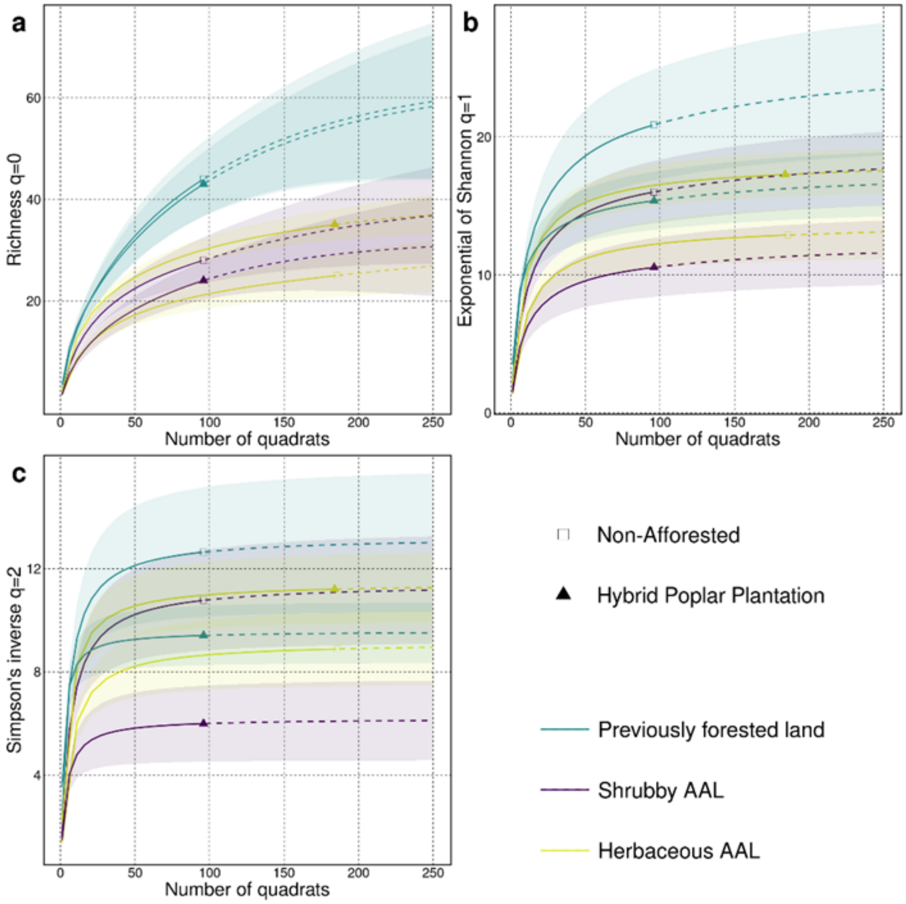

Figure 16
Regional scale species diversity (γ) for bryophytes based on sample size using Hill numbers of species richness q=0 (a), exponential of Shannon q=1 (b) and Simpson's inverse q=2 (c). Solid lines show rarefaction/interpolation and dotted lines show extrapolation with 95% interval confidence (shaded area). Symbols indicate the observed Hill numbers hybrid poplar plantation or non-afforested areas and colours indicate different site origins. AAL = Abandoned Agricultural Land.

1.3.3 Beta diversity

Beta diversity as measured by Sørensen's dissimilarity indicated that the differences observed between sites belonging to the same group were mainly due to a turnover effect (Table 3), which indicates that communities differed from one another by the presence or absence of certain species. It should be noted that the nestedness component was more important for bryophyte communities than for vascular plants, indicating that from one site to another the poorest community was a subset of the richest communities (Table 3).

Table 3 Values of overall β diversity measured as Sorensen dissimilarity (β Sor) and its nestedness (Nes) and turnover (Sim) components for each study group. AAL = Abandoned Agricultural Land.

Community	Treatment	Site origin	Nes	Sim	β Sor
Vascular plants	Hybrid poplar plantation	Previously forested land	0.024	0.61	0.64
		Shrubby AAL	0.057	0.53	0.59
		Herbaceous AAL	0.056	0.71	0.76
	Non-afforested	Previously forested land	0.046	0.56	0.60
		Shrubby AAL	0.070	0.60	0.67
		Herbaceous AAL	0.073	0.67	0.74
Bryophytes	Hybrid poplar plantation	Previously forested land	0.071	0.57	0.64
		Shrubby AAL	0.10	0.56	0.66
		Herbaceous AAL	0.10	0.65	0.75
	Non-afforested	Previously forested land	0.16	0.46	0.63
		Shrubby AAL	0.24	0.34	0.58
		Herbaceous AAL	0.19	0.53	0.72

1.3.4 Plant community composition

Plantations from previously forested lands and shrubby AALs harboured different vascular plant communities compared to their non-afforested counterparts (Figure 17a). In contrast, plantations and non-afforested areas from herbaceous AALs did not shift in vascular plant composition (Figure 17a). In addition, hybrid poplar plantations on sites of all origins were clustered in the ordination, whereas the non-afforested areas were not, meaning that the composition of vascular plant communities within plantations tended to be similar regardless of the origin of the site. When considering their relationships with environmental variables, sites originating from herbaceous AALs were distributed along a gradient formed by precipitation, temperature and soil pH, whereas non-afforested sites issued from shrubby AALs and forested lands were associated with a high amount of light intercepted by the canopy whereas afforested areas showed a lower percentage of light interception. Non-afforested forested lands had the highest number of indicator species associated with this group alone(Table 5, Figure 17b), including: *Dryopteris* spp., *Betula papyrifera*, *Ribes triste*, *Galium trifidum*, *Prunus pensylvanica*, *Galeopsis tretahit*, *Maianthenum canadense*, *Symphyotrichum puniceum*, *Impatiens capensis* and *Solidago rugosa*. Indicator species observed in plantations originating from previously forested lands were *Apocynum androsaemifolium* and *Juncus tenuis*. *Picea mariana*, *Prunus virginica* and *Alnus incana subsp. rugosa* were indicator species of both plantations and non-afforested areas originating from forested lands. *P. virginica* and *A. incana subsp. rugosa* were also indicator species for respectively plantation on herbaceous AALs and non-afforested areas from shrubby AALs. The following indicator species were shared between two or more studied groups: *Vicia craca* and *Ranunculus acris* were characteristic of sites originating from AALs. *Pyrola elliptica* was an indicator species of plantations from all origins and of non-afforested forested lands. *Trifolium pratense* was a distinct species found in both plantations and non-afforested areas originating from herbaceous AALs, which was similar for *Leucanthenum vulgare*, but this species was also characteristic of afforested shrubby AALs (Table 5).

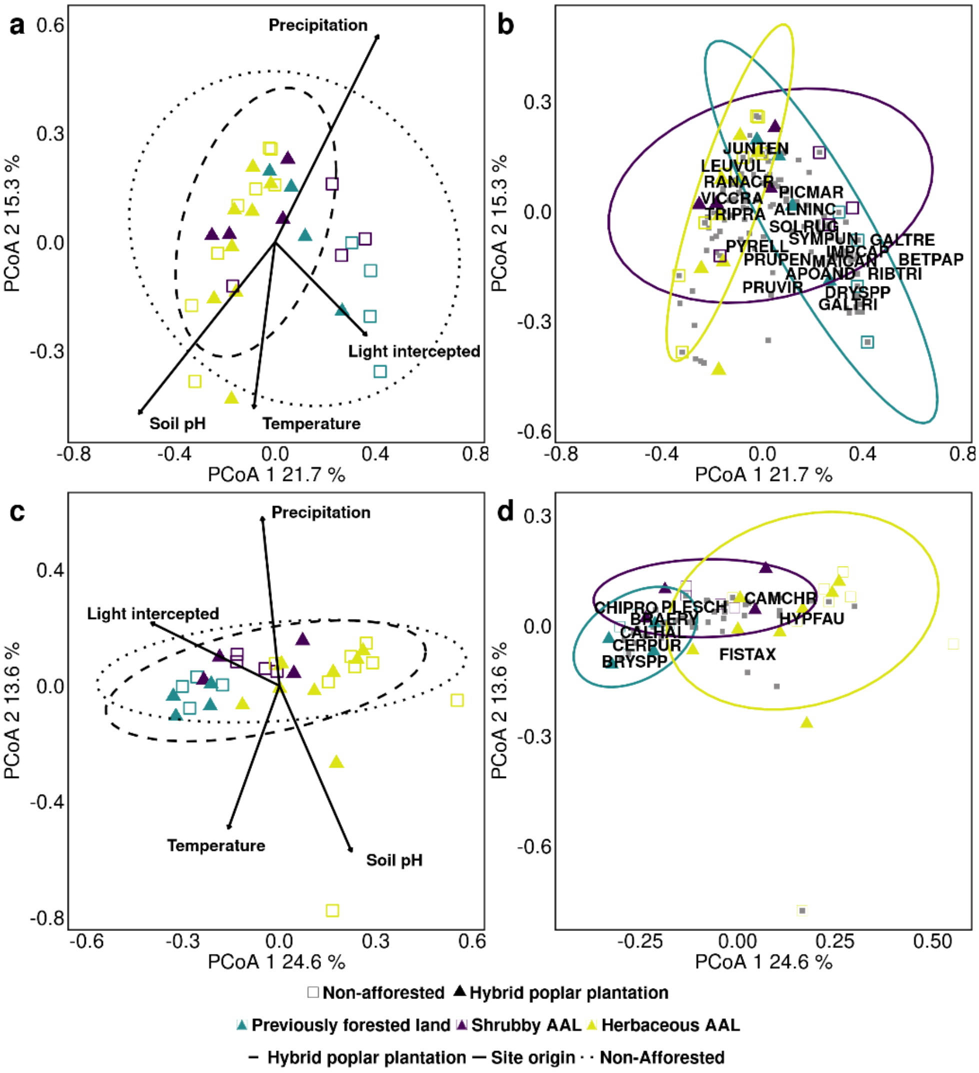

Figure 17
Principal coordinate analysis (PCoA) based on vascular plant (a and b) and bryophyte (c and d) communities using the Bray-Curtis dissimilarity index. Plant communities are represented as coloured shapes. Colours indicate different site origins and shapes indicate hybrid poplar plantations or non-afforested areas. Left plots indicate four environmental variables fitted onto the ordination. The right plots indicate species scores as grey squares. Code names of significant species (p<0.05) for each group selected with the function multipatt are shown in black font. Information on the species codes is available in annexe A-Table S1. In left plots, ellipses show afforested (long dash) and non-afforested (short dash) areas. In right plots, ellipses drawn with

solid lines show site origin with colour. All ellipses are drawn with a 95% confidence interval. AAL = Abandoned Agricultural Land.

Table 4
Summary of the permutational analysis of variance (permANOVA) with Bray-Curtis dissimilarity to test the effects of afforestation and site origin and environmental variables on species composition (10, 000 permutations). *Indicates a significant effect (p<0.05).

	Vascular plants				Bryophytes			
Studied Variables	Sum sq	R^2	F	Pr	Sum sq	R^2	F	Pr
Afforestation	0.42	0.067	2.62	<0.001*	0.21	0.033	1.22	0.252
Site origin	1.14	0.18	3.59	<0.001*	1.35	0.22	3.98	<0.001*
Afforestation: Site origin	0.56	0.09	1.77	0.013*	0.25	0.04	0.74	0.877
Residuals	4.13	0.66			4.41	0.71		
Environmental variables								
Mean annual temperature	0.46	0.073	2.94	<0.001*	0.42	0.07	2.42	0.046*
Mean annual precipitation	0.69	0.11	4.38	<0.001*	0.43	0.07	2.51	0.044*
Intercepted light	0.56	0.09	3.56	<0.001*	0.40	0.06	2.30	0.060
Soil pH	0.33	0.05	2.08	0.071	0.25	0.04	1.43	0.37
Residuals	4.23	0.68			4.71	0.76		

Bryophyte community composition did not shift with afforestation with hybrid poplars. However, composition differed with site origin (Table 4, Figure 17c). Position of the different sites along the PCoA axis 1 indicated that the greatest difference in composition was between previously forested lands and herbaceous AALs, while shrubby AALs communities were intermediate between the two (Figure 17d). Two indicator species were exclusively associated with plantations from previously forested lands (Table 5, Figure 17d): *Bryum* spp. and *Ceratodon purpureus*. *Fissidens taxifolius* was an exclusive indicator species found in afforested herbaceous AALs. Other indicator species were shared between multiple groups: *Hypnum faurei* and *Campylladelphus chrysophyllus* were indicator species of both afforested and non-afforested herbaceous AALs. *C. chrysophyllus* is also an indicator species for plantations on shrubby AALs. *Callicladium haldanianum*, *Pleurozium schreberi* and *Chiloscyphus profundus* were indicator species for both afforested and non-afforested forested lands. In addition, *P. schreberi* and *C. profundus* were also characteristic respectively of afforested and non-afforested shrubby AALs (Table 5).

Table 5

Summary showing vascular plant and bryophyte indicators species ($p<0.05$) selected with the multipatt function for each combination of studied factors (afforestation vs. origin of site). The origin of site is shown with different colours: Blue for previously forested lands, purple for shrubby AALs and yellow for herbaceous AALs

Vascular plants

Species name	Afforested			Non-afforested		
Apocynum androsaemifolium L.	🟦					
Juncus tenuis Wild.	🟦					
Picea mariana (Mill.) Britton, Sterns & Poggenburg	🟦			🟦		
Alnus incana subsp. rugosa (Du Roi) R.T. Clausen	🟦			🟦	🟪	
Prunus virginiana L.	🟦		🟨	🟦		
Trifolium pratense L.	🟦		🟨			🟨
Pyrola elliptica Nutt.	🟦	🟪	🟨	🟦		
Vicia craca L.	🟦	🟪	🟨		🟪	🟨
Ranunculus acris L.		🟪	🟨		🟪	🟨
Leucanthemum vulgare Lam.		🟪	🟨			🟨
Dryopteris spp Adans.				🟦		
Ribes triste Pall.				🟦		
Betula papyrifera Marshall				🟦		
Galium trifidum L.				🟦		
Prunus pensylvanica L.f				🟦		
Galeopsis tretahit L.				🟦		
Maianthemun canadensis Desf.				🟦		
Symphyotrichum puniceum (L.) Á. Löve & D. Löve				🟦		
Impatiens capensis Meerb.				🟦		
Solidago rugosa Mill.				🟦		
Bryophytes						
Bryum spp Hedw.	🟦					
Ceratodon purpureus (Hedw.) Brid.	🟦					
Brachythecium erythrorrhizon Shimp.	🟦				🟪	
Chiloscyphus profundus (Nees) J.J. Engel & R.M. Schust.	🟦			🟦	🟪	
Callicladium haldanianum (Grev.) H.A. Crum	🟦			🟦		
Pleurozium schreberi (Wild. ex Bird.) Mitt	🟦	🟪		🟦		
Campylladelphus chrysophyllus (Brid.) Kanda		🟪	🟨			🟨
Hypnum fauriei Cardot			🟨			🟨
Fissidens taxifolius Hedw.			🟨			

1.4 Discussion

1.4.1 Local plant diversity

We showed that establishing poplar plantations on herbaceous AALs, at least after 15 years, did not reduce richness, Shannon index and Pielou's evenness for vascular plant and bryophyte communities compared to non-afforested areas (Figures 13 and 14). Past studies have shown that AALs are likely to harbour a high biodiversity as forest species progressively recolonize the environment (Chazdon et al., 2020; Ustaoglu & Collier, 2018), and in the same sense other studies have shown that AALs afforestation could be detrimental to plant diversity due to the perturbations linked to plantations establishment (Löf et al., 2012). However, our study did not confirm these results, rather supporting other studies that found that abandoned farmlands are sensitive to the establishment of invasive species and to the rapid colonization by shrub species, which homogenize the environment and limit plant biodiversity (Flinn & Vellend, 2005; Rey Benayas & Bullock, 2015). Furthermore, the majority of previous studies on AALs were done in Europe, where agriculture has been practiced for thousands of years, and has favoured a diversity of species closely linked to open habitats (Hampicke, 2006; Queiroz et al., 2014). In contrast, farmlands in our study region have only been cultivated since the beginning of the twentieth century, in the oldest cases. Open habitat species are less numerous and often come from Europe, thus limiting the plant diversity of agricultural sites and, consequently, of AALs. Consequently, the similar diversity observed between plantations and non-afforested areas in our study is likely due to the low plant diversity of non-afforested agricultural environments.

Plantations of all origins contained similar levels of plant biodiversity (Figures 13 and 14). These results contradict our second hypothesis, which anticipated greater diversity in plantations established on previously forested sites and shrubby AALs compared to those established on herbaceous AALs because of the presence of a seed bank, propagules and vegetative materials of forest species in the soil. This bank of reproductive materials did not lead to greater diversity in plantations established on previously forested lands or shrubby AALs. Mechanical site preparation is required for the establishment of hybrid poplar plantations, which disturbs the soil, affects its chemical and physical properties, and alters the biodiversity found in the plantation (Cao et al., 2022; Poirier et al., 2016; Šebesta et al., 2021). In addition, it was also shown that ploughing reduces seed concentration in shallow layers (Luzuriaga et al., 2005). Therefore, we believe that soil disturbances associated with afforestation probably limited the establishment of forest species from the seed bank of previously forested sites and shrubby AALs, leading to similar plant diversity compared to plantations on herbaceous AALs.

1.4.2 Regional plant diversity

While local plant diversity was little affected by afforestation or the origin of sites, diversity on a regional scale showed greater variability (Figures 15 and 16). Our results highlighted that plantations on herbaceous AALs at regional scale housed a higher vascular plant richness and bryophyte diversity than their non-afforested counterparts (Figures 15 and 16). In addition, beta diversity analysis showed that the variation within the assembled vascular plant communities and to a lesser extent bryophytes communities was mainly due to a turnover effect rather than a nestedness effect (Table 3). This indicates that the less diverse communities had a different species composition rather than being a subset of the more diverse communities. Our study sites covered a large geographical area, and the most southern part of the region had a milder climate, which translated into a significant impact of climate (precipitation and mean annual temperature) in our PERMAnova on plant community composition (Table 4). A possible explanation for the high plant diversity at regional scale of planted herbaceous AALs could be heterogeneity of the landscape. Afforested herbaceous AALs in our study were located in agricultural landscapes with different habitats such as other AALs at different stages of succession, agricultural land still in use, and forest patches (Grondin et al., 2014). The presence and proximity of those habitats to our plantations differed from one site to another, which may have impacted plant diversity at the regional scale. Vanbeveren & Ceulemans, (2019) have shown that afforestation with short rotation coppices could increase biodiversity at the landscape scale, but their study focused on homogeneous European agricultural landscapes.

1.4.3 Community composition

Our findings showed that the composition of vascular plant communities within hybrid poplar plantations tended to be similar despite different site origins (Figure 17 and Table 4). All plantations contained ruderal and shade-intolerant vascular plants such as *V. cracca*, *T. pratense* and *R. acris* (Table 5). These results contradict our hypothesis, where we predicted that the plantation environment would be conducive to colonization by forest species. Afforestation of previously forested lands or AALs with hybrid poplars resulted in a plant diversity similar to that of adjacent non-afforested areas but did not yet promote the establishment of forest vascular plant species. Due to their high competitiveness, rapid growth and quick vegetative propagation, ruderal species are commonly found in the early stages of plantation establishment (Aubin et al., 2014). Mechanical weed control is normally used in Quebec during the first 3 to 5 years of plantation establishment, due to the restriction of herbicide use in forest plantations (Fortier et al., 2011). This practice promotes the persistence of ruderal species, which in turn limit colonization by forest species (Fløistad et al., 2018). Several forest species found in previously forested lands or, to a lesser extent, in shrubby AALs communities were absent from plantations such as *A. incana subsp. rugosa*, *R. triste* or *M. canadense* (Table 5). Our PCoA showed that plantations in previously forested lands and shrubby AALs were distinct from their non-afforested counterparts by the light intercepted by the canopy (Figure 17a). Most of non-afforested previously forested lands and shrubby AALs were colonized by shrub species, providing a dense, shaded plant cover beneath the canopy. This explains the low light levels in these environments, which favours the presence of shade-tolerant forest species. Consequently, we can suggest that the low presence of forest species in hybrid poplar plantations may be due to competition from ruderal species that were stimulated by mechanical weed control. Hybrid poplar plantations were less able to provide a darker environment for shade-tolerant species than non-afforested forested lands and shrubby AALs.

Surprisingly, site origin had a stronger impact than afforestation for bryophyte communities (Table 4). Our PCoA indicated that bryophyte communities in plantations were similar to their non-afforested counterparts (Figure 17c). For example, in the plantations established on previously forested lands, we found species commonly associated with forest environments such as *P. schreberi*, *C. haldanianum* or *C. profundus* that were also present in non-afforested previously forested lands (Table 5). Bryophytes reproduce sexually by producing spores and asexually by vegetative propagules. These reproductive structures enable bryophytes to disperse over long distances (Patiño & Vanderpoorten, 2018). Hylander, (2009) showed that the colonization rate of bryophytes after clear cuts was not linked to the presence of nearby propagules sources because of the low contribution of those sources to the global background spore level originating from more distant sources. Thus, we do not expect that the similarities found between plantations and non-afforested areas were due to the dispersal of spores and propagules from neighbouring non-afforested areas to plantations. Furthermore, Caners et al. (2009) demonstrated that the diaspore bank was a viable recruitment source for bryophyte communities after a disturbance such as forest harvest. The presence of spores and propagules ready to germinate in the diaspore bank could thus explain the absence of an afforestation effect on bryophyte communities in our study. That said, our results regarding bryophytes communities are not consistent within the scientific literature. For example, in the study by Randriamananjara et al. (2023), the composition of bryophyte communities was less sensitive to site origin than the community composition of vascular plants. This suggests that more research needs to be done to better understand the ecology of bryophytes, which remains understudied compared to that of vascular plants.

Our study also presents some notable results in the light of our current knowledge of bryophyte habitats and distribution. For example, *H. faurei* is a species that is usually mainly found in forested environments (Faubert, 2013), yet we identified this species in herbaceous AALs and their afforested equivalents (Figure 17d). Another unforeseen discovery was the presence of *F. taxifolius*, a species considered to be rare in Quebec, which we found in various plantations established on herbaceous AALs, well beyond the known northern distribution limit of this species (Faubert, 2013, Table 5). The lack of knowledge or understanding of these species' habitats could explain the unexpected presence of both species. Indeed, AALs and hybrid poplar plantations are environments that are unfortunately little investigated by bryologists and we hope that more studies about plant communities in fast growing plantations or AALs will include a bryology survey in the future.

1.4.4 Perspectives for further diversity investigations

The inclusion of bryophytes in our study adds another aspect of biodiversity and gives us a better overview of the links between plant community diversity and the reforestation of AALs with hybrid poplars. That said, other taxa could be investigated because of their different patterns of colonization and affinity with various forest habitat. In Europe, several studies have looked at the diverse bird communities that coexist within complex agricultural landscapes composed of woodland patches, farmlands and AALs (Rey Benayas & Bullock, 2015). Shrublands similar to some of the AALs in our study provide favorable habitats for species with a conservative concern while plantations are suitable for generalist forest species (Rey-Benayas et al., 2010; Sánchez-Oliver et al., 2014). There are fewer North American studies on this subject, and it would be wise to look at avian diversity in hybrid poplar plantations and AALs in North America in the future. Microbial communities could also be the subject of future studies, because it has been shown that hybrid poplar plantation establishment on cultivated lands decreased the species abundance of bacterial communities while the fungal community gained in species abundance and diversity (Yannikos et al., 2014; Zheng et al., 2017). Given the importance of these organisms in the nutrient cycle, particularly the carbon cycle, and the desire to use hybrid poplar plantations as tools for sequestering atmospheric CO_2 (Ameray et al., 2021; Cavicchioli et al., 2019), it would also make sense to explore the effects of AALs afforestation on the diversity of these taxa.

1.5 Conclusion

Fifteen years after establishment of hybrid poplar plantations, previously forested lands had lower richness and Shannon diversity of vascular plant communities in comparison to their non-afforested counterparts, and contained more ruderal species in the understory. Even though afforestation of AALs also favoured ruderal species, diversity indices were similar between plantations and non afforested areas for both vascular plants and bryophytes. Rather, afforestation of herbaceous AALs tended to increase plant diversity compared with non-afforested herbaceous AALs at a regional scale. Therefore, the use of intensively managed hybrid poplar plantations to take advantage of their high yield per hectare over a short period of time, should preferentially target herbaceous rather than previously forested lands or shrubby AALs, in order to limit the impacts on vascular plant and bryophyte diversity and community composition.

2. DOES AFFORESTATION BY HYBRID POPLAR AND SITE ORIGIN AFFECT THE DIVERSITY AND COMPOSITION OF THE SOIL MICROBIOME?

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Résumé

Le haut rendement des espèces à croissance rapide comme le peuplier hybride est largement exploité pour fournir d’importantes quantités de biomasse et est susceptible de séquestrer du carbone, contribuant ainsi à atténuer les effets du changement climatique. Les microorganismes du sol jouent un rôle clé dans le bon fonctionnement des écosystèmes, notamment dans la décomposition de la matière organique, la croissance des plantes et le cycle du carbone. Comprendre comment la diversité et la composition du microbiome sont impactées par l'établissement d'une plantation de peupliers hybrides représente donc un enjeu majeur. Outre les propriétés physico-chimiques du sol et le type de couvert végétal, les caractéristiques des communautés microbiennes sont à même de dépendre de l'origine du site précédant la plantation. Afin d’aider les gestionnaires concernant le choix de sites propices à l'établissement de plantations, nous avons cherché à évaluer l'impact de l’afforestation par du peuplier hybride sur le microbiome du sol en comparant entres elles des plantations établies sur trois différents types de sites ainsi qu’avec leurs homologues non plantés : friches agricoles avec végétation herbacée, friches agricoles avec végétation arbustive et sites forestiers. Les communautés fongiques sont plus sensibles à l’afforestation que les communautés bactériennes, et l’établissement de plantations dans un contexte forestier a entraîné une diminution plus importante de la diversité fongique que le reboisement de friches agricoles. De plus, si un changement dans l'abondance de certains phylum bactériens est causé par le reboisement et l'origine du site, ces changements sont aussi possiblement liés aux propriétés édaphiques comme le pH ou la teneur en nutriments. En raison des perturbations moins intenses lors de l’afforestation de friches par rapport aux sites forestiers, nous pensons qu'il serait judicieux de favoriser l'établissement de plantations sur les friches plutôt que sur les sites forestiers, afin de maintenir la diversité et la richesse des communautés microbiennes du sol.

Mots clés : Microbiome du sol, Diversité, Peuplier hybride, Friches agricoles, ADN environnemental

Abstract

The rapid growth rate of hybrid poplars is widely used to produce large quantities of biomass while enabling carbon sequestration, thus helping to mitigate the effects of climate change. As soil microorganisms play a key role in the proper functioning of ecosystems, understanding how the diversity and composition of the microbiome are impacted by the establishment of a hybrid poplar plantation is an important issue. In addition to the soil physico-chemical properties, the characteristics of the microbial communities are likely to depend on the origin of the site, i.e its vocation preceding the plantation. To facilitate decision-making concerning the choice of sites for the establishment of plantations, we conducted a study to evaluate the impact of afforestation by hybrid poplar on the soil microbiome by comparing plantations on different types of sites and their non-afforested counterparts: Abandoned agricultural lands (AAL) with herbaceous vegetation, AALs with shrubby vegetation and previously forested sites. Fungal communities are more sensitive to afforestation than bacterial communities and afforestation of previously forested lands led to a greater decrease in fungal diversity than the afforestation of AALs. Furthermore, while a change in abundance of some bacterial phyla was induced by afforestation and site origin, those changes were also possibly linked to edaphic properties such as pH or nutrient content. Because of the less intense disturbances when afforesting AALs compared to previously forested sites, we believe it would be wise to favor the establishment of plantations on AALs rather than on previously forested sites, to maintain the diversity and richness of soil microbial communities.

Keywords: Soil Microbiome, Bacteria, Fungi, Hybrid Poplar, Abandoned Agricultural land, environmental DNA

2.1 Introduction

Microorganisms are the most widespread living organisms on the planet, present in all biomes, where they play key roles in nutrient cycles and carbon sequestration, helping to mitigate the effects of climate change (Cavicchioli et al., 2019; Saccá et al., 2017). Within terrestrial ecosystems such as forests, microorganisms occupy numerous habitats from plant tissues to mineral soil (Baldrian, 2017). Among these, soil contains one of the most abundant and diverse microbial communities (Buée et al., 2009; Saccá et al., 2017). Their structure, composition and activity are highly associated with edaphic properties. Soil pH has been observed to be the best predictor of bacterial community composition, while fungal community composition has been associated with soil nutrient concentrations such as nitrogen and phosphorus, and both have been correlated to silt and clay contents (Lauber et al., 2008; Rousk et al., 2010; Xia et al., 2020). Land use conversion, such as the establishment of tree plantations on abandoned agricultural lands (AALs), can also lead to a shift in soil microbial community composition whether by directly affecting edaphic properties or through symbiotic associations between plants and certain microorganisms such as arbuscular mycorrhiza or ectomycorrhiza that can influence non-symbiotic taxa (Lang et al., 2011; Urbanová et al., 2015; Yu et al., 2021).

Afforestation initiatives aim to mitigate climate change by sequestering carbon, restoring ecosystems or producing biomass and often target croplands for conversion to forest environments (Government of Canada, 2025; Mayer et al., 2020). In Quebec and Canada, fast growing trees such as hybrid poplar are often used when converting agricultural lands to plantations (Derbowka et al., 2012; Ménétrier, 2008). Several studies have examined the impact of this type of land conversion on the soil microbiome. Fungal communities benefit most from the transition from cultivated land to forest. The input of degradable woody matter and the possibility of mycorrhizal associations with the planted trees lead to an increase in the richness, diversity and abundance of fungal communities (Yannikos et al., 2014; Zheng et al., 2017). For bacterial communities, many authors have studied their response to afforestation of croplands, with contradictory results, ranging from an increase in both microbial biomass and diversity to a decrease in richness or diversity (Kong et al., 2022; Liu et al., 2018; Ren et al., 2016). The recent review by (Huang et al., 2022) confirms the positive effect of afforestation on fungal communities and shows that afforestation has no impact on bacterial community diversity. They also add that the effect of afforestation on microbial communities varies according to climatic zones. However, most of the studies reported in this review are located in China, and none in a boreal biome, as is the case for most of the Canadian forest. In addition, these studies focussed on plantations established directly or shortly after the cessation of agricultural activities, whereas it is also common for afforestation programs to target abandoned agricultural lands (AAL) that have been left fallow for several years or decades (Fayet et al., 2022; Subedi et al., 2022).

Following farmland abandonment, secondary succession progresses with the development of perennial herbaceous or shrubby vegetation, which sometimes leads to the restoration of a forest ecosystem (Chazdon et al., 2020; Ustaoglu & Collier, 2018). Several studies have shown that during this successional process, fungal and bacterial communities undergo several changes, but the nature of these changes vary from one study to another, and none that we know of has taken place in the boreal biome. In the Loess plateau in China, Zhang et al. (2016) found an increase in diversity of bacterial communities during secondary succession while G. Wang et al. (2021), in warm and humid south China, observed a change in fungal and bacterial community composition and an overall decrease in diversity with succession. Balami et al. (2021) also found a species shift in fungal community composition during secondary succession in a temperate monsoon climate, but no differences in richness or Shannon diversity, partly explained by the absence of host trees for mycorrhizal associations in AALs. Therefore, afforestation of AALs and its consequences on microbial communities could depend on the state of advancement of secondary succession when the plantation is established, considering the changes brought in the microbiome during secondary succession. The conversion of natural forests to plantations also induces varied responses in microbial communities, in some cases leading to an alteration and a decrease in the diversity of microbial communities

(Cheng et al., 2022; Vitali et al., 2016), while in others, the bacterial diversity increases (Sawada et al., 2021).

The variety of microbial community responses observed in the literature during afforestation does not allow us to identify clear trends on the impact of site origin on the fate of microbial communities after tree plantations are established. Given the potential of fast growing plantations to enhance carbon sequestration in soils and biomass (Ameray et al., 2021; Kämpf et al., 2016), and the role of the microbiome in carbon cycling within ecosystems (Cavicchioli et al., 2019), it is important to know which sites are best suited for these plantations. This study was designed to assess the impact of afforestation with hybrid poplar on the soil microbiome composition and diversity present in sites with different origins: herbaceous AAL, shrubby AAL and previously forested sites.

2.2 Materials and methods

2.2.1 Study sites

The sampling design consisted of 16 sites, mostly scattered across the Abitibi-Témiscamingue region of Quebec and two located in neighbouring territories (Ontario and Northern Quebec). The sites shared comparable weather conditions, where the mean annual temperature ranged from 0.1°C to 2.8°C and mean annual precipitations from 785 mm to 950 mm (Government of Canada, 2011). Soil types were mainly heavy clay apart from one loamy site (ND). For more details on sites, see Annexe B-Table S1. Each site was divided into a hybrid poplar plantation established between 2003 and 2009, and an adjacent non-afforested area chosen to be representative of the vegetation of the site. Several hybrid poplar clones were planted within each site, but to limit the variability related to clonal identity, we only sampled planting blocks of clone 915319 (*Populus maximowiczii x Populus balsamifera*), since it showed high productivity and survival rates at all sites. Before plantation establishment, four of the sites were poorly regenerated harvested forest stands (AD, DP1, DP3 and ND), eight were abandoned agricultural lands (AAL) with herbaceous vegetation (DO, DY, ND, PC, SG, TA, TR and VP) and four were AALs with patches of shrubby vegetation (AM, LS, RH and SD). These three different site origins are referred to in this study as previously forested lands, herbaceous AAL and shrubby AAL. Mechanical site preparation was necessary prior to planting, the intensity of which depended on the amount of vegetation and woody debris to be removed. The intensity was greater for forest sites and lower for herbaceous AALs sites. In addition, during the first few years of the plantation, the undergrowth was mechanically weeded and woody debris removed.

2.2.2 Sample collection

Our sampling campaign took place during the summer of 2022. We selected 12 random sampling points for each site, 6 within the plantation and 6 within the non-afforested area that were equidistant from two trees within a row for the hybrid poplar plantations (Figure 18). After removing the dead vegetation and the litter (L), fermentation (F) and humus (H) layers, we sampled the first 15 cm of mineral soil with an auger. We concentrated on mineral soil to be consistent between sites, as some sites had a very thin or no organic layer. The soil samples were individually stored on ice pending return to the laboratory where we prepared a composite sample for each of the associated plantation and non-afforested areas. Using sterile equipment, we cut each sample lengthways in half to access the middle of the sample where soil had not been exposed to the outside environment during in situ manipulations. Then, 1 g of soil from each sample was mixed to obtain a 6 g composite sample for each site. Pending DNA extraction, composite samples (N=32) were placed in a freezer at -80°C.

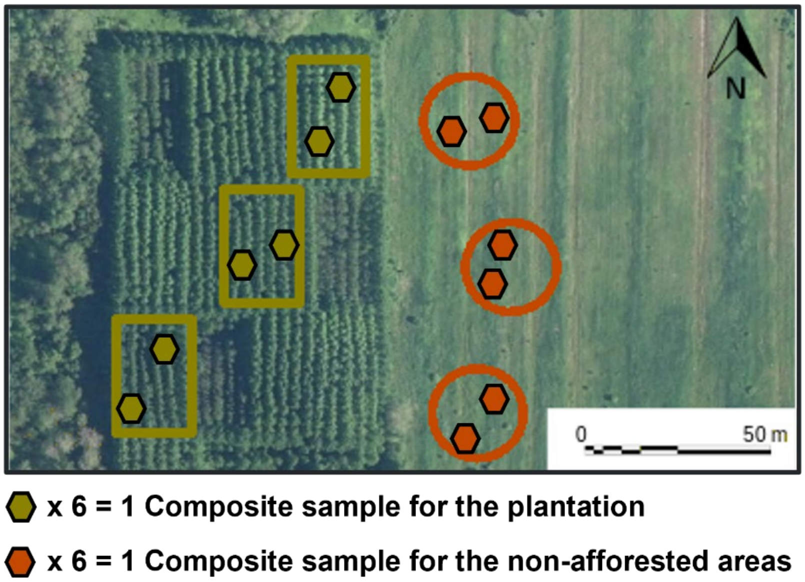


Figure 18
Map of the Val-Paradis site (VP). Illustrating the location of soil samples for microbial DNAe analysis

2.2.3 DNA extraction, amplification and sequencing

Soil DNA from our samples was extracted with the DNeasy PowerSoil Pro Kit (Qiagen, USA) following the manufacturer's instructions. Soil DNA was PCR-amplified with primers 515bF/926R (515bF : GTGYCAGCMGCCGCGGTAA – 926R : CCGYCAATTYMTTTRAGTTT) from The V4-V5 region of the 16S rRNA gene for bacteria and primers ITS-9F/ITS4R (ITS-F9 : AACGCAGCRAAIIGYGA - ITS4R : TCCTCCGCTTATTGATATGC) from the ITS2 region for fungi (Parada et al., 2016; White et al., 1990). Sequencing was performed on a MiSeq PE300 sequencing system (Illumina Inc., USA). Amplification, metabarcoding library preparation and sequencing were performed by Genome Quebec (Montreal, Canada).

2.2.4 Bioinformatic processing

The high throughput Illumina sequencing produced a total of 2,130,852 reads for bacterial 16S and 1,880,351 reads for Fungal ITS. We had 2 extraction controls during sequencing that generated 321 and 1,412 reads for bacterial 16S and 8 and 2 for fungal ITS, respectively. After checking that the composition of the controls differed from that of the samples, we excluded them from the analyses. The paired-end sequence reads in FASTQ format were processed using the DADA2 R package (Callahan et al., 2016). Through the "DADA2" pipeline, we used the function "filterAndTrim" to truncate the sequences after 300 pb for forward and 240 pb for reverse reads to remove low-quality sequences. ITS sequences were truncated after 280 pb for both forward and reverse strands. The truncation size was defined with the visualization of quality score with the function "plotQualityProfile". The forward and reverse reads were then merged together using "mergePairs". After merging we counted 1,438,637 bacterial reads and 1,795,741 fungal reads. Chimeras were removed with the function "removeBimeraDnovo" and corresponding sequences were clustered into amplicon sequence variants (ASVs) obtaining 1,158,018 bacterial reads and 1,512,898 fungal reads. We excluded the rarest ASVs from our study, keeping only those present in at least 2 samples and whose abundance was greater than 10. After the last cut off we obtained 953,993 bacterial reads and 1,158,221 fungal reads distributed among 13,693 unique bacterial ASVs and 1,872 unique fungal ASVs. We assigned the ASVs to a taxonomic group using the "assignTaxonomy" function based on the SILVA database (V138.1) for the 16S gene and the UNITE database (V10.0) for the ITS2 fungal region (Abarenkov et al., 2010; Quast et al., 2012).

We used FUNGuild (V1.1) to assign ecological guilds to each fungal ASV (Nguyen et al., 2016). In this study, we retained associations between guilds and ASV with a confidence ranking of "highly probable" or "probable" while discarding association with a confidence ranking of "possible". The abundance of any ASV designated in more than one guild was divided by the total number of guilds associated with this specific ASV to obtain a guild abundance matrix weighed by the number of guilds found for each ASV.

2.2.5 Soil properties

We used the remainder of our soil samples to determine soil pH, total carbon and total nitrogen concentrations (C_{tot} and N_{tot}), soil water and clay contents (SWC and SCC), and bulk density (BD). Soil samples were weighed before and after being air-dried to evaluate SWC. Following weighting, dry samples were sieved through a 2 mm mesh and ground with a Humboldt hammer mill (Dayton Electric Mfg. Co., USA). No significant amounts of organic or non-organic coarse materials were found in our soil samples during sieving. We estimated mineral soil pH using the electrometric method (Government of Quebec, 2023) and soil texture was assessed using the hydrometer method (Bouyoucos, 1962) based on the size classes from the Canadian Soil Classification Working Group (1998). Sub-samples were ground more finely using a ball grinder (MM301, Retch, Germany) and sieved through a 250 µm mesh for total C and N determination by dry combustion (CR-412, LECO Inc., USA). The total C concentration in our samples was considered equal to organic C since no significant concentration of carbonates was found in our samples.

We used the following equation [1] from Federer et al. (1993) to calculate bulk density (D_b).

$$D_b = \frac{(b_1 \times b_2)}{\left(\frac{(b_1 \times Ctot}{1000}\right) + \left(b_2 \times \left(\frac{1 - Ctot}{1000}\right)\right)} \qquad \text{(Eq. 1)}$$

Where b1 and b2 are respectively equal to 1.460531 and 0.106068 and C_{tot} is equal to total carbon concentration in g.kg^{-1}. b1 and b2 were determined using the data from the study of Thibault et al. (2022), available online (Thiffault et al., 2021).

To calculate soil water content (SWC) we used the following equation [2] which includes soil wet mass (m_w) and soil dry mass (m_d):

$$SWC = \frac{m_d}{m_w} \times 100 \qquad \text{(Eq. 2)}$$

2.2.6 Vegetation survey

In each sampling area, we randomly placed 1 m² quadrats with the condition that half of the quadrats were placed at the foot of a tree and the other half between the tree rows. The number of quadrats per sampling area was inversely related to the total number of sampling areas in the plantation corresponding to the number of areas planted with the clone 915319: 24 quadrats for 1 sampling area (RH), 4 quadrats for 5 sampling areas (TR and SG) and 8 quadrats for 3 sampling areas (all other sites). For the non-afforested areas, we delimited 3 circular sampling areas of 150 m², chosen to be representative of the vegetation of the site and we randomly placed 8 x 1 m² quadrats in each of them. In each quadrat, we identified all vascular plant species, and their percent cover within the quadrat was assessed by two observers. For bryophyte species, we collected samples from colonies on soil and tree bark within the quadrats for subsequent identification in the laboratory. Names of the different plant species were determined using the nomenclature of vascular plants of Canada (Canadensys, 2024) for vascular plants and “Flore des bryophytes du Québec-Labrador” (Faubert, 2013) for bryophytes.

2.2.7 Statistical analysis

Data transformation. We rarefied the dataset with the function “rarefy_even_depth” from the R package “phyloseq” (McMurdie & Holmes, 2013) to 16,051 reads per sample for bacteria, and to 15,714 reads per sample for fungi (Annexe B-Figure S1). The rarefied data set resulted in 13,692 ASVs and 513,632 reads for bacteria, and 1,872 ASVs and 502,848 reads for fungi (Annexe B-Figure S1). ASVs richness, Shannon index and Pielou’s evenness (Pielou, 1966; Shannon, 1948) were estimated using the functions “specnumber” and “diversity” from the R package “vegan” (Oksanen et al., 2022). Phyla and guild abundance data were transformed by applying a centred log-ratio (clr) transformation on our dataset with the function “decostand” (pseudocount = 1) from the R package “vegan”. In addition, we divided the *Proteobacteria* phyla into Alpha and Gamma proteobacteria Class.

ANOVA and mixed linear models. To assess the effects of afforestation and site origin on soil properties, alpha diversity and phylum and fungal guild abundance we completed an analysis of variance (ANOVA) for fitted mixed models. We built our models with alpha diversity indices (Richness, Shannon’s and Pielou’s evenness), soil properties (pH, C_{tot}, N_{tot}, SWC, SCC and BD) and centered log-ratio (clr) transformed phylum and guild abundance as explanatory variables. In each model, the site was included as a random effect while afforestation and site origin were fixed effects. Because of the importance of soil properties in structuring microbial communities, we also included soil properties as fixed effects in models describing alpha diversity index and phylum abundance. To determine which soil property variables to include in our models, we used a model selection analysis based on the Akaike Information Criterion for small samples (Akaike, 1998). We compared models including a different combination of soil property variables and selected for our analyses the ones with the best weighted AICc score. We built our models with the function “lmer” from the R package “lme4” (Bates et al., 2015). We evaluated diagnostic plots to check for normality of residuals and of the random effects using qqnorm, qqline, ranef and plot functions from “stats” and “lme4” R packages (Bates et al., 2015; R Core Team, 2023). Some guild and phylum data were too skewed to be analyzed with an ANOVA, and in these cases, we completed a non-parametric Kruskal-Wallis test (Kruskal & Wallis, 1952). To perform pairwise comparisons, we used the function "emmeans" from the eponymous R package (Lenth et al., 2024) and the function "pairwise.wilcox.test" in R (Bauer, 1972).

Dissimilarity distance and permANOVA. We computed Bray-Curtis distances on rarefied and Hellinger transformed bacterial and fungal ASV abundance with the function “vegdist” from vegan (Bray & Curtis, 1957; Legendre & Gallagher, 2001). The obtained distance matrix was used to carry out a principal coordinate analysis (PCoA) with the function “wcmdscale” from vegan (Oksanen et al., 2022). We fitted environmental, phylum and vegetation abundance vectors onto the ordination with the function “envfit” also from vegan. We tested the effect of afforestation and site origin on the composition of microbial communities by performing a multivariate analysis of variance with permutations (permANOVA; McArdle & Anderson, 2001) with the “adonis2” function from “vegan” on the Bray-Curtis distance matrix of fungal and bacterial communities. The variable “site” was set as strata and we also used soil properties as co-variables in the analysis. Before interpreting the results of the permANOVA, we tested the dispersion of our data using vegan's “betadisperse” and “permutest” functions (Oksanen et al., 2022). We also carried out pairwise tests using the “pairwise.adonis2” function (Arbizu, 2017).

To process to the fitting of vegetation abundance onto the ordination, we constructed two community matrices with sites as rows and species as columns. In the vascular plant matrix, we converted percent cover into classes based on a 9-point Braum-

Blanquet scale (Braun-Blanquet et al., 1932; Wood et al., 2013). The other matrix was for bryophytes and based on the sum of the species presence in each quadrat for plantations and non-afforested areas at each site.

Analyses presented in this study were carried out using R 4.3.1 (R Core Team, 2023), visual representation using the R packages ggplot2 and cowplot (Wickham, 2016; Wilke, 2024).

2.3 Results

2.3.1 Microbial alpha diversity

Bacterial communities in soils of hybrid poplar plantations and non-afforested areas showed similar richness, Shannon's diversity and evenness regardless of site origin (Figure 19a, b and c). In contrast, afforestation with hybrid poplars induced a decrease in fungal ASVs richness compared to non-afforested areas but only for plantations established on previously forested lands (Figure 19d). Plantations on previously forested lands also harboured lower fungal richness than those established on both herbaceous and shrubby AALs (Figure 19d). Diversity of fungi in afforested AALs was similar to their non-afforested counterparts, while afforestation with hybrid poplars on previously forested lands reduced Shannon diversity of fungal communities (Figure 19e). Lastly, Pielou's evenness of ITS ASV was lower in hybrid poplar plantations compared to their non-afforested counterparts (Figure 19f).

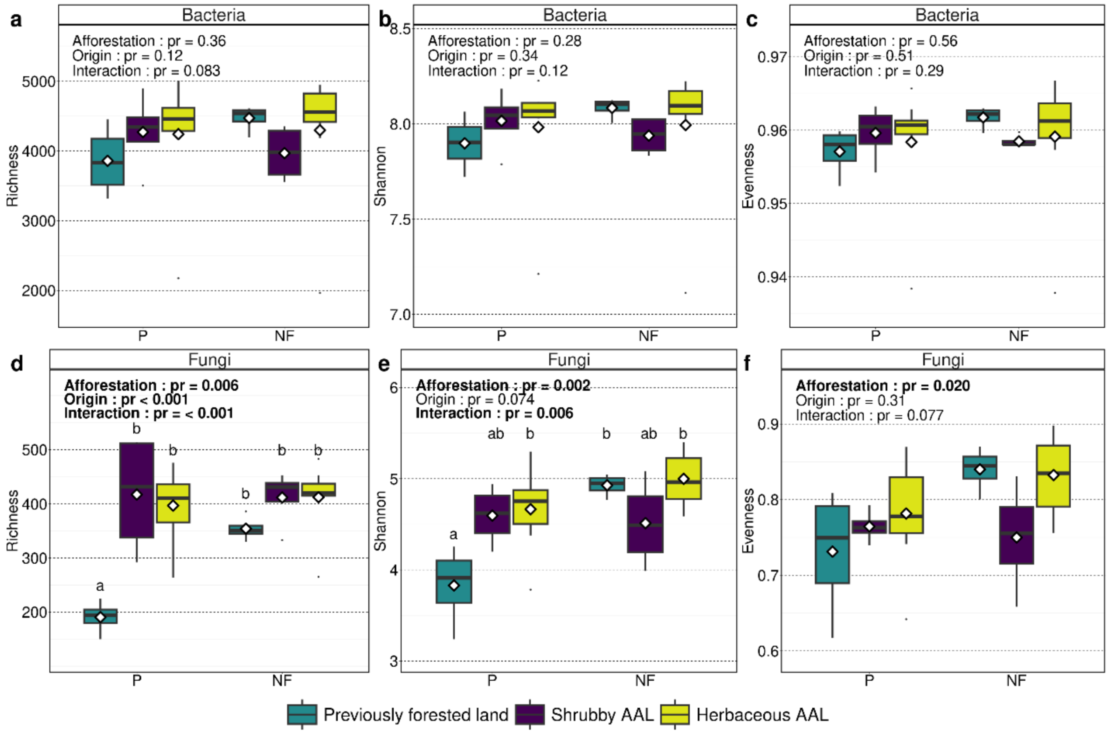


Figure 19
Box plot statistic of richness (a and d), Shannon's index (b and e) and evenness (c and f) of amplicon sequence variants for hybrid poplar plantations (P) and non-afforested areas (NF) by site origin. Solid lines indicate the median, hinges indicate 1st and 3rd quantiles and whiskers indicate inter quantile ranges multiplied by 1.5. Outlying values are shown as black dots. Means are shown with white diamonds. ANOVA results are shown with a bold font when significant ($P<0.05$). When interaction is significative, lower-case letters above box plots indicate significant differences at $p<0.05$.

2.3.2 ASV ordination

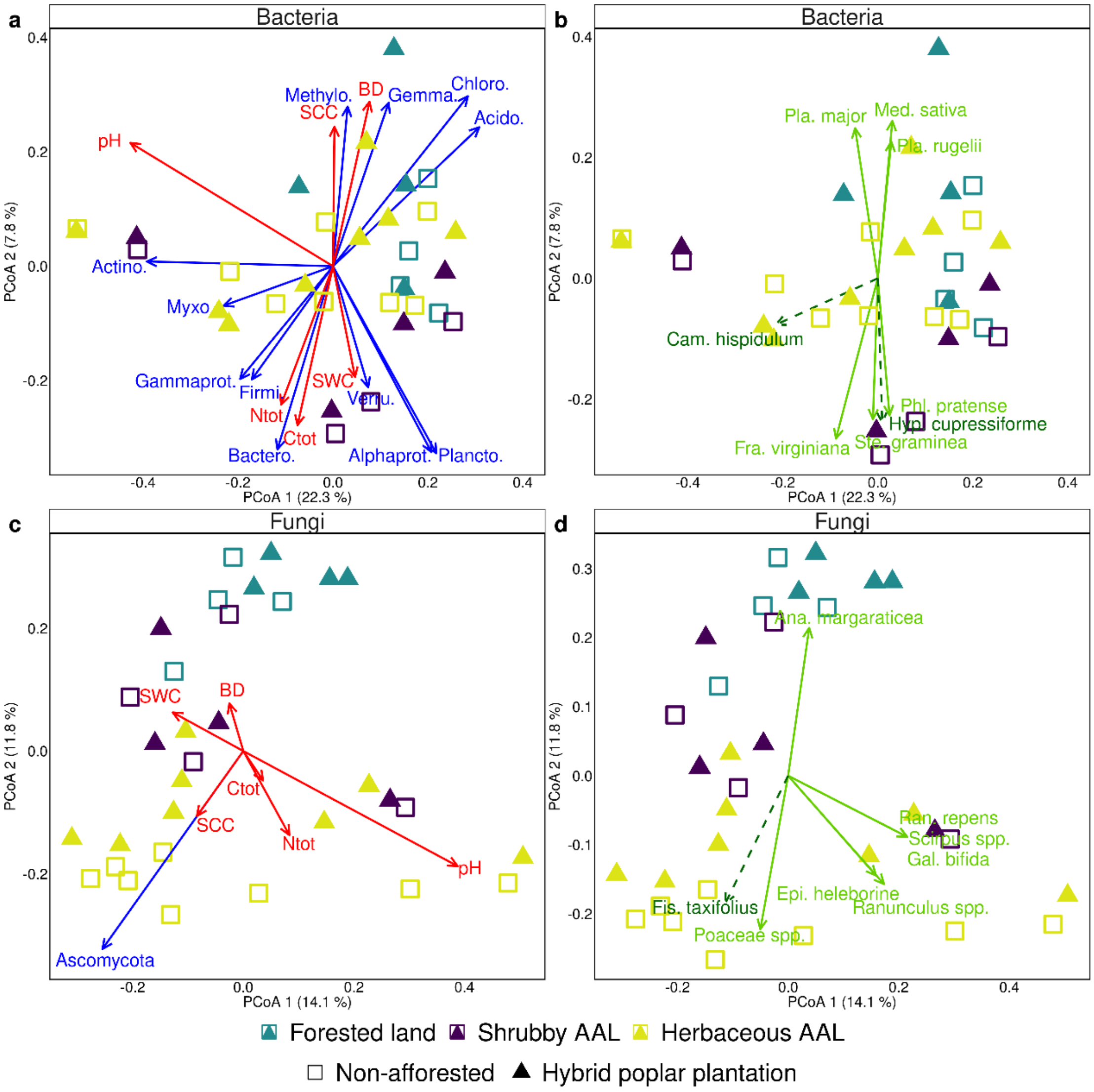
For both fungal and bacterial communities, site origin explained a larger proportion of the variation in composition than afforestation (11% and 14% of site origin, vs 2.5% and 5.5% of afforestation, for bacteria and fungi respectively; Table 6). Fungal communities were also impacted by soil pH, carbon concentration and clay content, whereas the bacterial community was only impacted by soil pH (18% of the variability; Table 6). *Chloroflexi* (Chloro.) and *Acidobacteriota* (Acido.) were associated with previously forested sites, while *Alphaproteobacteria* (Alphaprot.) and *Planctomycita*

(Plancto.) were associated to shrubby AALs. For fungi, there was a strong link between Ascomycota and herbaceous AALs (Figure 20a and b).

Table 6
permANOVA results for the effects of afforestation, site origin and soil properties on bacterial and fungal ASVs composition.

	Bacteria		Fungi	
Factor	R²	P value	R²	P value
Afforestation	0.025	**0.010**	0.055	**<0.001**
Site Origin	0.11	**0.016**	0.14	**<0.001**
- Forested vs S.AAL	*0.11*	***0.022***	*0.11*	***0.013***
- Forested vs H.AAL	*0.09*	***0.007***	*0.14*	***<0.001***
- S.AAL vs H.AAL	*0.06*	*0.13*	*0.08*	***0.016***
Interaction	0.040	0.69	0.050	0.091
pH	0.18	**0.010**	0.11	**<0.001**
C_{tot}	0.032	0.49	0.029	**0.049**
N_{tot}	0.036	0.22	0.029	0.54
SWC	0.037	0.24	0.036	0.27
SCC	0.033	0.22	0.042	**0.017**
BD	0.025	0.47	0.035	**<0.001**
Residuals	0.49		0.47	

Ctot : total Carbon, Ntot : total Nitrogen, SWC : Soil Water Content, SCC : Soil Clay Content, BD : Bulk Density, S.AAL : Shrubby Abandoned Agricultural Lands, H.AAL : Herbaceous Abandoned Agricultural Lands



Notes: Ctot: total Carbon, Ntot: total Nitrogen, SWC: Soil Water Content, SCC: Soil Clay Content, BD: Bulk Density

Figure 20
Principal coordinate analysis (PCoA) based on rarefied bacterial and fungal amplicon sequence variants composition using the Bray-Curtis dissimilarity index. Plots on the left show microbial phylum (blue) and edaphic properties (red). Plots on the right show vascular plants species (light green) and bryophytes (dark green dotted lines). Vegetation variables are fitted onto the ordination with P < 0.05.

Composition of bacterial and fungal communities were correlated with the abundance of vascular plants and moss species found in the vegetation cover of the hybrid poplar plantations and the non afforested areas (Figure 20b and d). *Fragaria virginiana* (Frag. Virginiana), *Stelaria graminea* (Stel. graminea), *Phleum pratense* (Phl. pratense) and the moss *Hypnum curpessiforme* (Hyp. cupressiforme) were correlated to bacterial composition mostly within sites originating from shrubby AALs. *Plantago major* (Pla. major), *Plantago rugelii* (Pla. rugelii) and *Medicago sativa* (Med. sativa) were associated to bacterial ASVs in previously forested sites and the bryophyte *Campylophyllum hispidulum* (Camp. hispidulum) in sites originating from herbaceous AALs (Figure 20b). *Ranunculus* spp., *Ranunculus repens* (Ran. repens), *Galium bifida* (Gal. bifida), *Scirpus spp*, *Epipactis helleborine* (Epi. helleborine), *Poaceae spp.* and the moss *Fissidens taxifollius* (Fis. taxifolius) were correlated to fungal ASVs within sites originating from herbaceous AALs while *Anaphalis margaritacea* were associated to fungal composition in previously forested sites (Figure 20d).

2.3.3 Phylum abundance

Among the 12 bacterial phyla with a relative abundance over 2%, eight of them were affected by either afforestation, site origin or both, but none by the interaction of these two factors (Table 7 and Figure 21a). Acidobacteriota, Chloroflexi, Gemmatimonadota and Methylomirabilota were more relatively abundant in plantation soils compared to non-afforested areas (respectively 25% vs. 23%, 8.6% vs. 7%, 2.5% vs. 2.1 and 2.1% vs. 1.5%). Sites originating from herbaceous AALs had a greater relative abundance of ASVs identified as Actinobacteriota, Firmicutes and Verrumicrobiota compared with sites originating from previously forested lands, whether afforested or not (respectively 14 vs. 10%, 3.4% vs. 1.8% and 3.8% vs. 2.6). ASVs identified as Methylomirabilota were less relative abundant in soils of shrubby AALs (1.2%) compared to soils from previously forested lands (3.8%).

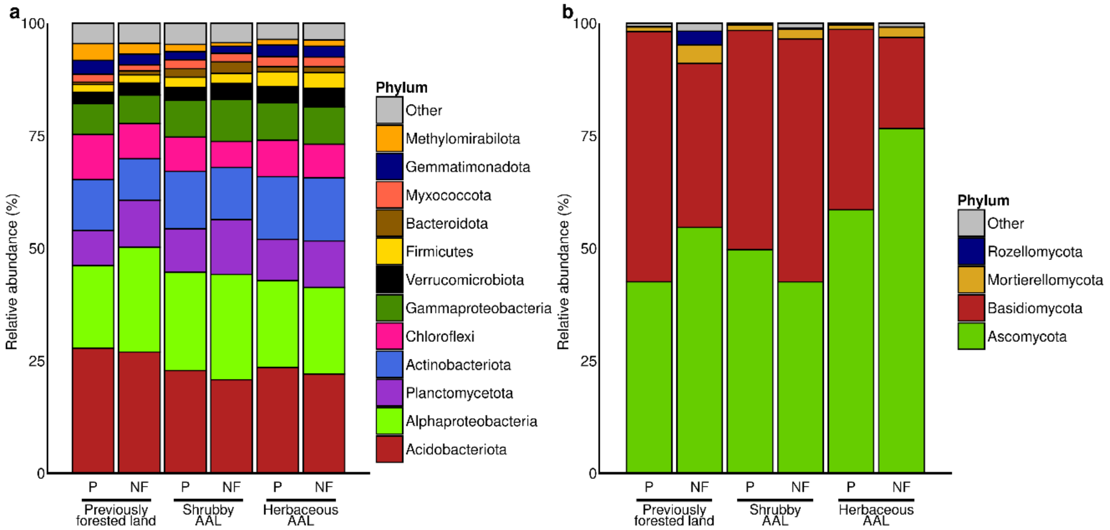


Figure 21
Relative abundance of dominant (>2%) bacterial phyla (a) and fungal phyla (b) for hybrid poplar plantations (P) and non-afforested areas (NF) by site origin. Proteobacteria phylum is divided into Alpha and Gamma proteobacteria class.

The relative abundance of ASVs identified as *Ascomycota* varied within afforestation depending on site origin (Table 7). Hybrid poplar plantations established on previously forested lands had less relatively abundant ASVs identified as *Ascomycota* equivalent to 43% compared to plantations on herbaceous and shrubby AALs with a relative abundance of 59% and 50% respectively (Figure 21b). *Basidiomycota* relative abundance was only affected by site origin, with lower relative abundance in herbaceous AALs sites (30%) and highest relative abundance in shrubby AALs sites (51%) (Figure 21b). Regardless of site origin, the fungal community of non-afforested areas included more relatively abundant *Mortierellomycota* (2.8%) compared to plantations (1%). *Rozellomycota* were also more relatively abundant in non-afforested areas compared to plantations (1.1% vs. 0.08%).

Table 7
ANOVA summary showing the effect of afforestation and site origin on dominant (>2%) bacterial and fungi phylum based on centered log ratio transformed compositional data. Phyla for which relative abundance was affected either by afforestation, site origin or their interaction are shown with a bold font (P<0.05).

Phylum	Afforestation		Site origin		Interaction	
	F stat	P value	F stat	P value	F stat	P value
Bacteria						
Acidobacteriota	**4.82**	**0.043**	0.48	0.63	2.45	0.12
Actinobacteriota	0.002	0.97	**4.37**	**0.037**	0.58	0.57
Alphaproteobacteria	0.18	0.68	1.99	0.18	**4.60**	**0.031**
Gammaproteobacteria	0.36	0.56	1.55	0.25	2.14	0.16
Bacteroidota	**10.43**	**0.006**	**8.27**	**0.005**	**4.20**	**0.039**
Chloroflexi	**19.1**	**<0.001**	0.20	0.82	3.50	0.067
Firmicutes	0.02	0.90	**4.85**	**0.027**	0.99	0.40
Gemmatimonadota	**4.66**	**0.047**	1.77	0.21	0.072	0.93
Methylomirabilota	**9.05**	**0.011**	**4.16**	**0.040**	3.13	0.078
Myxococcota	0.67	0.43	2.61	0.11	0.23	0.80
Planctomycetota	0.36	0.56	1.56	0.25	2.20	0.15
Verrucomicrobiota	0.078	0.78	**4.74**	**0.031**	0.076	0.93
Fungi						
Ascomycota	4.23	0.061	**13.76**	**<0.001**	**6.36**	**0.012**
Basidiomycota	3.43	0.087	**3.91**	**0.047**	1.47	0.27
Mortierellomycota	**24.59**	**<0.001**	1.41	0.28	2.19	0.15
Rozellomycota	**3.96**	**0.047**	4.04	0.13	-	-

Note: Due to skewed data, we used a non-parametric Kruskal-Wallis test for *Rozellomycota abundance* that did not allow us to test for interaction.

2.3.4 Fungal guild

Plant pathogens, ericoid mycorrhizae and plant saprotrophs were not affected by site origin or afforestation (Table 8). Afforestation did reduce the relative abundance of fungal parasites, endophytes, dung saprotrophs, wood saprotrophs and undefined saprotrophs compared to non-afforested area (respectively 4% vs. 5.5%; 2.4% vs. 4.1%; 4.1% vs. 5.8% and 24% vs. 32%) (Figure 21). Among these guilds, the relative abundance of dung saprotrophs was higher in soils of herbaceous AALs (5.8%) compared to shrubby AALs (1%) and previously forested lands (3%, Table 8). The relative abundance of lichenized fungi was greater in soils of previously forested lands (1.6%) compared to herbaceous AALs where the relative abundance was the lowest (<0.01%).

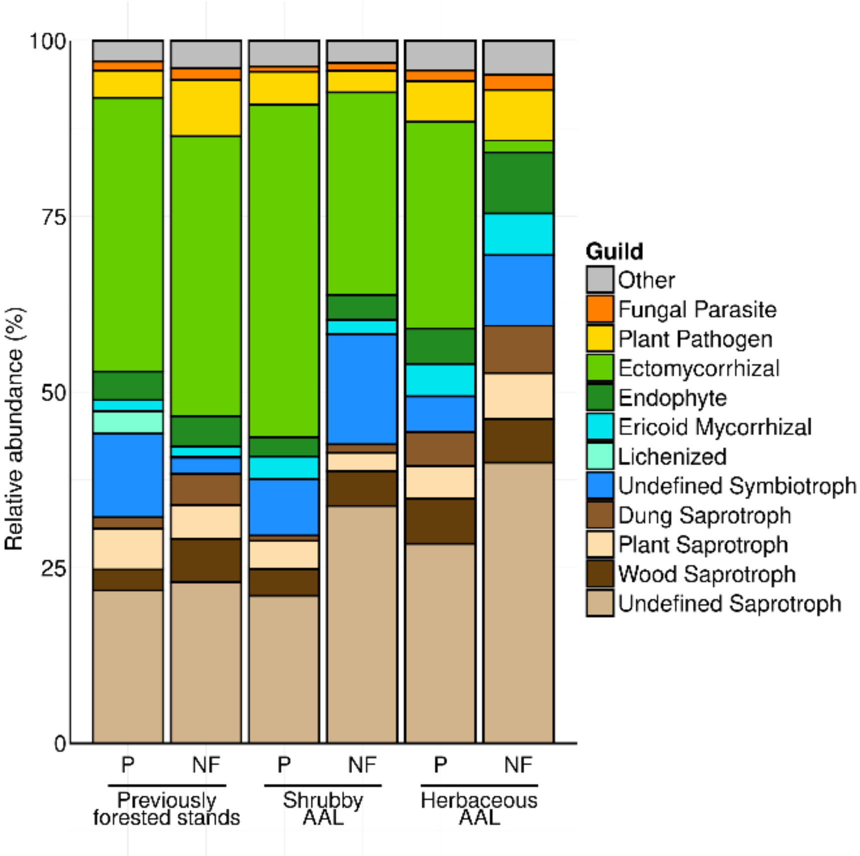


Figure 22
Relative abundance of dominant fungi guilds (>2%) for hybrid poplar plantations (P) and non-afforested area (NF) by site origin.

The effect of afforestation on the relative abundance of ectomycorrhizal and undefined symbiotrophs depended on the origin of the afforested site (Table 8); Among the non-afforested areas from sites of different origins, only herbaceous AALs were depleted in ectomycorrhizas compared to plantations (1.7% vs. 30%), while for sites originating from previously forested areas or shrubby AALs, ectomycorrhiza relative abundance did not differ between plantations and non-afforested areas (Figure 22). The relative abundance of undefined symbiotrophs tended to increase after afforestation on previously forested sites, from a relative abundance of 2.3% in non-afforested areas to 12% in plantations. However, an opposite trend was observed for plantations on AALs where afforestation tended to decrease the relative abundance of undefined symbiotrophs, from 16% to 8% for shrubby AALs and from 10% to 5% for herbaceous AALs (Figure 22).

Table 8
ANOVA summary showing the effect of afforestation and site origin on dominant fungi guilds (>2%) based on centered log ratio transformed compositional data. Guilds for which relative abundance is affected either by afforestation, the site of origin or their interaction are shown with a bold font (P<0.05).

Guild	Afforestation		Site origin		Interaction	
	F stat	P value	F stat	P value	F stat	P value
Fungal parasites	**10.24**	**0.006**	0.21	0.81	0.35	0.71
Plant pathogens	4.21	0.059	0.45	0.65	1.96	0.18
Ectomycorrhizal fungi	**25.8**	**<0.001**	**19.5**	**<0.001**	**23.4**	**<0.001**
Endophyte fungi	**8.7**	**0.011**	0.90	0.43	3.65	0.055
Ericoid mycorrhizal fungi	3.99	0.061	1.22	0.33	0.46	0.64
Lichenized fungi	1.06	0.30	**6.57**	**0.037**	-	-
Undefined symbiotrophs	0.004	0.95	0.17	0.85	**4.18**	**0.040**
Dung saprotrophs	**6.95**	**0.021**	**5.28**	**0.021**	1.32	0.30
Plant saprotrophs	0.96	0.34	0.10	0.91	**4.40**	**0.034**
Wood saprotrophs	**11.3**	**0.004**	0.26	0.78	1.56	0.25
Undefined saprotrophs	**6.73**	**0.022**	3.65	0.055	2.23	0.15

Note: due to skewed data, we used a non-parametric Kruskal test for lichenized fungi abundance that did not allow us to test the interaction.

2.3.5 Soil properties

The soil clay content was similar in plantations and non-afforested areas, whatever the site origin (Table 9). The relatively high clay concentrations at all sites are related to the location of our study, in the Ontario-Quebec clay belt (Vincent & Hardy, 1977). Soil pH and water content were the only two parameters affected independently by afforestation (Annexe B-Table S2). Soil pH was higher in plantations, while water content was lower. The remaining edaphic parameters (carbon and nitrogen concentration and bulk density) were affected by afforestation, but this effect was dependent on the site origin (Table 9). Nitrogen and carbon concentrations were lower in plantations established on previously forested sites, while bulk density was higher. These effects were not observed for plantations established on AALs (Table 9).

Table 9
Soil properties (mean ± SE) in hybrid poplar plantations and non-afforested areas according to the site origin. Different lowercase letters in parentheses indicate a significant difference (P<0.05).

Soil properties	Site origin	Treatment	
		Afforestation	Non-afforested
pH	Previously forested	5.72±0.19(a)	5.37±0.10(b)
	Shrubby AAL	5.76±0.30(a)	5.57±0.29(b)
	Herbaceous AAL	5.95±0.22(a)	5.82±0.24(b)
C_{tot} (g.kg^{-1})	Previously forested	14.5±2.22(a)	32.25±4.61(b)
	Shrubby AAL	31.75±5.38(ab)	44.75±9.63(b)
	Herbaceous AAL	25.25±2.97(ab)	28.25±3.26(ab)
N_{tot} (g.kg^{-1})	Previously forested	0.88±0.10(a)	2.23±0.38(b)
	Shrubby AAL	2.03±0.29(ab)	2.68±0.44(b)
	Herbaceous AAL	1.81±0.21(ab)	2.11±0.25(ab)
SWC (%)	Previously forested	29.1±2.6(a)	39.4±4.1(b)
	Shrubby AAL	36.2±3.4(a)	52.3±9.6(b)
	Herbaceous AAL	30.9±2.6(a)	33.7±3.9(b)
SCC (%)	Previously forested	62.0±15.4	63±10.4
	Shrubby AAL	59.4±5.3	61.4±6.6
	Herbaceous AAL	67.9±4.7	63.0±3.7
BD (g.cm^{-3})	Previously forested	1.24±0.03(a)	1.04±0.04(b)
	Shrubby AAL	1.05±0.05(ab)	0.95±0.07(b)
	Herbaceous AAL	1.11±0.03(ab)	1.08±0.03(ab)

Notes: C_{tot} = Total Carbon; N_{tot} = Total Nitrogen; SWC = Soil Water Content; SCC = Soil Clay Content; BD = Bulk density.

2.4 Discussion

2.4.1 Fungal communities are more sensitive to changes in their habitat than bacteria

The richness and Shannon's diversity of fungal communities were sensitive to the establishment of plantations, with a general decrease in richness observed in plantations compared to non-afforested areas, particularly for the previously forested sites (Figure 19c). Fungi are renowned for their ability to degrade carbohydrates such as lignin and cellulose (Boer et al., 2005), and these recalcitrant compounds are usually present in greater quantities in environments with woody vegetation compared to those with herbaceous vegetation (Lindahl et al. 2006). We might have therefore expected an increase in the richness and diversity of fungal communities in hybrid poplar plantations, as observed in other publications (Yannikos et al., 2014; Zheng et al., 2017), but this was not the case in our study. Hybrid poplar plantations require regular and intensive maintenance. In the first few years after plantation establishment, the undergrowth was mechanically weeded and woody debris removed from the plantations. The lack of lignin compounds within the plantations has probably limited the colonization of the plantation by fungal species leading to lower fungal diversity than expected for such ecosystems. Another possible reason for the decline in fungal diversity in plantations is the use of a poplar clone with an exotic parent. Tree and shrub species build mycorrhizal associations such as ectomycorrhizae (ECMs) or arbuscular mycorrhizae that form a close link between the plant cover and soil fungal communities (Smith & Read, 2008; Urbanová et al., 2015). Although many other factors influence the colonization of tree roots by mycorrhizal fungi, in species of the Populus genus this is also influenced by the phylogeny of the host tree (Zanin et al., 2024). Our study focused on clone 915319, a hybrid formed by crossing a balsam poplar (*P. balsamifera*), indigenous to our study area, with a Japanese poplar (*P. maximoviczii*), an exotic species. It is possible that the presence of an exotic ancestry of the clone targeted in the study limited the colonization of the environment by fungal species associated with the poplar species native to our study area, also limiting fungal diversity within the plantations. It would be wise to study mycorrhizal communities within hybrid poplar plantations in greater detail focusing on host specificity for different hybrid poplar clones, as the composition of mycorrhizal communities can vary widely depending on the phylogeny of the planted tree (Liu et al., 2023; Zanin et al., 2024).

The absence of disturbances linked to agricultural practices in AALs may have contributed to the establishment of a more diverse fungal community in our study within non-afforested areas compared to plantations. Since the cessation of agricultural activity, communities present in the soil of the plantations have undergone numerous disturbances: ploughing, disking, mechanical or chemical weeding and sudden changes in plant cover. In contrast, the communities present in the non-afforested areas, which have undergone little disturbance, have been progressively enriched with both carbon inputs from the vegetation and the colonization of new species over time. However, the pattern of evolution in fungal communities after agricultural abandonment is not clearly established in the literature. Some authors have shown an increase in fungal biomass in AALs following the cessation of tillage (van der Wal et al., 2006) while others observed no difference in diversity, explaining this by the absence of host trees in AALs (Balami et al., 2021). Studies focusing on the monitoring of fungal communities during secondary succession following the end of agricultural activities would help to clarify the effects of abandonment on the evolution of these communities. In addition, our study focused on deciduous tree plantations. The work of Rodríguez-Rodríguez et al. (2023) showed that, in our study region, soil bacterial and fungal communities were sensitive to the type of forest, deciduous or coniferous, forming the vegetation cover. It would therefore be wise to explore the effect of reforestation on the diversity and composition of microbial communities of AAL with coniferous species native to our study area, such as black or white spruce.

While fungal diversity decreased with afforestation, *Mortielmomycota* and *Rozellomycota* were the only two fungal phyla that decreased in relative abundance with afforestation, regardless of site origin (Table 7). As *Rozllomycota* are obligate intracellular parasitic single-celled organisms (Tedersoo et al., 2018), their depletion within plantations also explains the depletion within plantations of the “fungal parasite” guild (Table 8). We can assume that the decline in fungal diversity within plantations reduced parasitism possibilities targeting fungi and therefore resulted in a decreased relative abundance of fungi specialized in the parasitism of other fungi including *Rozellomycota*. Soil-associated *Mortielomycota* play a key role in nutrient cycles and usually abundant in fertile soils (Ma et al., 2024; Ozimek & Hanaka, 2021). This suggests that our poplar plantations were nutrient-deficient, as evidenced by declining C and N concentrations in plantations established on previously forested sites (Table 9). However, the wide distribution of this taxon and its many functions limit the scope of this conclusion (Telagathoti et al., 2022). Ectomycorrhizae (ECMs) mainly form symbiotic associations with tree and shrub roots, but rarely with herbaceous plants (Smith & Read, 2008). It is therefore not surprising that non-afforested areas of herbaceous sites that are devoid of tree or shrub vegetation harbor a fungal community largely depleted in ECM. Interestingly afforestation of herbaceous AALs with hybrid poplars increased ECM relative abundance to levels similar to those observed in the other site origin types in our study (Figure 22). In forest ecosystems, ECMs promote nutrient uptake and contribute to the sequestration of C into soils, helping to mitigate climate change (Cairney, 2012; S. E. Smith & Read, 2008). The increase in ECM relative abundance within plantations on herbaceous AALs is thus encouraging, if there is a wish to use these plantations as a tool to restore forest ecosystems.

Our results showed that endophytes had lower relative abundance in the soils of hybrid poplar plantations (Figure 22) compared to non-afforested sites. In soils, endophytes are mostly found in plant roots, but since our study focused on the mineral soil microbiome, it is difficult to draw conclusions from these observations as the number of roots in our soil samples was low if not zero. Given the importance of endophytes for plant health, it would be wise to explore the rhizosphere microbiome in order to improve our knowledge of endophytes in a context of reforestation of old AALs with hybrid poplars. Lastly, we showed that lichenized fungi were abundant in plantations and non-afforested areas of formerly forested lands (Table 8 and Figure 22), confirming that hybrid poplar plantations can offer refuge for certain lichen species, as shown in Randriamananjara et al. (2023).

2.4.2 Changes in bacterial community composition but not in diversity

In contrast to the trends of fungal communities, our results showed that 15 years after plantation establishment, bacterial alpha diversity remained similar between hybrid poplar plantations and non-afforested areas among the different site origins (Figure 19). Bacteria are known for their resistance and resilience to disturbance, as well as their ability to metabolize a wide variety of compounds (Hartmann et al., 2012, 2014; Uroz et al., 2016). In microbial ecology, microorganisms can be divided into 2 large families: r and k strategists, where bacteria are more generally associated with r strategies and fungi with k strategies (Fierer et al., 2007). R-strategists can adapt quickly to a disturbance thanks to their high growth rate (Andrews & Harris, 1986). This argument is often put forward in studies and reviews to explain why bacterial communities thrive in plantations and degraded forests (Cuer et al., 2018; Y. Wang et al., 2021; Zhou et al., 2018). The similarity in bacterial diversity observed among our treatments can be explained by the resilience of bacterial communities to plantation disturbances. In addition, since environmental DNA analysis of the microbiome does not distinguish between active and inactive cells, microorganisms, especially bacteria, can become dormant under unfavorable conditions and could make up to 96 % percent of the bacterial cells present in the soil (Fierer & Lennon, 2011; Lennon & Jones, 2011; L. Li et al., 2024). It is therefore possible, on the one hand, that we have analyzed inactive organisms in the soil of our study sites that were present prior to afforestation and have become dormant following the disturbances associated with the change in land use. But little is known about the dormancy time of bacteria in plantations. It would be useful to know whether bacteria present before planting could still be detected by molecular analysis techniques 15 years after planting.

While the diversity of bacterial communities was little affected by afforestation or site origin, relative abundance of most bacterial phyla, (8 of the 12 dominant phyla) was affected by afforestation, site origin or both (Table 7, Figure 21a). *Acidobacteriota*, with the highest relative abundance in our study, had a higher relative abundance within hybrid poplar plantations along with *Chloroflexi*, *Gemmatimonadota* and *Methylomirabilota* (Figure 21a). *Acidobacteriota* are often associated with acidic soils (Jones et al., 2009; Kielak et al., 2016), but non-afforested areas were more acidic than hybrid poplar plantations (Table 9). Even though soil pH in our plantations was low (below 6 on average), we expected more *Acidobacteriota* in the unplanted areas. *Acidobacteriota* is one of the most widespread phyla in the planet's soils, possessing great diversity and occupying a wide variety of ecological niches, making their ecological characterization imprecise (Kielak et al., 2016). Many representatives of *Acidobacteriota*, along with *Chloroflexi* bacteria are oligotrophs, meaning that these organisms proliferate in nutrient-poor environments (Dou et al., 2023; Fierer et al., 2007). The shift observed in bacterial communities in oligotrophic phyla could illustrate the loss of C and N observed in plantations, mainly for those established on previously forested sites (Table 9). In addition, *Chloroflexi* and *Gemmatimonadota* have a pronounced affinity for low soil moisture and are able to proliferate in drier environments (DeBruyn et al., 2011; Jiao et al., 2021). For these two phyla, the decline in their relative abundance in plantations were possibly linked to the observed decrease in soil water content. This suggests that the compositional changes observed in bacterial communities during afforestation are probably linked to changes in edaphic properties such as soil fertility or soil water content.

2.4.3 Relationship between soil microbiome and vegetation cover

Relationships between plant cover and soil microbiome are tight due to the specific host association established between plant and microbial species. In natural or lightly managed forests of boreal biomes, forest understories plant species adapted to low-light are associated with numerous species of microorganisms, such as ericoid mycorrhizal fungi found forming symbiosis with Ericaceae family (Adamczyk et al., 2016; Luo et al., 2024; Uroz et al., 2016). By establishing hybrid poplar plantations on former agricultural lands, we could expect forest plant species to colonize the understory of the plantations due to the shaded environment provided in a short time by the rapid growth of hybrid poplars. Our previous work has shown that hybrid poplar plantations have allowed ruderal species to persist in the understories in plantations established on AALs and favored the colonization by these same species in plantations on previously forested sites (Zanin et al., 2025). The abundant presence of ruderal species in plantations may limit the colonization potential of symbiotic microbial species specific to forest species. This was highlighted in the present study, where we observed a correlation between the composition of microbial communities and the presence of non-shade tolerant ruderal species, such as *Poaceae* spp., *Ranunculus* spp. or *Anaphalis margaritacea* for fungi, and *Medicago sativa* or *Fragaria virginiana* for bacteria (Figure 20b and d). To enrich the soil communities of hybrid poplar plantations, it could be interesting to encourage the presence of forest plant species in the understories of plantations. For example, by reducing the intensity of certain silvicultural practices conducive to ruderal species, such as mechanical weeding.

2.5 Conclusion

Fifteen years post-establishment of hybrid poplar plantations, diversity and composition changes induced by afforestation on soil microbiome were more noticeable within fungal communities than bacterial communities. Those differences depended on the site origin of the plantation. Afforestation of AALs, whatever their vegetation stage, caused little change in the soil microbial community compared with the afforestation of previously forested lands, where a significant drop in fungal diversity was observed after plantation establishment. Because the silvicultural work involved in AAL afforestation was lighter than on previously forested sites, we believe this has resulted in less disturbance for the soil microbiome and would therefore be preferred as a target in afforestation programs involving hybrid poplar. Further research could be carried out to study less intense methods of mechanical site preparation, in order to consider the afforestation of these lands as a viable option in regard to the microbial community.

3. CONVERTING ABANDONED AGRICULTURAL LANDS TO PLANTATIONS: EFFECTS ON SOIL ORGANIC CARBON STOCKS

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Résumé

La sylviculture intensive peut assurer une part non négligeable de la production mondiale de bois et ainsi supporter les efforts de préservation des stocks de carbone accumulés dans les écosystèmes forestiers naturels ou peu aménagés. Cependant, il est également essentiel de s’assurer qu’une plantation de peupliers hybrides accumule plus de carbone durant son existence qu’elle n’engendre de perte lors de son établissement, notamment en raison de l’intensité des travaux de préparation de terrain. En outre, la capacité d’une plantation à être un puits ou une source de carbone peut dépendre du stock initial de carbone présent sur le site de la plantation lors de son établissement. Le choix du site s‘avère donc être crucial pour minimiser voire permettre l’accumulation de carbone au sein d’une plantation de peuplier hybride. Notre étude vise à déterminer l’impact sur les stocks de carbone de la litière et du sol du reboisement par du peuplier hybride de 3 types de site d’origine : friche agricole avec un couvert de végétation herbacée; friche agricole arbustive et ancien site de coupe forestière. Nos résultats montrent que les sites forestiers reboisés avec du peuplier hybride ont des stocks de carbone plus faibles que les sites homologues non plantés et que les autres plantations établies sur des friches agricoles. Tandis que ces mêmes plantations sur friches présentent des stocks équivalents à leurs contreparties non reboisées. Les friches agricoles semblent donc être des environnements à privilégier pour profiter du haut rendement des peupliers hybrides tout en préservant les stocks de carbone.

Mots clés : Carbone organique, Sol minéral, Litière, Peuplier hybride, Friche agricole, Chimie du sol

Abstract

Intensively managed fast growing plantations can provide a significant portion of the world's wood biomass and preserve natural or extensively managed forest ecosystems by limiting harvesting pressure and associated disturbances. However, the establishment of plantations should not be at the expense of soil organic carbon stocks, and their potential as a carbon source or sink may depend on their initial stocks prior to planting. The choice of plantation sites is therefore crucial in minimising losses or allowing the accumulation of carbon from a hybrid poplar plantation. The aim of our study was to determine the impact of afforestation with fast growing hybrid poplars on soil carbon stocks of sites of different origins: abandoned agricultural land (AAL) with a herbaceous vegetation cover; shrubby AAL and logged (previously forested) sites. Our results showed that 15 years post-afforestation, previously forested sites where fast growing hybrid poplar plantations were established had lower carbon stocks than their non-afforested equivalents and than other plantations established on AALs, while plantations on AALs had similar carbon stocks to their non-afforested counterparts. AALs would therefore appear to be the preferred establishment site for taking advantage of the high yield of hybrid poplars while preserving soil carbon stocks.

Keywords: Organic carbon, Mineral soil, Litter, Hybrid Poplar, Abandoned Agricultural land, Soil chemistry

3.1 Introduction

Forest soils are an important carbon (C) reservoir, representing more than 40% of the total carbon stored in terrestrial ecosystems (IPCC, 2007; Lal, 2005; Mayer et al., 2020). Preserving and increasing C stocks could help to mitigate the effects of global warming caused by greenhouse gas emissions from fossil fuel combustion (Bossio et al., 2020; IPCC, 2021). Several silvicultural practices can lead to a better management of C stocks (Mayer et al., 2020). For example, soil carbon is more stable after partial than clear cutting (Strukelj et al., 2015) and carbon accumulates more rapidly in plantations and managed forest when nitrogen fertilizers are used or when nitrogen-fixing trees are planted due to the effect of nitrogen inputs on plant growth, litter production and C stabilization (Forrester et al., 2013; Nave et al., 2009). Afforestation of cropland is also a strategy to enhance C sequestration in soils (Bárcena et al., 2014; S. Shi et al., 2016). In conventional agriculture, repeated ploughing, soil exposure and intensive use of fertilizers increase the mineralization rate of organic C leading to its depletion in cropland soils (Del Galdo et al., 2003; Drewniak et al., 2015). Therefore, establishing plantations on agricultural lands might offer a good potential to increase soil carbon stocks by increasing the supply of organic matter to the litter (Guo & Gifford, 2002; Jégou et al., 2000; Laganière et al., 2010). However, transforming prime agricultural land into plantations is not always desirable as it puts food supply in competition with wood-based products (Erb et al., 2012; P. Smith et al., 2013). Instead, marginalized territories such as abandoned agricultural lands (AAL) could be an alternative for afforestation programs (Fayet et al., 2022).

During secondary succession following farmland abandonment, ecosystems gradually evolve from an herbaceous dominated to a shrub dominated state. These ecosystems could ultimately resemble a forest ecosystem, with its associated biodiversity (Chazdon et al., 2020; Plieninger et al., 2014; Wilson et al., 2017) and services such as carbon sequestration (Bell et al., 2021; Kämpf et al., 2016; Wertebach et al., 2017). Conversely, plantation establishment requires the use of mechanical site preparation techniques such as scarification, mounding or stump and wood debris removal (Löf et al., 2012). The disturbance caused by these methods in addition to the lack of vegetation cover during the first few years could break the progression of the secondary succession and lead in the short to medium terms to C loss from increased decomposition rates of organic matter (Ameray et al., 2021; Chazdon et al., 2020; Guo & Gifford, 2002).

A meta-analysis by Guo et al. (2021) highlighted a greater gain from afforestation of barren lands than that of croplands or pastures because of their low initial stocks of soil C. However, they had grouped very different types of environments in the category of “barren lands”, such as abandoned farmlands, sand dunes or degraded lands. Other studies focusing only on agricultural lands have shown by modelling or by *in situ* measurements that afforestation of AALs resulted in greater accumulation of soil carbon than passive regeneration relying on natural vegetation invasion (Fradette et al., 2021; Tremblay & Ouimet, 2013). However, in both studies, comparisons were made with recently abandoned agricultural lands. In contrast, Thibault et al. (2022) studied afforested AALs of different ages to show that non-afforested AALs harboured greater soil C stocks than AALs planted with white spruce (*Picea glauca [(Moench) Voss]*). The use of a coniferous species in afforestation could explain these results as they are often less effective for soil C sequestration than deciduous trees (Guo & Gifford, 2002; Thibault et al., 2022). Fast-growing tree species such as hybrid poplars are also heavily used in afforestation programs for their fast growth rates that sequester large amounts of C in their above-ground biomass (Arevalo et al., 2011; Bazrgar et al., 2022; Winans et al., 2015). In addition, the output of these plantations can be a substitute for numerous fossil fuel products such as biomass for bioenergy (Davis, 2008). Unfortunately, little is known on the capacity of hybrid poplar plantations to sequester organic carbon in the soil after establishment on AALs.

While AALs are potential targets for the establishment of hybrid poplar plantations, it is also common to establish hybrid poplar plantation on previously forested sites such as old harvest sites with this species (Chomel et al., 2014; Royer-Tardif et al., 2018; Trottier-Picard et al., 2016). As forest soils are considered to be richer in organic carbon than agricultural soils (Jackson et al., 2017), we can assume that initial carbon stocks before planting differ between previously forested sites and AALs. In addition, AALs exist at different stages of succession. As AALs accumulate carbon during secondary succession after the cessation of agricultural activity (Bell et al., 2021; Wertebach et al., 2017), a more recent AAL with herbaceous vegetation will potentially be less rich in SOC than a more advanced AAL with shrubby vegetation. Organic carbon stocks within a plantation can therefore be expected to depend on the site chosen for afforestation. Improving our knowledge on the effects of site origin on carbon stocks in hybrid poplar plantations is crucial to enable us to select the best suited sites to accumulate soil carbon following afforestation. Lastly, organic carbon is unevenly distributed between the organic and mineral layers, and is distributed along a depth gradient where carbon concentration decreases as one progresses towards the lower layers (Jackson et al., 2017; Jobbágy & Jackson, 2000). The conversion of agricultural lands to plantations mainly impacts the first 10 cm of mineral soil with few effects at deeper layers (Bárcena et al., 2014; S. Shi et al., 2016, p. 201). However, some results have shown that deeper layers can also accumulate carbon over the longer term, for example 50 years after planting (Zak et al., 1990).

The present study aimed to investigate the effects on soil carbon in organic and mineral soil layers at different depths of afforesting AALs that are at different vegetation stages (herbaceous vs shrubby) and previously forested sites with intensively managed hybrid poplar plantations. We expected that the rapid growth rate of hybrid poplars would lead to greater carbon sequestration in the soils of plantations than in non-afforested lands of the same type despite the disturbances linked to plantation establishment and initial weed control. We hypothesized that the carbon gain would be greater in afforested herbaceous AALs, intermediate in afforested shrubby AALs and lowest in plantations established in previously forested lands. Finally, we thought that organic carbon stocks would mainly be affected within the organic soil and the superficial layer of the mineral soil as the short rotation time of hybrid poplars does not allow time for organic carbon to migrate to the deeper soil horizons.

3.2 Materials and methods

3.2.1 Study site

Our study took place in Abitibi-Témiscamingue, a region of the Canadian province of Quebec (Figure 23). This region is characterized by a flat topography and the presence of the Quebec-Ontario clay belt formed by the glaciolacustrine deposits from the glacial lake Barlow-Ojibway (Vincent & Hardy, 1977). We had at our disposal 16 hybrid poplar (PEH) plantations established between 2003 and 2009 with the clone 915319 (*Populus maximowiczii* x *Populus balsamifera*), associated with a neighbouring non-afforested area (Figure 23, Annexe C-Table S1). Before plantation establishment, eight of our sites were AALs with herbaceous-like vegetation with scarce shrubs; four were AALs mostly covered with a shrubby-like vegetation with patches of *Alnus* spp., *Salix* spp. and few deciduous trees like paper birch (*Betula papyfera [Marshall]*) and/or poplars (*Populus* spp.); and four were poorly regenerated forest cut blocks located in the balsam fir -yellow birch and balsam fir-paper birch bioclimatic zones. These site origins will be referred to in this study respectively as herbaceous AAL, shrubby AAL and previously forested land. Discussions with the landowners, observations in the field and previous studies allowed us to obtain information on the state of the sites before planting. Among our sites, mean annual temperature ranged from 0.1 °C to 2.8 °C and mean annual precipitation from 785.1 mm to 950 mm (Government of Canada, 2024).

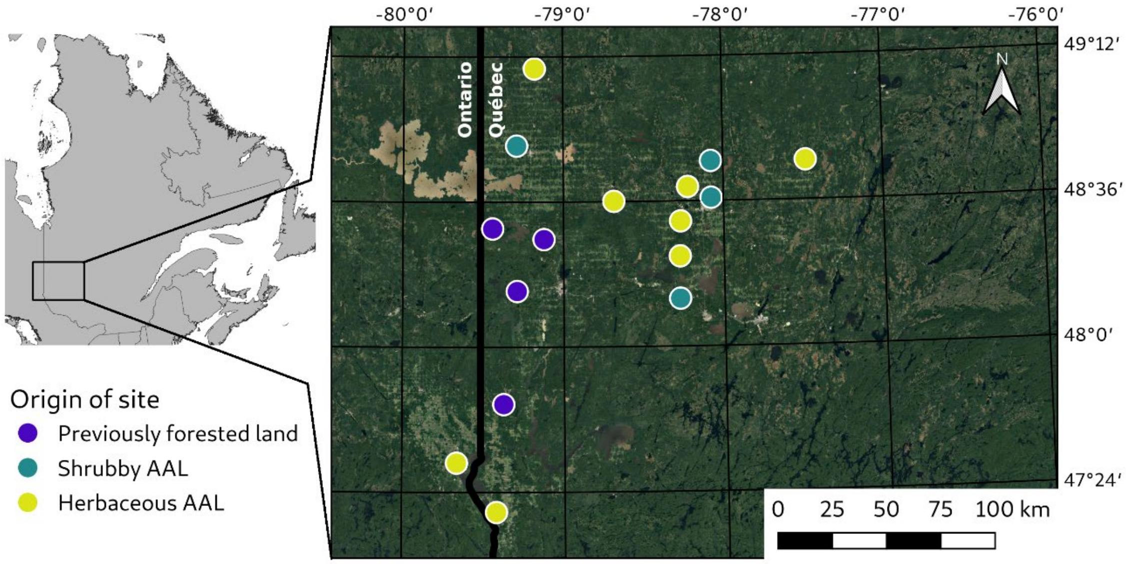


Figure 23
Map showing our 16 study sites and their origin within the province of Quebec.

3.2.2 Soil and litter sampling

The sampling campaign took place during the summer of 2022. In each site we selected 12 sampling points, six in the hybrid poplar plantation and six in the non-afforested area. Those sampling points were selected randomly but placed at equidistance from two trees within a row in the plantations. At each sampling point, we sampled the litter in a 177 cm² area containing dead vegetation and the L, F and H layers (Litter, Fermentation and Humus). Throughout the manuscript, the term litter will refer to layers L, H, and F, as well as plant and wood debris. Then, with a manual auger, we sampled 3 carrots of 15 cm from mineral soil at different depths (0-15 cm, 15-30 cm and 30-45 cm). We grouped our samples into plastic bags to form a composite sample for each soil layer, one for the hybrid poplar plantation, and one for the non-planted area. With 16 sites, one plantation and one non-afforested area par site and 4 soil layers, we collected a total of 128 samples. The samples were stored in a cooler for transport to the lab, where they were stored at -20°C, pending further analysis. In addition to soil sampling, we measured the diameter at breast height (dbh) of hybrid poplars to estimate carbon and nitrogen content within their biomass.

3.2.3 Laboratory

Samples were thawed at room temperature, then oven-dried during 48h for litter samples or air-dried for two weeks in a greenhouse for soil samples. Once dried, samples were ground with a Humboldt hammer mill (Dayton Electric Mfg. Co., USA) and sieved through a 2 mm mesh. No significant proportion of coarse materials (organic or non-organic) were found in our soil samples during sieving. We measured mineral soil pH using the electrometric method in deionized water with a soil-to=solution ratio of 1:1 (Government of Quebec, 2023). The soil texture (Annexe C-Table S1) was assessed in samples from the first layer of mineral soil (0-15 cm) with a hydrometer (Bouyoucos, 1962) based on the size classes from the Canadian Soil Classification Working Group (1998): sand (50–2000 µm); coarse silt (20–50 µm); fine silt (5–20 µm); clay (0–5 µm). Due to a carbon content in excess of 5%, granulometry of the sample from the non-afforested area of the SD site could not be carried out. Being adjacent to the plantation, we considered the soil texture of this sample to be similar to that of the plantation. Concentrations in exchangeable cations in mineral soil

(P, K, Ca and Mg) were obtained by Mehlich-3 method (Mehlich, 1984). Sub-samples were ground more finely using a ball grinder (MM301, Retch, Germany) and sieved through a 250 µm mesh for total C and N determination by dry combustion (CR-412, LECO Inc., USA). Total C was considered equal to organic carbon in most of our samples, except for 12 with a pH above 7. To distinguish organic from inorganic carbon, we treated 5g sub-samples with LECO’s default hydrochloric acid method to eliminate the carbonates present, then reanalysed the quantity of carbon by dry combustion to obtain the organic C concentrations.

3.2.4 Computing

The Dutch auger we used for our sampling did not allow us to accurately measure the volume of the samples collected and therefore their bulk-density. We used the following equation [1] to compute bulk density (D_b) based on the study of Federer et al., (1993).

$$D_b = \frac{(b_1 \times b_2)}{\left(\frac{b_1 \times [C]}{1000}\right) + \left(b_2 \times \left(\frac{1 - [C]}{1000}\right)\right)} \qquad \text{(Eq. 1)}$$

Where b_1 and b_2 are respectively equal to 1.460531 and 0.106068 and [C] is equal to total carbon concentration in g.kg^{-1}. The soils at our sites all contain more than 40% clay and are categorized as clay/heavy clay soils (Annexe C-Table S1). Nédelec (ND) site is the only exception but still had a high proportion of clay (18% for the plantation and 37% for the non-afforested area). To estimate the parameters b_1 and b_2, we followed the study of Thibault et al. (2022), whose samples also came from the Quebec-Ontario clay belt and had similar characteristics to ours. The database is available on line (Thiffault et al., 2022). We also used the same values of b_1 and b_2 for all soil horizons.

We estimated carbon and nitrogen stocks in each layer of the mineral soil and in the litter by following the equations [2] and [3] respectively.

$$Q_{soil} = 0.1 \times D_b \times [Q_{soil}] \times E \qquad \text{(Eq. 2)}$$

Where Q_{soil} is equal to mineral soil carbon or nitrogen stocks in $Mg.ha^{-1}$, D_b is equal to the bulk density computed in equation [1], $[Q_{soil}]$ is the concentration of carbon or nitrogen in $g.kg^{-1}$ in the mineral soil and E is the thickness of the layer in cm.

$$Q_{lit} = \frac{0.1 \times [Q_{lit}] \times W_{dry}}{S} \qquad \text{(Eq. 3)}$$

Where Q_{lit} is equal to litter carbon or nitrogen stocks in $Mg.ha^{-1}$, $[Q_{lit}]$ is the concentration of carbon or nitrogen in the litter, W_{dry} is the dry litter mass in g and S is the sampled area in cm².

We used allometric equations to estimate the dry aboveground biomass (A_b) of hybrid poplars within plantations with equation [4] from Truax et al. (2014). We applied a 0.49 factor to the computed dry biomass to obtain the C content within the hybrid poplars (Matthews, 1993).

$$A_b = 0.0937 \times dbh^{2.3499} \qquad \text{(Eq. 4)}$$

Where dbh is the diameter at breast height.

We calculated cumulative soil carbon stocks in plantations and non-afforested areas by summing the stocks present in litter and mineral soil at depths of 0-15 cm, 15-30 cm and 30-45 cm. For plantations only, we also calculated cumulative carbon stocks by taking into account the stocks present in the above-ground biomass of hybrid poplars for inter-plantation comparisons.

3.2.5 Statistical analysis

To test the effect of afforestation with hybrid poplars on soil carbon by site origin, we completed an analysis of variance (ANOVA) for a fitted mixed model. We built mixed models with the R package “lme4” (Bates et al., 2015) for each soil layer including litter and for each studied response variable independently (Table 11). Site was included as a random effect, while afforestation and site origin were fixed effects. For models analysing cumulative C and C stocks in mineral soils, litter and PEH, we added the clay percentage measured in the 0-15 cm soil layer as co-variable. Models were checked with diagnostic plots for normality and homoscedasticity of residuals and of random effect using the R functions plot, qqnorm, qqline and ranef from “stats” and “lme4” packages (Bates et al., 2015; R Core Team, 2023). No transformation was needed to respect the ANOVA postulate. We use the package “emmeans” to perform pairwise tests with a significance level of $p<0.05$ (Lenth et al., 2024). We carried out a principal component analysis (PCA) including the concentrations of carbon, nitrogen, phosphorus, potassium, calcium, magnesium and pH by first standardising our data using the “scale” function in R and then performing PCA using the “prcomp” function in R stat. We tested if our studied factors affected the soil properties by performing a multivariate analysis of variance with permutations (PermANOVA; McArdle & Anderson, 2001) with the adonis2 function (999 permutations, package “vegan”). The variable site was set as strata. The distance matrix was calculated with the function “vegdist” from “vegan” and the euclidian method (Oksanen et al., 2025).

Analyses presented in this study were carried out using R 4.3.1 (R Core Team, 2023), visual representation using the R packages ggplot2 and cowplot (Wickham, 2016; Wilke, 2024)

3.3 Results

3.3.1 Carbon stocks

Changes in organic carbon stocks resulting from the establishment of hybrid poplar plantations could only be observed in the litter and the first 15 cm of the mineral soil, and depended on site origin (Figure 24). Plantation establishment in previously forested sites led to a decrease in carbon stocks within the litter and the 0-15 cm horizon, compared with their non-afforested counterparts. The litter in plantations had mean SOC stocks of 14.1 $Mg.ha^{-1}$ *vs* 29.6 $Mg.ha^{-1}$ for non-afforested areas, while the 0-15 cm horizon contained 26.6 $Mg.ha^{-1}$ in plantations *vs* 49.4 $Mg.ha^{-1}$ in the non-afforested areas. In sites originating from AALs, SOC stocks were similar between plantations and non-afforested areas (Figure 24). The SOC stock differences we observed in litter and in the first 15 cm of mineral soil were also reflected in the cumulative carbon stocks that were lower in plantations of previously forested sites compared to their non-afforested equivalent, with 80.3 $Mg.ha^{-1}$ *vs* 122 $Mg.ha^{-1}$ of carbon accumulated in the litter and the first 45 cm of mineral soil (Figure 25). This result was not observed between plantations and non-afforested areas of sites originating from AALs. Cumulative carbon stocks within plantations, including those of the three mineral soil horizons, litter and above-ground biomass of hybrid poplars, varied with site origin (Figure 26). Of the 3 site origins studied, plantations on previously forested sites showed lower cumulative stocks compared with plantations in shrubby and herbaceous AALs, with a total value of 94.8 Mg.ha^{-1} compared with 143.4 Mg.ha^{-1} for plantations on herbaceous and shrubby AALs.

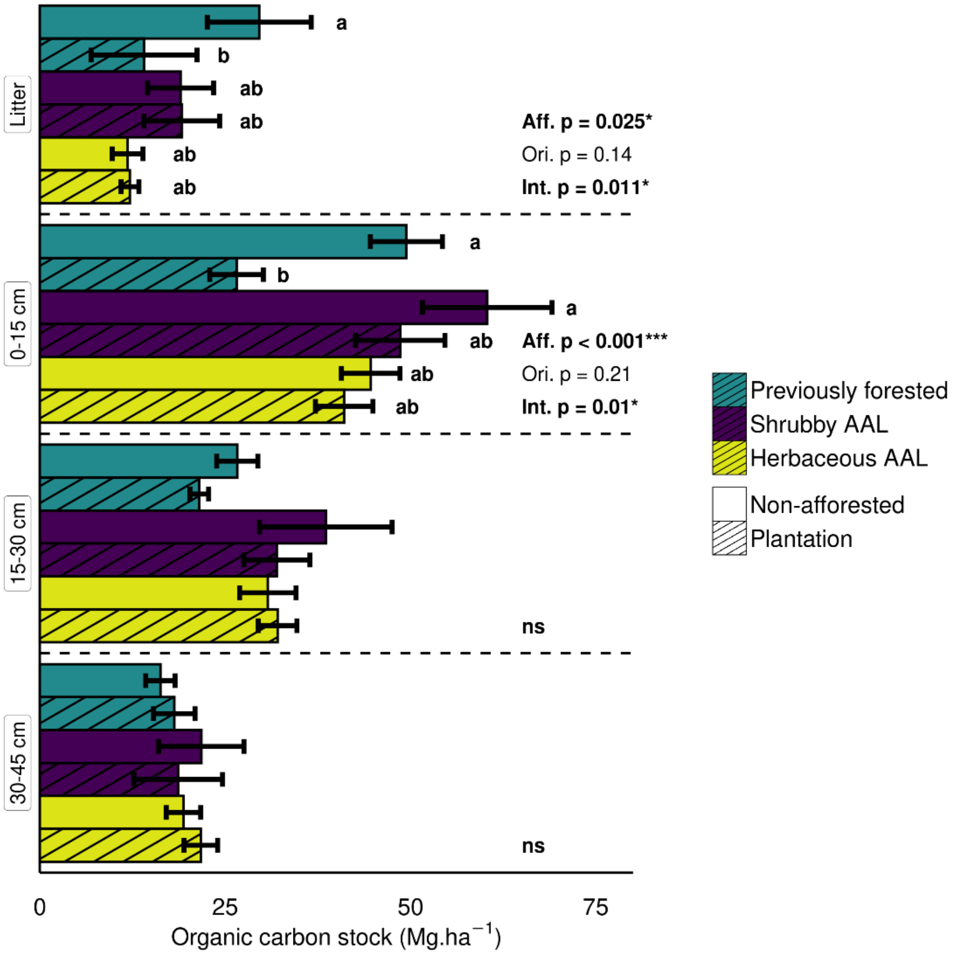


Figure 24
Bar plot representing carbon stocks within litter and three layers of mineral soil (0-15 cm, 15-30 cm and 30-45 cm) for hybrid poplar plantations and non-afforested areas by site origin. Whiskers indicate the mean ± standard error. ANOVA results are shown if significant (* = p<0.05, ** = p<0.01, *** = p<0.001, ns = non-significant) for each studied factor (Aff. = afforestation, Ori. = site origin, Int. = interaction). Different lowercase letters indicate significant difference at p<0.05 for pairwise test.

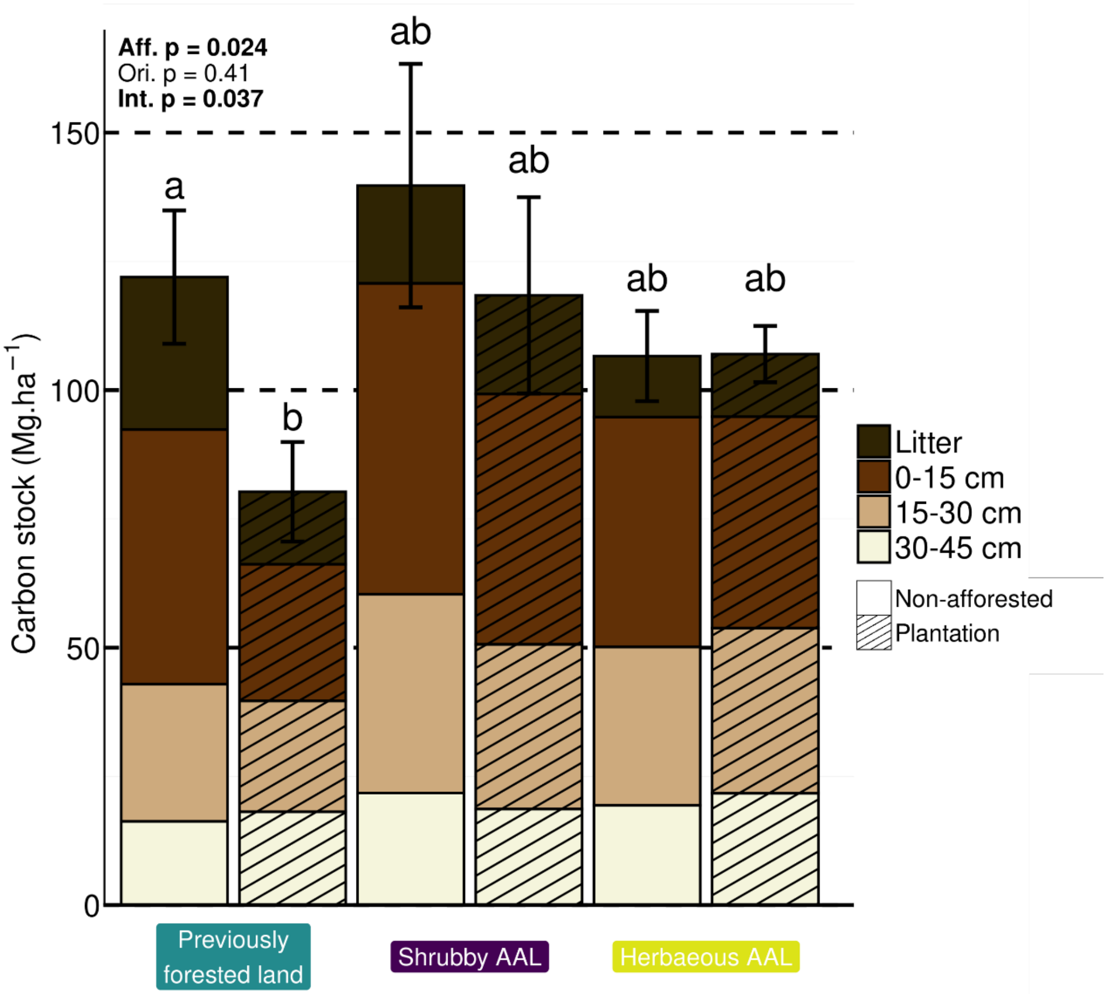


Figure 25
Bar plot representing cumulative stocks of organic carbon in organic and mineral soil at different depths of hybrid poplar plantation and non-afforested areas. Whiskers show mean ± standard error on total cumulative stocks. ANOVA results are shown in bold when $p<0.05$ for each studied factor (Aff. = afforestation, Ori.= Site origin, Int. = Interaction). Different lowercase letters indicate significant difference at $p<0.05$ for pairwise tests.

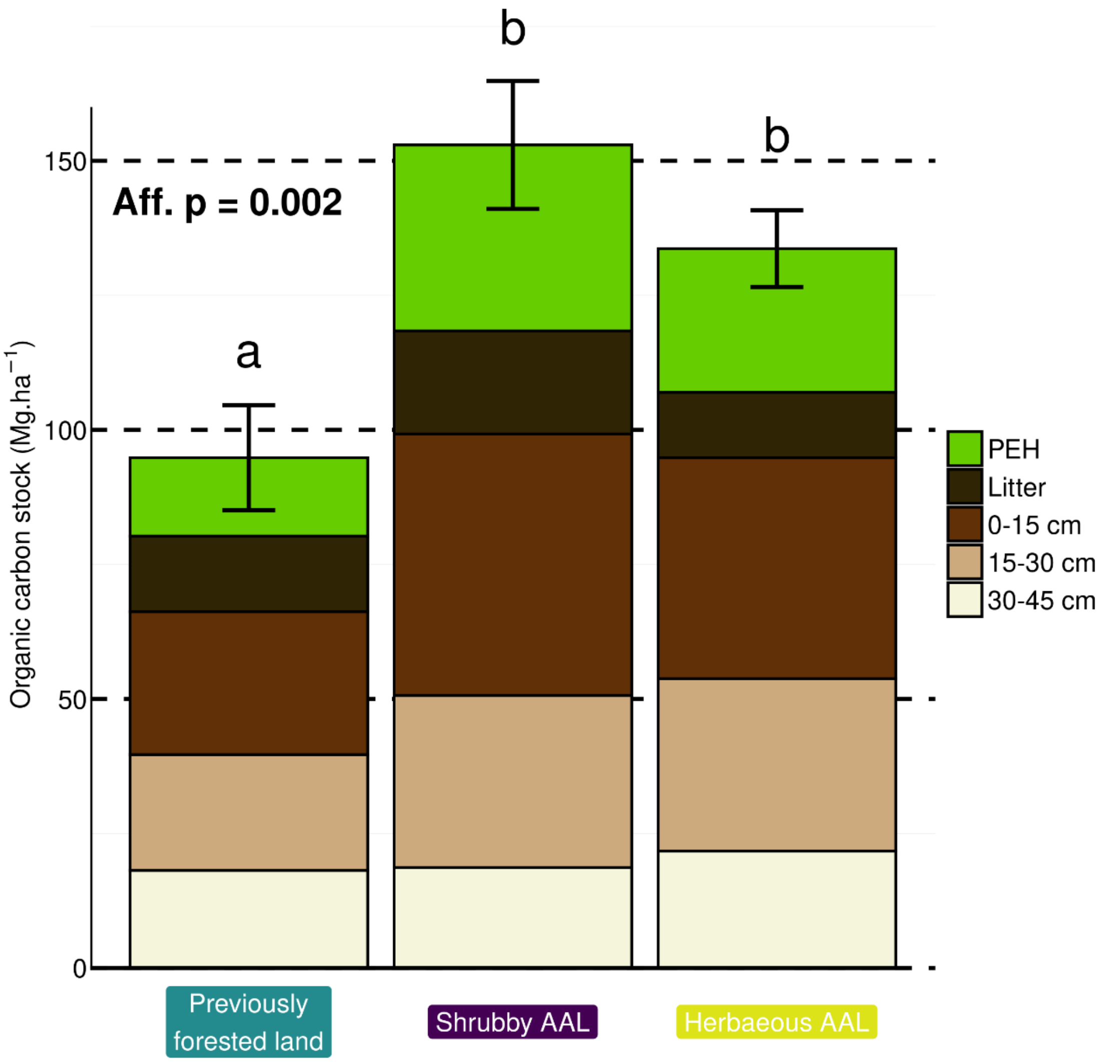


Figure 26
Bar plot representing cumulative stocks of carbon in aboveground biomass of hybrid poplar (PEH), litter and three layers of mineral soil (0-15 cm, 15-30 cm and 30-45 cm) within plantations. Whiskers show mean ± standard error on total cumulative stocks. ANOVA result is shown within the plot (Aff. = afforestation). Different lowercase letters indicate significant difference at $p<0.05$ for pairwise tests.

3.3.2 Litter attributes

Carbon concentrations in the litter of hybrid poplar plantations was similar to that measured in the litter of non-afforested areas adjacent to the plantations, whatever the site origin of the plantations (Table 10). Afforestation with hybrid poplars led to a decrease in nitrogen concentration compared to non-afforested areas, and this decrease was observed for plantations originating from previously forested lands, shrubby AALs and herbaceous AALs (Table 10). However, this decrease in nitrogen concentration did not impact C:N ratios which remained similar between plantations and non-afforested areas (Table 10). The dry mass of litter collected in our sample areas was negatively affected by the establishment of hybrid poplar plantations in previously forested sites only (Table 10).

Table 10
Litter organic carbon, nitrogen, C:N ratio and dry mass (mean±SE) in hybrid poplar plantations (Aff) and non-afforested areas (NF). Lowercase letters in parentheses indicate a significative difference ($P<0.05$) between groups.

Site Origin	Type	OC ($g.kg^{-1}$)	N ($g.kg^{-1}$)	C:N	Dry litter mass ($kg.m^{-2}$)
Forest	NF	283±35.4	13.5±1.9 (a)	21.2±1.6	11.6±4.2 (a)
	Aff	206±47.9	7.38±1.2 (b)	27.25±3.2	6.0±1.8 (b)
S AAL	NF	299±35.5	9.82±0.87 (a)	30.37±2.1	6.7±1.7 (ab)
	Aff	322±10.5	9.6±0.36 (b)	33.52±0.50	5.9±1.5 (ab)
H AAL	NF	338±24.3	11.97±1.1 (a)	29.01±2.5	3.4±0.51 (b)
	Aff	290±19.2	8.32±0.65 (b)	36.18±3.4	4.3±0.55 (b)

OC: Organic Carbon; N: Nitrogen; S: Shrubby; H: Herbaceous; AAL: Abandoned Agricultural Land

3.3.3 Mineral soil biochemical properties

Phosphorus, calcium and magnesium concentrations were similar between afforested and non-afforested areas in all soil horizons, and were unaffected by site origin (Table 11). Potassium concentrations varied between afforested and non-afforested areas depending on site origin, revealing a significant interaction between afforestation and site origin. Potassium tended to increase in afforested herbaceous AALs while it tended to decrease in afforested shrubby AALs or previously forested lands, but differences were small and failed to be significantly detected by our pairwise tests

(Table 11). The concentrations in organic carbon and nitrogen decreased while soil bulk density of mineral soil increased by afforestation with hybrid poplars, but only in the 0-15 cm horizon and only for plantations on previously forested sites (Table 11). Soil pH increased by afforestation in the first 15 cm mineral soil layer for sites of all origins (Table 11).

The multivariate analysis of our study shows the distribution of our sampling zones according to their origin and whether they were afforested with hybrid poplar or not (Figure 27). The first and second axes represented respectively 39.7% and 27.2% of the variability in the dataset. Soil pHh, magnesium and calcium concentrations were mostly associated with the first axis with loadings respectively of -0.4, -0.4 and -0.53. Nitrogen and soil organic carbon were principally associated with the second axis with loadings respectively of -0.49 and -0.56. The ordination shows that plantations and non-afforested areas from both shrubby and herbaceous AALs sites were more variable than those from previously forested sites, particularly hybrid poplar plantations, illustrating the variability in the chemical composition of mineral soil in formerly agricultural sites. Plantations from previously forested sites were also associated with low concentrations of potassium, organic carbon and nitrogen (Figure 27). Soil properties were affected by both afforestation and site origin independently, without an interaction effect (Table 12).

Table 11
Soil physico-chemical properties (mean±SE) in hybrid poplar plantations (Aff) and non-afforested areas (NF). Lowercase letters in parentheses indicate a significative difference ($P<0.05$).

Strate	Site origin	Type	P (mg.kg^{-1})	K (mg.kg^{-1})	Ca (mg.kg^{-1})	Mg (mg.kg^{-1})	SOC (g.kg^{-1})	N (g.kg^{-1})	C:N	Bd (g.cm^{-3})	pH
0-15	Forest	NF	11.0±2.48	201±33.7	1766±469	402±102.4	32.3±4.6 (a)	2.22±0.38 (a)	14.7±0.6	1.04±0.04 (a)	5.37±0.10 (a)
		Aff	8.8±1.03	168±36.6	1837±602	442±173.6	14.5±2.2 (b)	0.88±0.09 (b)	16.3±1.1	1.23±0.03 (b)	5.72±0.19 (b)
	S.AAL	NF	11.0±2.16	210±36.4	1877±851	370±89.5	44.8±9.6 (a)	2.67±0.43 (a)	16.3±1.0	0.95±0.07 (a)	5.57±0.29 (a)
		Aff	8.5±1.32	188±30.4	1983±871	403±82.0	31.8±5.4 (ab)	2.02±0.29 (ab)	15.5±0.8	1.05±0.05 (ab)	5.76±0.29 (b)
	H.AAL	NF	10.3±1.33	182±22.4	2105±416	457±46.1	28.3±3.3 (ab)	2.11±0.25 (ab)	13.6±0.8	1.08±0.03 (ab)	5.82±0.24 (a)
		Aff	10.0±1.31	204±17.6	2383±383	558±63.6	25.3±3 (ab)	1.81±0.21 (ab)	13.9±0.4	1.11±0.03 (ab)	5.95±0.22 (b)
15-30	Forest	NF	13.0±5.21	185±30.4	2226±511	590±73.5	14.5±1.9	0.95±0.18	15.8±1.1 (ab)	1.23±0.02	5.89±0.11
		Aff	7.0±1.47	143±44.0	2497±1131	438±153.9	11.3±0.8	0.68±0.06	17.0±1.4 (ab)	1.28±0.01	6.04±0.26
	S.AAL	NF	7.3±1.11	149±26.2	1969±868	470±125.4	24.3±8	1.27±0.23	17.9±2.2 (a)	1.13±0.08	5.94±0.37
		Aff	8.5±2.72	154±29.3	3361±2087	538±75.8	19±3.19	1.05±0.12	17.1±1.0 (a)	1.19±0.04	6.17±0.44
	H.AAL	NF	8.3±1.05	151±21.5	2290±429	527±53.2	17.6±2.8	1.39±0.26	13.1±0.6 (b)	1.20±0.03	6.16±0.24
		Aff	8.5±0.98	157±10.0	2447±463	576±50.7	18.3±1.9	1.32±0.12	13.8±0.6 (b)	1.19±0.02	6.06±0.22
30-45	Forest	NF	12.5±4.84	181±29.0	2602±525	729±80.9	8.3±1.11	0.68±0.11	12.6±1.1	1.32±0.02	6.23±0.21
		Aff	8.0±2.86	149±46.7	3865±2198	496±169.7	9.4±1.6	0.58±0.13	20.3±6.7	1.31±0.02	6.20±0.35
	S.AAL	NF	7.8±1.93	156±31.2	3485±2010	633±101.3	11.8±3.7	0.58±0.08	19.3±3.2	1.28±0.05	6.45±0.54
		Aff	8.0±2.65	161±34.4	3807±2245	668±76.1	10.0±3.7	0.58±0.15	16.8±2.5	1.30±0.05	6.55±0.45
	H.AAL	NF	7.1±0.87	162±20.1	3120±861	635±49.2	10.1±1.4	0.71±0.10	14.5±0.8	1.30±0.02	6.57±0.25
		Aff	7.5±1.16	159±15.3	3026±816	672±86.6	11.5±1.4	0.81±0.08	14.0±0.8	1.28±0.02	6.40±0.24

P: Phosphorus; K: Potassium; Ca: Calcium; Mg: Magnesium; SOC: Soil Organic Carbon; N: Nitrogen; Bd: Bulk density; S: Shrubby; H: Herbaceous; AAL: Abandoned Agricultural Land

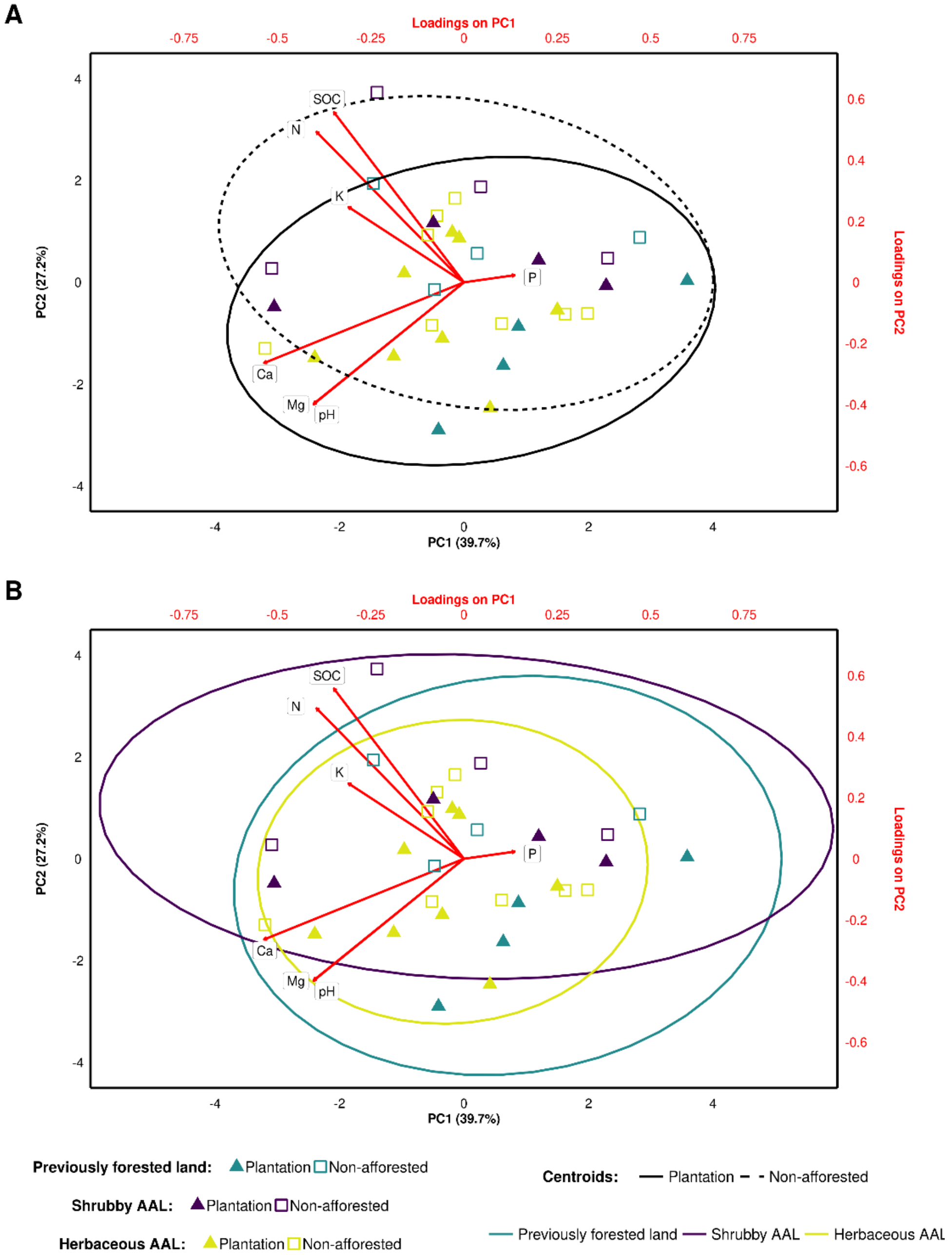


Figure 27
Principal component analysis (PCA) based on the chemical properties of the first layer (0-15 cm) of mineral soil (P = Phosphorus, K = Potassium, Ca = Calcium, Mg = Magnesium, N = Nitrogen, SOC = Soil organic carbon).

Table 12
Summary of the permutational analysis of variance (permANOVA) to test the effects of afforestation and site origin and environmental variables on soil properties (999 permutations). *Indicates a significant effect (p<0.05)

Tested variables	Sum sq	R^2	F	Pr
Afforestation	13.3	0.061	1.92	0.004*
Site origin	16.8	0.076	1.20	0.004*
Afforestation: Site origin	7.29	0.034	0.53	0.28
Residuals	179.8	0.83		

3.4 Discussion

3.4.1 Carbon loss in plantations on previously forested sites

After 15 years, hybrid poplar plantations established on forest cut blocks had lower carbon stocks in the first 15 cm of mineral soil compared with their non-afforested equivalent, while plantations originating from AALs had similar carbon stocks to those found in non-afforested AALs (Figure 24). Establishing hybrid poplar plantations, and more generally plantations of fast-growing species, requires extensive site preparation due to their high nutrient demand and sensitivity to competition (Bilodeau-Gauthier et al., 2011; Thiffault et al., 2020). This most likely results in the mineralization of a significant proportion of the SOC (Egnell et al., 2015). In previously forested sites, soil preparation is more intensive due to the need to remove stumps, branches and residual trees prior to plantation establishment in order to allow the passage of machinery for weed maintenance in the first few years of plantation establishment (Desrochers & Sigouin, 2014). As a result, much of the carbon-rich organic horizon is also removed. Abandoned agricultural lands, especially those with herbaceous vegetation, require less intensive site preparation due to the low proportion or even absence of woody vegetation (usually a simple ploughing), which could explain why no carbon was lost from these soils within plantations compared to their non-afforested counterparts. Plantations established on shrubby AALs had a carbon concentration 40% lower in the first 15 cm of the mineral soil than their non-planted equivalent (Table 11). Despite a non-significant statistical effect, we can highlight a trend which shows that the establishment of plantations on shrubby AALs can also lead to carbon losses. This trend could be explained by an increasing gradient in the intensity of site preparation from herbaceous AALs through shrubby AALs to forested sites leading to, as well, losses in carbonwithin the soil. Further research should be carried out to validate this hypothesis.

Our results showed that litter from our plantations, whatever the site origin, had lower nitrogen concentrations than litter from their non-afforested counterparts (Table 10). Because of their rapid growth, hybrid poplars have an important demand for nutrients, which can lead to a decrease in nitrogen concentration in litter and shallow soil horizons (K. Wang et al., 2021). This may explain the results observed in our study. Herbaceous plant litter is rich in nitrogen with a high decomposition rate (Zhang et al., 2008). The study by Chomel et al. (2016) demonstrated that adding herbaceous litter to hybrid poplar plantations accelerated the rate of decomposition of organic matter, resulting in a greater quantity of assimilable N for the trees. AALs are environments where the vegetation cover is dominated by herbaceous plant species. The difference in nitrogen concentration between plantations and non-afforested areas could therefore be explained, at least in the case of AALs, by an N-rich herbaceous plants litter. Nitrogen-rich litter is conducive to more intense microbial activity, resulting in an accelerated rate of organic matter decomposition and greater C transfers to deeper soil layers (Chomel et al., 2016; Ge et al., 2018). Therefore, a drop in N concentration in the litter can be associated with a reduction in carbon stocks in the lower soil horizons. As the litter is less rich in N, the activity of decomposers is reduced, reducing the transfer of carbon to the mineral soil. However, the decrease in SOC stocks was only observed for plantations established on previously forested sites, where afforestation also led to a significant reduction litter dry mass matter compared to non-afforested counterparts (Table 10). Perhaps the heavier site preparation required to establish fast growing plantations in previously forested sites caused a greater loss of organic matter than in the AALs following the plantation establishment, leading to slower reconstitution of the litter.

3.4.2 Past agricultural use and soil chemical properties

Plantations and non-afforested areas from AALs were a little more heterogeneously distributed on our ordination compared to those from forested sites (Figure 27). Our AALs sites, located in agricultural areas, had varied historical uses: some were cultivated for cereal production, others were cultivated for hay to feed cattle, and some were pastured or may even have had different successive uses before being abandoned. In addition, management and agricultural practices could vary from one farm to another, for example one of our sites was farmed organically, with limited fertilizer and pesticide inputs. Farming activities have a major impact on the physico-chemical properties of soils through tillage, biomass removal and fertilizer applications, and are highly dependent on the type of farming activity practised (Cade-Menun et al., 2017; Omer et al., 2024). Organic farming tends to improve soil quality compared with conventional farming (Gomiero et al., 2011). The same is true for different types of grazing management, where light or moderate management is beneficial for soil properties (Mayel et al., 2021). In addition, the changes induced by the presence of agricultural activity can persist within a plantation several decades after it has been established (Bergès et al., 2017; Nadal-Romero et al., 2016). In this study we investigated the effects of afforestation with PEH on the SOC stocks of AALs at different states of secondary succession (herbaceous-like vegetation and shrub-like vegetation). The variability of soil properties related to the different AALs agricultural histories shows that the afforestation of AALs with hybrid poplar and its consequences on SOC stocks may depend on the type of agricultural activity practised before farmland abandonment. Comparing the effects of plantation establishment on AALs originating from different practices such as cereal cropping, cattle grazing or even organic cropping will provide new useful knowledge to facilitate site selection for plantation.

3.4.3 The future of carbon stocks in poplar plantations

Plantations of fast-growing species such as hybrid poplars are seen as a potential opportunity to sequester carbon and mitigate the effects of climate change, due to their rapid biomass production and high contribution to the litter organic matter (Arevalo et al., 2011; Ménard et al., 2023). Our study showed that, despite the progressive accumulation of carbon in the soil of a secondary succession following the abandonment of agricultural lands, their afforestation with hybrid poplars did not lead to SOC losses in plantations after 15 years, compared with non-reforested AALs. If the sole aim of establishing hybrid poplar fast growing plantations was to sequester carbon in soil horizons, afforestation of AALs would be equivalent to letting secondary succession take its course. However, given the global demand for a renewable, non-fossil fuel-based resource like wood, hybrid poplars can be an important source of woody material while preserving SOC stocks. In addition, intensive silviculture can help reduce wood harvesting pressure in natural carbon-rich forests, such as the boreal forests (Arevalo et al., 2011; Thibault et al., 2022). However, the lifespan of hybrid poplar products such as pulp is generally short, which is not conducive to carbon sequestration in wood products (Arehart et al., 2021; Ménard et al., 2023; Stanton et al., 2002). Developing longer-lasting products from poplar wood would further enhance its capacity to store carbon and mitigate climate change.

Although it has been shown that productivity of different hybrid poplar clones was not related to SOC, differences where observed between clones in their capacity to stock carbon in the soil, probably due to differences in their root traits (Rabearison et al., 2023). Management methods applied to plantations throughout their life can also influence carbon stocks, such as thinning intensity (Lutter et al., 2024) or when the wood will be harvested which can disturb the soil and activate mineralization of SOC also leading to C losses (Berhongaray & Ceulemans, 2015; Yanai et al., 2003). For example, clear-cutting of a poplar plantation in China transformed the plantation into a carbon source for several months after cutting (Gao et al., 2015). While many studies were carried out over the last few decades on C accumulation capacity of fast-growing plantations, few of them focused on the potential carbon losses during harvesting and how they can be mitigated.

3.5 Conclusion

Our study showed that, 15 years after the establishment of hybrid poplar plantations, soil organic carbon (SOC) stocks were similar to those in non-afforested areas in the case of afforestation of abandoned agricultural lands (AALs), whereas afforestation of previously forested sites led to a decrease in SOC stocks in the litter and the first 15 cm of mineral soil. These results are probably due to a more intensive site preparation and biomass removal on previously forested sites than on AALs. Without changes in silvicultural practices within forest sites to limit carbon losses, AALs remain the best choice of site for establishing PEH plantations to take advantage of their high yield while preserving existing carbon stocks. Finally, we believe that herbaceous AALs are a better option due to their less dense vegetation, which requires less intensive clearing and is therefore less likely to result in the mineralisation of organic carbon. However, further research is needed to confirm this.

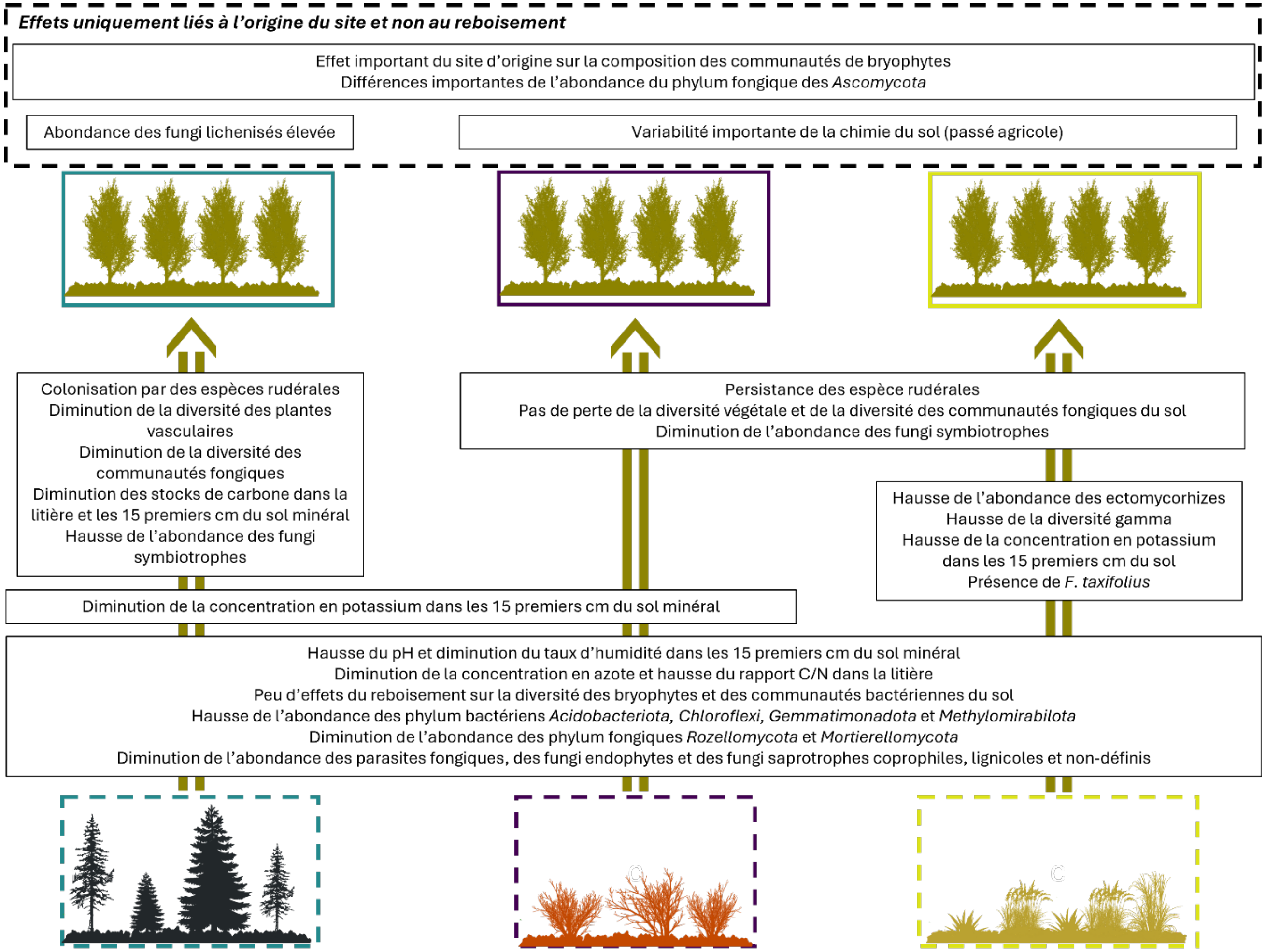
CONCLUSION GÉNÉRALE

Les peupliers hybrides dans un contexte forestier. Reboiser d'anciennes coupes forestières avec du peuplier hybride (PEH) permet de bénéficier du taux de croissance élevé de ces arbres, restreignant la production de bois à des zones réduites, offrant ainsi la possibilité de limiter les prélèvements dans les environnements peu ou pas aménagés de la forêt boréale (Barrette et al., 2014; McEwan et al., 2020; Royer-Tardif et al., 2018). Dans cette thèse nous montrons que l'établissement de peupliers hybrides sur d'anciennes coupes forestières est préjudiciable pour certaines caractéristiques écologiques des plantations. En comparant ces dernières avec des zones adjacentes non reboisées, on constate une perte de diversité des plantes vasculaires dans la végétation du sous-bois et des communautés fongiques du sol ainsi qu'une baisse des stocks de carbone dans la litière et les 15 premiers centimètres du sol minéral (Figure 28). Ces conséquences sont propres au cas des plantations issues de sites forestiers et n'ont pas été observées lors du reboisement de terres agricoles abandonnées. L'un des principaux éléments pouvant expliquer cette disparité est la préparation de terrain effectuée avant l'établissement de la plantation. Ces pratiques perturbent le microclimat du sol accélérant la décomposition de matière organique et la minéralisation du carbone (Cao et al., 2022; Egnell et al., 2015; Šebesta et al., 2021). Or, les préparations de terrain sont plus intenses en milieu forestier, car il est nécessaire de retirer du site les résidus de coupe, les souches et la végétation ligneuse restante afin de pouvoir faire circuler la machinerie qui sera utilisée pour l'entretien intensif des plantations. Contrairement à ce que notre hypothèse, la croissance rapide du peuplier hybride n'a pas permis de compenser cette perte et de reconstituer le couvert de matière organique ainsi que les stocks de carbone perdu à la suite des perturbations pré-plantation. L'intensité de la préparation de terrain a probablement également joué un rôle dans la baisse de diversité fongique au sein des plantations. En effets, ces organismes sont plus sensibles que les bactéries aux perturbations de leur milieu en raison de leur stratégie de vie principalement basée sur des stratégies de conservation plutôt que de reproduction (Fierer et al., 2007).

À l'instar des plantations établies sur des friches agricoles, la végétation du sous-bois des plantations sur d'anciennes coupes est principalement composée d'espèces rudérales adaptées à des milieux ouverts et perturbés. Contrairement à nos hypothèses initiales, les conditions de sous-bois propices aux espèces forestières amenées par la formation rapide de la canopée des peupliers n'ont pas permis la colonisation des plantations par des espèces tolérantes à l'ombre. Les plantations de peuplier hybride offrent donc des environnements propices à l'épanouissement d'espèces rudérales adaptées aux milieux perturbés et intolérantes à l'ombre. À la lumière de ce qui précède, il semble logique d'observer une baisse de diversité lorsqu'elles sont établies sur d'anciennes coupes forestières. En effet, ces plantations sont entourées par des environnements forestiers où les espèces rudérales sont absentes tandis que celle établie sur des friches sont proches d'autres milieux riches en espèces rudérales. L'absence d'une source proche de graines et propagules d'espèces susceptibles d'évoluer dans la plantation a visiblement limité les possibilités de colonisation et ainsi fait des plantations sur d'anciens sites forestiers des environnements peu riches et peu diversifiés en plantes vasculaires.

Bien que les désavantages soient nombreux à l'établissement de plantations de PEH dans les environnements forestiers, on a observé une abondance importante de champignons appartenant à la guilde des champignons lichenisés et l'étude de Randriamananjara et al. (2023) montre également une diversité importante de lichen dans les plantations. Cela suggère que les peuplements de PEH peuvent être des refuges pour ces espèces en milieux forestiers. De plus, le mode de dispersion des lichens est basé principalement sur une reproduction sexuée et la propagation de spores (Murtagh et al., 2000; Ronnås et al., 2017). Une étude approfondie des lichens permettrait de confirmer la nature de refuge des plantations de PEH en forêt pour ces organismes tout en permettant de comprendre les dynamiques de colonisation d'espèces depuis les environnements bordant la plantation.

À l'aune des résultats présentés dans cette thèse, le reboisement de sites forestiers n'est a priori pas souhaitable. Est-il tout de même possible d'envisager une poursuite de l'établissement de plantations de peuplier hybride après coupes forestières dans des environnements forestiers ? Une piste de réflexion serait de repenser les méthodes de préparation de terrain afin de limiter les pertes en carbone lors de cette transition cruciale vers une plantation. On peut envisager de réduire l'intensité des méthodes de préparation de terrain ou bien incorporer de la matière organique aux horizon plus profonds pour stabiliser le carbone organique (Ameray et al., 2021; Mayer et al., 2020). Ensuite certains hybrides de peuplier sont réputés pour leur capacité de résistance et de croissance confrontés à un stress. Ces hybrides pourraient être envisagés comme solution de reboisement là où les conditions environnementales sont trop stressantes pour les essences natives de la forêt boréale.



Effets uniquement liés à l'origine du site et non au reboisement

Effet important du site d'origine sur la composition des communautés de bryophytes
Différences importantes de l'abondance du phylum fongique des *Ascomycota*

Abondance des fungi lichenisés élevée

Variabilité importante de la chimie du sol (passé agricole)

Colonisation par des espèces rudérales
Diminution de la diversité des plantes vasculaires
Diminution de la diversité des communautés fongiques
Diminution des stocks de carbone dans la litière et les 15 premiers cm du sol minéral
Hausse de l'abondance des fungi symbiotrophes

Persistance des espèce rudérales
Pas de perte de la diversité végétale et de la diversité des communautés fongiques du sol
Diminution de l'abondance des fungi symbiotrophes

Hausse de l'abondance des ectomycorhizes
Hausse de la diversité gamma
Hausse de la concentration en potassium dans les 15 premiers cm du sol
Présence de *F. taxifolius*

Diminution de la concentration en potassium dans les 15 premiers cm du sol minéral

Hausse du pH et diminution du taux d'humidité dans les 15 premiers cm du sol minéral
Diminution de la concentration en azote et hausse du rapport C/N dans la litière
Peu d'effets du reboisement sur la diversité des bryophytes et des communautés bactériennes du sol
Hausse de l'abondance des phylum bactériens *Acidobacteriota, Chloroflexi, Gemmatimonadota* et *Methylomirabilota*
Diminution de l'abondance des phylum fongiques *Rozellomycota* et *Mortierellomycota*
Diminution de l'abondance des parasites fongiques, des fungi endophytes et des fungi saprotrophes coprophiles, lignicoles et non-définis

Figure 28
Schéma bilan résumant les résultats du présent manuscrit.

Les friches agricoles et leur reboisement avec du PEH. À la suite de l'abandon d'une terre agricole, une succession secondaire se met en place, faisant évoluer l'écosystème d'une friche herbacée vers une friche arbustive et peut à terme, permettre la reconstitution d'un écosystème forestier (Ustaoglu & Collier, 2018). Progressivement, la diversité végétale s'accroit du fait de la colonisation du milieu par de nouvelles espèces, le microbiome s'enrichit d'espèces fongiques et le carbone organique s'accumule dans la litière et les horizons superficiels du sol. Les perturbations induites par l'établissement d'une plantation de peuplier hybride sont susceptibles d'être délétères pour la biodiversité et les stocks de carbone. Cela soulève donc des interrogations quant à la nécessité de transformer les friches agricoles en plantations intensives de peuplier hybride. Notre étude montre que pour la majorité des variables étudiées, les plantations de PEH restaient proches de leur équivalent non reboisé (Figure 28). Le reboisement n'a pas engendré de pertes de carbone, ni de diminution de richesse et de diversité au sein des communautés de plantes vasculaires, des bryophytes et des communautés microbiennes du sol. Comme évoqué dans la section précédente, la préparation du site avant la plantation est moins intense sur les sites issus de friches agricoles, en particulier pour les friches herbacées, car peu de débris de végétation nécessitent d'être retirés. Cette faible intensité de perturbation a limité l'impact sur le carbone organique et les communautés microbiennes du sol. Le peu de différences observées entre plantations et friches agricoles environ 15 ans après l'établissement des plantations est peut-être également lié à une diversité biologique et à des stocks de carbone moins importants qu'attendu au sein des friches de notre région d'étude. Nous avions, lors de l'élaboration de nos hypothèses, suggéré que les friches seraient durement impactées par le reboisement de peuplier hybride en raison de l'accumulation de carbone et de la hausse progressive de la diversité végétale au cours de la succession secondaire en nous basant principalement sur des études européennes. En Europe, certaines terres sont cultivées depuis plusieurs siècles, voire millénaires. Ce laps de temps a permis à de nombreuses espèces végétales adaptées aux milieux ouverts de coloniser les environnements agricoles européens pouvant s'épanouir dans les espaces abandonnés (Hampicke, 2006; Queiroz et al., 2014). Dans la région québécoise de l'Abitibi-Témiscamingue, les terres agricoles sont cultivées pour les plus anciennes depuis seulement un siècle, époque correspondant à l'arrivée des premiers colons dans la région. Le nombre d'espèces susceptibles de coloniser les friches est potentiellement faible, ce qui est corroboré par la présence d'espèces européennes rudérales introduites. De plus, le climat boréal de notre région limite la saison de croissance et donc la captation de carbone par la photosynthèse pouvant limiter les capacités de séquestration des friches comparativement à leur homologue européen localisé dans des biomes tempérés. La conduite d'études se focalisant principalement sur l'évolution de la biodiversité et des stocks de carbones au sein de successions secondaires dans les biomes boréaux d'Amérique du Nord permettrait de mieux connaitre ces écosystèmes uniques à mi-chemin entre milieu anthropisé et milieu naturel. Après 15 ans de plantations et au regard des variables étudiées, les friches agricoles semblent être une meilleure cible pour l'implantation de peuplier hybride comparé aux environnements forestiers. Mais quelles friches sont à privilégier pour un reboisement, les friches herbacées ou arbustives ?

Notre choix de distinguer les friches herbacées des friches arbustives repose sur l'hypothèse qu'une friche arbustive, ayant été abandonnée depuis plus longtemps en raison du temps nécessaire au développement d'une végétation arbustive, abriterait des communautés végétales et microbiennes plus diverses et des stocks de carbone plus important, augmentant ainsi l'effet des perturbations liées au reboisement. Mais dans l'ensemble, la majorité des variables étudiées n'ont pas varié significativement entre le reboisement d'une friche herbacée et le reboisement d'une friche arbustive. En raison de l'absence d'éléments nous permettant de juger l'âge exact de la friche, nous nous sommes basés sur l'état de la végétation lors de l'établissement de la plantation en nous informant à l'aide des études précédentes, des récits des propriétaires terriens et de nos observations *in situ*. Cependant, les friches agricoles demeurent des environnements difficiles à catégoriser. Il n'existe pas de définition précise de ce qu'est une friche et la distinction entre friche herbacée et arbustive est nécessairement empreinte de subjectivité. De plus, les friches peuvent présenter des strates de végétation similaire, mais différer par bien d'autres aspects comme la composition spécifique de la communauté végétale ou bien les propriétés du sol. La frontière fine qui existe entre friche herbacée et friche arbustive explique peut-être le peu de différence observée entre le reboisement de friches arbustives et herbacées. Il semble donc peu évident de conclure sur la préférence entre les deux types de friches vues ici pour être l'objet de l'établissement d'une plantation de PEH. Cependant, certains résultats tendent à nous faire penser que la préférence devrait être accordée aux friches herbacées.

Le reboisement des friches herbacées a permis une hausse de l'abondance des ectomycorhizes au sein des plantations comparativement à leurs équivalents non reboisés. Ces champignons forment des associations symbiotiques avec des espèces végétales ligneuses et sont particulièrement abondants dans les milieux forestiers. L'accroissement conséquent de leur abondance lors de la transition entre friches herbacées et plantations est un potentiel signe de la restauration de la friche vers un écosystème forestier. Nous avons également démontré que la diversité végétale à l'échelle du paysage des plantations sur friches herbacées (diversité gamma) y était plus importante comparé à leur équivalent non reboisé et comparé aux plantations sur friches arbustives. Nos sites de friches agricoles herbacées, donc abandonnées plus récemment, évoluent dans un paysage varié ou l'on compte des terres agricoles toujours exploitées, d'autres friches à différents stades dans leur succession secondaire et des correctifs forestiers. L'influence des différents environnements a certainement contribué à une forte diversité gamma tandis que les friches arbustives étaient principalement voisines par des milieux homogènes. Enfin, notons que les plantations issues de friches herbacées peuvent être un habitat pour certaines espèces rares comme *Fissidens taxifolius*, une espèce de bryophyte dont nos observations sont les plus septentrionales de la province du Québec à ce jour.

Le bon choix du clone. Nous nous sommes concentrés sur un seul clone de peuplier hybride pour notre étude, le 915 319 issu du croisement d'un peuplier baumier et d'un peuplier du japon (*Populus balsamifera x P. Maximowiczii)*. Nous avons sélectionné ce peuplier, car il offre l'un des meilleurs rendements pour notre région d'étude. Si l'objectif de productivité est le seul considéré pour l'établissement d’une plantation, il semble alors logique de privilégier le clone offrant le taux de croissance le plus élevé pour le site ciblé. Néanmoins si l’on cherche également à minimiser l’impact du reboisement, voir même à favoriser la séquestration de carbone, la diversité végétale et la diversité du microbiome du sol alors d’autres facteurs sont à prendre en considération dans le choix du clone. En raison de la variabilité des traits racinaires entre différents clones de peupliers hybrides, ces derniers peuvent posséder des capacités de séquestration de carbone différentes qui ne sont pas corrélées à leur productivité (Rabearison et al., 2023). De plus, la présence d’un parent exotique dans l’ascendance du clone peut influencer d’autres aspects de notre étude comme la qualité de la litière ou la composition du microbiome. L’un des principaux processus d’accumulation du carbone dans le sol est l’apport à la litière. Si l’apport provient d’espèces exotiques, il est possible que la décomposition de la matière organique de la litière et donc son transfert vers les horizons plus profond du sol soient ralentis en raison de la non-adaptation du microbiome local à décomposer la litière de l’espèce exotique (Chomel et al., 2016). Il en va de même pour la composition du microbiome car de nombreux microorganismes forment des relations symbiotiques hôte spécifiques avec les espèces végétales. La présence d’un parent exotique peut donc limiter les possibilités de colonisation pas des microorganismes indigènes réduisant ainsi la diversité du microbiome.

En dernier lieu, il est également nécessaire de s’interroger sur la dispersion des peupliers hybrides dans les environnements bordant les plantations. Dès qu’une espèce exotique commence à s’installer en dehors des plantations, son contrôle peut s’avérer couteux et peu efficace. Néanmoins, en dépit des fortes capacités de reproduction végétative des peupliers, le risque lié à la dispersion des hybrides est faible en raison de leur faible compétitivité hors plantation (Vance et al., 2014). En revanche, l’hybridation avec les peupliers indigènes et la dispersion de gènes issue de parents exotiques au sein des populations locales est un risque important qui pèse sur les écosystèmes voisins de plantations. En Europe, il a été montré que des gènes issus de l’hybride *Populus Xcanadensis* pouvaient s’immiscer dans le génome des populations de peuplier noir (*Populus nigra [L.]*), réduisant la diversité génétique de cette espèce menacée dans certains territoires européens (Heinze, 2008; Ziegenhagen et al., 2008). En Amérique du Nord, d'autres auteurs notent un transfert de gènes provenant d'espèces eurasiatiques (*P. nigra* et *Populus laurifolia [Ledeb.]*) vers les populations natives de *P. balsamifera* et de *P. trichocarpa* (DiFazio et al., 2012; P. Talbot et al., 2012). L'étude de Meirmans et al. (2010) s'est intéressée aux hybridations entre clones ayant comme parent *P. maximowiczii* et les populations naturelles de peupliers. Leurs résultats montre qu'une hybridation est possible et que celle-ci est plus susceptible de se produire avec *P. balsamifera* que *P. deltoïdes* en raison de sa proximité phylogénique avec *P. maximowiczii*. Néanmoins, de plus amples recherches sont nécessaires afin de mieux comprendre les transferts de gènes des plantations vers les populations sauvages et de déterminer s'il est judicieux d'utiliser des clones ayant un parent exotique. Dans l'ensemble, la recherche devrait se concentrer sur les effets de tel ou tel clone sur la diversité végétale et microbienne des plantations ainsi que de leur capacité de séquestration de carbone afin de déterminer les meilleurs clones dans le cadre d'un reboisement de friches agricole.

Contrôler la végétation pour contrôler les stocks de carbone et l'activité microbienne ? Le couvert végétal influence les flux de carbone dans un écosystème par la diversité des traits fonctionnels de la végétation, la qualité et la quantité de matière organique amenée à la litière ou bien par la sécrétion d'exsudats racinaire (De Deyn et al., 2008; Jobbágy & Jackson, 2000). Ces mêmes exsudats agissent sur l'activité et la composition du microbiome du sol en plus des associations spécifiques plantes-microorganismes (Bardgett et al., 2014). À leur tour, les microorganismes sont impliqués dans les mécanismes de séquestration de carbone en formant des micros et macro-agrégats participant à la stabilisation du carbone organique dans le sol (Liang et al., 2017; Wiesmeier et al., 2019). Quelle que soit l'origine du site de la plantation, l'établissement de peupliers hybrides favorise les espèces rudérales et souvent exotiques comme *Vesca craca*, *Ranunculus arcis* ou encore *Taraxacum* spp., ainsi que de nombreuses espèces de poacées et de *Carex* spp. au détriment d'espèces forestières et locales. Nous avons avancé dans cette thèse plusieurs hypothèses pour justifier ces résultats. La proximité d'autres environnements agricoles, la grande capacité de dispersion des espèces rudérales, le couvert de peuplier hybride ne fournissant pas assez d'ombre pour les espèces forestières ou encore le choix du clone de peuplier. Mais ce qui nous semble être déterminant pour la colonisation et la persistance de ces espèces est le désherbage mécanique durant les premières années de la plantation qui favorise les espèces compétitives que sont les espèces rudérales. Au sein d'une plantation, une végétation de sous-bois arborant une grande proportion d'espèces herbacées contribue à la formation d'une litière riche en nutriments, notamment en azote, stimulant l'activité microbienne et conduit à l'accélération des cycles du C et N. À terme, cela peut engendrer une augmentation du taux de minéralisation du C et diminuer les stocks de carbone présent dans le sol minéral de la plantation (Chomel et al., 2016; Poirier et al., 2016). La persistance d'une végétation herbacée non forestière et exogène peut également limiter la reconstitution d'un microbiome similaire à celui des forêts environnantes. Certaines associations mycorhiziennes sont hôtes spécifiques et nécessitent donc la présence de leur plante hôte pour s'établir (Smith & Read, 2008). Plus généralement, le manque d'espèces ligneuses en dehors des arbres plantés limite la colonisation du milieu par les ectomycorhizes ou mycorhizes arbusculaires, principalement associées à des arbustes ou arbres (Onet et al., 2025; S. E. Smith & Read, 2008; Urbanová et al., 2015). Le changement des caractéristiques de la litière modifie également la composition et l'activité des microorganismes. Les espèces rudérales présentes dans les plantations de peuplier hybride peuvent donc représenter une barrière au retour d'espèces microbiennes forestières dans le microbiome des plantations. Intervenir directement sur le microbiome du sol via l'inoculation de microorganismes vivants pour faciliter la séquestration du carbone est une pratique abondamment discutée dans la recherche agronomique (Mason et al., 2023). Par exemple, l'inoculation de certaines mycorhizes arbusculaires peut faciliter le transfert du carbone labile vers des stocks de carbone récalcitrant (Cavagnaro & Martin, 2011; Mason et al., 2023). Mais jusqu'ici ces méthodes n'ont pas été expérimentées, à notre connaissance, dans un cadre sylvicole et les conséquences de l'inoculation de taxons exogènes sur le microbiome natif doivent être plus amplement étudiées. Au regard de l'importance du couvert végétal du sous-bois et de l'influence mutuelle qui existe entre le couvert, le microbiome et le carbone organique du sol, il est également envisageable d'agir directement sur la composition floristique de la plantation afin de faciliter le recouvrement de caractères propres aux forêts environnantes. En restauration écologique, la réintroduction active d'espèces natives via la production de matériel reproductif en pépinière ou la transplantation d'individus mature depuis les environnements naturels permet d'augmenter les chances de succès de la restauration (Reis et al., 2025; Silva Pedro et al., 2017). Ces techniques de réintroduction pourraient être utilisées en plantation afin de faciliter la colonisation du sous-bois par des espèces forestières. L'étude de Boothroyd-Roberts et al. (2013), prenant place dans le sud du Québec, montre que certaines espèces d'herbes forestières d'intérêt écologique, économique et culturel pouvaient être réintroduites avec succès dans des plantations de peuplier hybride. En plus d'aider la plantation à recouvrer des caractéristiques proches des forêts voisines, la présence de ces plantes d'intérêt dans les plantations permet également de diminuer la pression de cueillette qui pèse sur ces espèces dans leur milieu naturel. Néanmoins, cette étude prend place dans le sud de la province et les espèces réintroduites ici sont absentes de notre zone d'étude située plus au nord. La conduite d'études similaire s'intéressant à la réintroduction active d'espèces native du biome de la forêt boréale mixte représente donc un grand potentiel de recherche future. Enfin, l'association du peuplier hybride a des essences indigènes comme l'épinette blanche en plantation mixte pourrait également faciliter la colonisation du sous-bois par des espèces forestières.

Limites et contraintes. Comme toute étude, les résultats et conclusions discutées dans ce manuscrit sont contraints par des limites inhérentes à notre dispositif expérimental. Nos sites d'études sont dispersés sur un vaste territoire plus ou moins homogène. D'un site à l'autre, il existe des variations liées au climat, à la végétation, aux propriétés du sol ou encore aux paysages et aux activités humaines qui ont pu influencer en partie nos résultats. Par exemple, certains de nos sites sont localisés dans le domaine bioclimatique de la sapinière à bouleau jaune tandis que la majorité se situe dans celui de la sapinière à bouleau blanc. Bien que cette disparité ait pu influencer nos résultats, elle nous permet de disposer d'un nombre important de sites d’études. Nous nous sommes également concentrés sur l’échantillonnage de variables à un instant donné. Cependant, plusieurs variables d’études sont sujettes à des variations annuelles ou saisonnières comme la végétation, le microbiome ou les stocks de carbone du sol. De plus amples connaissances à ce propos nous permettraient de mieux comprendre les dynamiques temporelles à l’œuvre au sein des plantations et des zones non reboisées laissées en libre évolution.

Les zones non reboisées adjacentes aux plantations de peupliers peuvent également représenter une source de biais. Si cela nous permet de disposer de témoins ayant un historique similaire aux plantations, cela peut entrainer une importante dépendance notamment concernant la végétation et le microbiome, car ces zones non reboisées peuvent influence les plantations via la colonisation d’espèces végétales ou microbiennes de la zone non reboisée vers la plantation. Bien que cette interdépendance soit prise en compte dans nos modèles statistiques, elle peut toutefois avoir influencé les résultats de notre étude. Nous disposons également de peu d’échantillons avec un n=32 dans la majorité de nos tests statistiques. Cela peut conduire à une perte de puissance statistique et à une non-significativité de nos tests malgré un non-chevauchement des erreurs standards sur nos figures (ex. Figure 24).

Enfin, malgré la recherche d’informations auprès des propriétaires et au cours de la lecture de précédentes publications, nous manquions de plusieurs informations concernant le passé agricole des friches. Quelle était l’intensité de l’activité agricole ? Y avait-il un usage de produits phytosanitaires ? Combien de temps a duré l’exploitation ? De plus, dans le contexte de notre zone d’étude, le début de l’activité agricole date d'il y a un siècle et est relativement récent en comparaison d’autres territoires dans le monde et même en comparaison des terres du sud du Québec. Il serait intéressant pour de futures études de prendre en compte ces paramètres pour déterminer si certaines friches se prêtent mieux que d’autres au reboisement par du peuplier hybride.

Conclusion – Où planter du peuplier hybride. Notre étude montre qu’après 15 ans, les plantations de peupliers hybrides sur friches agricoles n’ont pas altéré les stocks de carbone ni la diversité végétale et microbienne comparativement à leurs équivalents non reboisés. À l’inverse, établir du peuplier hybride sur d’anciennes coupes forestières a conduit à une diminution des stocks de carbone du sol, de la diversité végétale et de la diversité fongique. De plus, le reboisement de friches herbacées a entrainé une hausse de diversité à l’échelle du paysage et l’accroissement de l’abondance relative des ectomycorhizes. Les friches herbacées semblent offrir la meilleure option pour profiter du taux de croissance élevé des peupliers hybrides et ainsi permettre de dérouter une partie de la production issue des peuplements naturels ou peu aménagée de la forêt boréale vers les plantations intensives.

ANNEXE A – PLANT DIVERSITY

Table S1
Species code use in figure 17b and d. The code is structured as follows : 3 first uppercase letters referred to the 3 first letters of the genus and the 3 last uppercase letters referred to the 3 first letters of the species. SPP stand for species (pl).

Vascular plants		**Bryophytes**	
Code	**Species**	**Code**	**Species**
ALNINC	*Alnus incana subsp. rugosa*	BRAERY	*Brachythecium erytrorrhizon*
APOAND	*Apocynum androsaemifolium*	BRYSPP	*Byrum spp*
BETPAP	*Betula papyrifera*	CALHAL	*Calicladium haldanianum*
DRYSPP	*Dryopteris spp*	CAMCHR	*Campylladelphus chrysophyllus*
GALTRE	*Galeopsis tretahit*	CERPUR	*Ceratodon purpureus*
GALTRI	*Galium trifidum*	CHIPRO	*Chiloscyphus profundus*
IMPCAP	*Impatiens capensis*	FISTAX	*Fissidens taxifolium*
JUNTEN	*Juncus tenuis*	HYPFAU	*Hypnum fauriei*
LEUVUL	*Leucanthemum vulgare*	PLESCH	*Pleurozium schreberi*
MAICAN	*Maianthemun canadensis*		
PICMAR	*Picea mariana*		
PRUPEN	*Prunus pensylvanica*		
PRUVIR	*Prunus virginiana*		
PYRELL	*Pyrola elliptica*		
RANACR	*Ranunculus acris*		
RIBTRI	*Ribes triste*		
SOLRUG	*Solidago rugosa*		
SYMPUN	*Symphyotrichum puniceum*		
TRIPRA	*Trifolium pratense*		
VICCRA	*Vicia craca*		

ANNEXE B – MICROBIOME

Table S1

Detailed information on the study sites, each site is divided into two: the hybrid poplar plantation and the neighbouring non-afforested area. Longitude and latitude are given in the WGS84 coordinate system.

							Hybrid poplar plantation					Non-afforested area	
Code	**Municipality**	**Longitude**	**Latitude**	**Mean annual T* (°C)**	**Mean annual P* (mm)**	**Origin of site**	**Year of plantation**	**Soil pH**	**Light intercepted by canopy (%)**	**Tree density (tree/ha)**	**Productivity ($m^3.ha^{-1}.y^{-1}$)**	**Soil pH**	**Light intercepted by canopy (%)**
AD	Arntfield	-79.289153	48.229618	1.7	883	Previously forested land	2005	6.03	47.22	1000	3.11	5.58	94.68
AM	Amos	-78.076250	48.612869	1.2	918	Shrubby AAL*	2003	5.54	75.25	1111	6.80	5.32	51.51
DO	Duhamel-Ouest	-79.419326	47.317287	2.8	819	Herbaceous AAL*	2005	5.82	94.29	833	12.3	5.7	0
DP1	Duparquet	-79.440552	48.490015	0.7	950	Previously forested land	2005	5.56	59.1	833	3.33	5.37	95.64
DP3	Duparquet	-79.120807	48.445066	0.7	950	Previously forested land	2004	6.04	40.3	1000	0.40	5.43	88.64
DY	Despinassy	-77.481485	48.762800	0.5	914	Herbaceous AAL*	2006	5.86	93.88	1000	9.56	6.04	50.97
LS	La Sarre	-79.290523	48.832356	0.7	890	Shrubby AAL*	2006	6.61	83.51	816	6.75	6.41	0
ND	Nédélec	-79.374244	47.763660	1.9	916	Previously forested land	2003	5.28	51.31	1111	6.36	5.1	92.25
NL	New Liskeard (ON*)	-79.664576	47.520836	2.3	785	Herbaceous AAL*	2007	7.22	93.98	816	16.74	7.34	0
PC	Preissac	-78.273785	48.372717	1.2	918	Herbaceous AAL*	2004	6.04	85.42	1000	0.53	5.73	50.85
RH	Rivière-Héva	-78.275070	48.197415	1.2	914	Shrubby AAL*	2003	5.26	68.05	1111	12.55	5.13	73
SD	Saint-Dominique-du-Rosaire	-78.076137	48.764188	0.2	909	Shrubby AAL*	2006	5.61	93.49	1000	9.18	5.43	89.25
SG	Sainte-Gertrude	-78.269317	48.517258	1.2	918	Herbaceous AAL*	2008	5.26	37.23	833	1.72	5.16	0
TA	Taschereau	-78.684490	48.601604	0.7	950	Herbaceous AAL*	2007	6.41	91.76	833	13.47	5.74	0
TR	Trécesson	-78.222183	48.659018	1.2	918	Herbaceous AAL*	2009	5.47	39.82	833	1.81	5.5	0
VP	Val-Paradis (NQ*)	-79.177988	49.151510	0.1	910	Herbaceous AAL*	2005	5.5	79.44	833	4.57	5.39	0

Table S2
ANOVA summary showing the effect of afforestation and site origin on soil properties.

Factor		pH	C_{tot}	N_{tot}	SWC	SCC	BD
Afforestation	P value	**0.002**	**<0.001**	**<0.001**	**0.002**	0.91	**<0.001**
	F stat	14.4	24.5	26.6	14.5	0.014	27.72
Site origin	P value	0.59	0.10	0.20	0.13	0.83	0.11
	F stat	0.55	2.78	1.85	2.41	0.18	2.59
Interaction	P value	0.27	**0.034**	**0.031**	0.10	0.56	**0.015**
	F stat	1.47	4.42	4.62	2.71	0.60	5.95

Notes: C_{tot} = Total Carbon; N_{tot} = Total Nitrogen; SWC = Soil Water Content; SCC = Soil Clay Content; BD = Bulk density

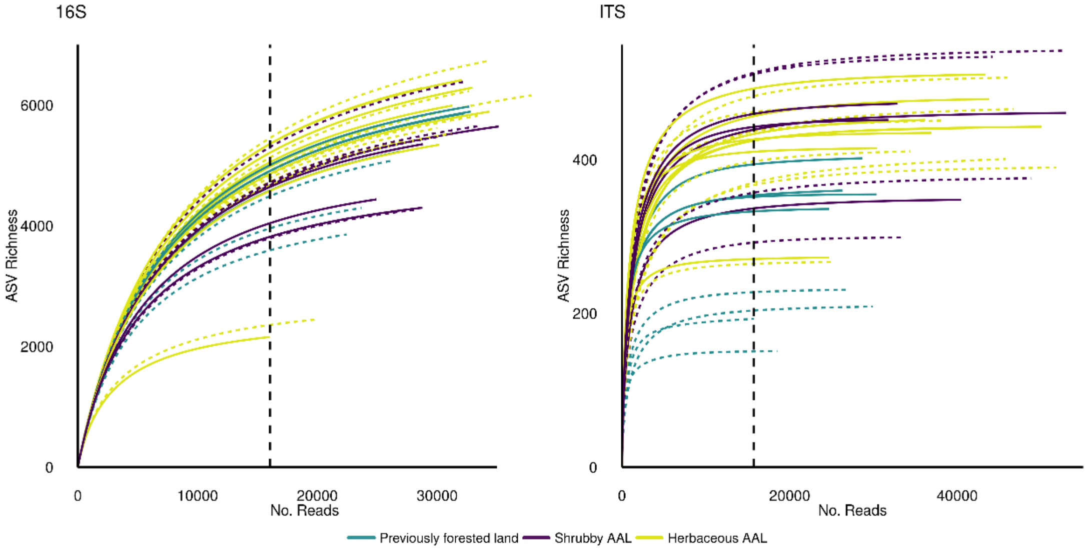


Figure S1
Rarefaction curves of 16S and ITS reads for each sample. Vertical Blacked dashed lines represent the size of the subsample use for rarefaction (16,051 sequences for bacteria and 15,714 for fungi). Plein curves are for samples from non-afforested areas while dotted curves are for samples from hybrid poplar plantations.

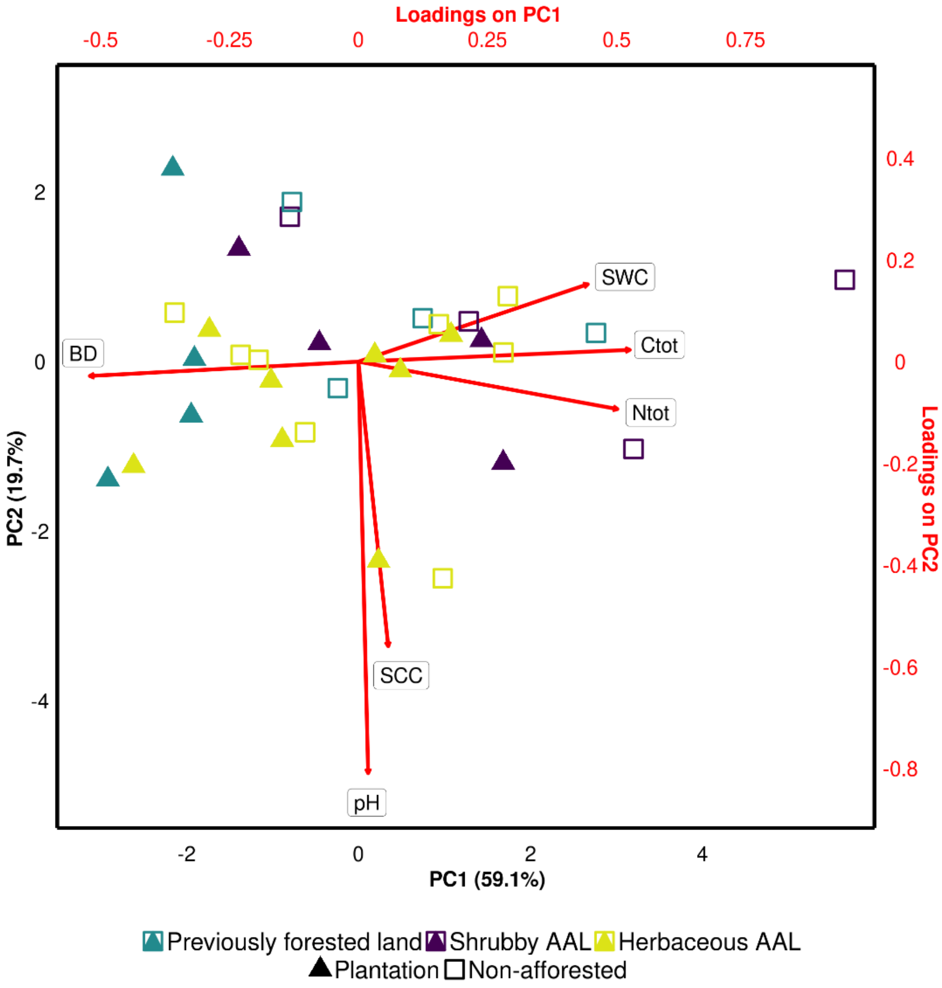


Figure S2
ANOVA summary showing the effect of afforestation and site origin on soil properties.

ANNEXE C – CARBONE

Table S1

Detailed information on the study sites, each site is divided into two: the hybrid poplar plantation and the neighbouring non-afforested area. Longitude and latitude are given in the WGS84 coordinate system.

Code	Municipality	Longitude	Latitude	Mean annual T* (°C)	Mean annual P* (mm)	Origin of site	Plantation			Non-afforested	
							Year of plantation	Clay content (%)	Soil texture	Clay content (%)	Soil texture
AD	Arntfield	-79.289153	48.229618	1.7	883	Previously forested land	2005	70.1	Heavy clay	57.9	Clay
AM	Amos	-78.076250	48.612869	1.2	918	Shrubby AAL	2003	67.8	Heavy clay	69.7	Heavy clay
DO	Duhamel-Ouest	-79.419326	47.317287	2.8	819	Herbaceous AAL	2005	45.8	Clay	41.9	Clay
DP1	Duparquet	-79.440552	48.490015	0.7	950	Previously forested land	2005	70.0	Heavy clay	71.8	Heavy clay
DP3	Duparquet	-79.120807	48.445066	0.7	950	Previously forested land	2004	90.0	Heavy clay	85.5	Heavy clay
DY	Despinassy	-77.481485	48.762800	0.5	914	Herbaceous AAL	2006	59.7	Clay	73.8	Heavy clay
LS	La Sarre	-79.290523	48.832356	0.7	890	Shrubby AAL	2006	61.9	Heavy clay	69.9	Heavy clay
ND	Nédélec	-79.374244	47.763660	1.9	916	Previously forested land	2003	18	Loam	36.8	Loam clay
NL	New Liskeard (ON*)	-79.664576	47.520836	2.3	785	Herbaceous AAL	2007	63.7	Heavy clay	62.6	Heavy clay
PC	Preissac	-78.273785	48.372717	1.2	918	Herbaceous AAL	2004	84.0	Heavy clay	64.0	Heavy clay
RH	Rivière-Héva	-78.275070	48.197415	1.2	914	Shrubby AAL	2003	43.8	Clay	41.9	Clay
SD	Saint-Dominique-du-Rosaire	-78.076137	48.764188	0.2	909	Shrubby AAL	2006	63.9	Heavy clay	63.9	Heavy clay
SG	Sainte-Gertrude	-78.269317	48.517258	1.2	918	Herbaceous AAL	2008	80.3	Heavy clay	73.8	Heavy clay
TA	Taschereau	-78.684490	48.601604	0.7	950	Herbaceous AAL	2007	60.9	Heavy clay	63.8	Heavy clay
TR	Trécesson	-78.222183	48.659018	1.2	918	Herbaceous AAL	2009	81.8	Heavy clay	71.9	Heavy clay
VP	Val-Paradis (NQ*)	-79.177988	49.151510	0.1	910	Herbaceous AAL	2005	66.7	Heavy clay	59.9	Clay

Notes: T = Temperature; P = Precipitation; AAL = Abandoned Agricultural Land; ON = Ontario; NQ = Northern Quebec

Table S2

ANOVA summary showing the effect of afforestation and site origin on litter and soil physico-chemical properties. Significative results (P<0.05) are shown in bold.

Strate	Factor		[P]	[K]	[Ca]	[Mg]	[SOC]	[N]	Bd	C/N	pH	Dry litter mass
Litter	Afforestation	P value	-	-	-	-	0.18	**0.0023**	-	0.059	-	**0.040**
		F stat	-	-	-	-	1.92	**14.27**	-	4.26	-	**5.20**
	Site origin	P value	-	-	-	-	0.066	0.86	-	0.054	-	0.079
		F stat	-	-	-	-	3.04	0.15	-	3.70	-	3.11
	Interaction	P value	-	-	-	-	0.43	0.077	-	0.59	-	**0.012**
		F stat	-	-	-	-	0.88	3.15	-	0.54	-	**6.27**
0-15	Afforestation	P value	0.16	0.22	0.29	0.16	**<0.001**	**<0.001**	**<0.001**	0.27	**0.002**	-
		F stat	2.17	1.62	1.23	2.21	**19.6**	**26.6**	**27.72**	1.32	**14.4**	-
	Site origin	P value	0.98	0.94	0.83	0.53	0.19	0.20	0.11	0.10	0.59	-
		F stat	0.02	0.06	0.19	0.67	1.91	1.85	2.59	2.80	0.55	-
	Interaction	P value	0.62	**0.02**	0.77	0.69	**0.026**	**0.031**	**0.015**	0.40	0.27	-
		F stat	0.49	**4.99**	0.27	0.38	**5.11**	**4.62**	**5.95**	0.99	1.47	-
15-30	Afforestation	P value	0.32	0.35	0.13	0.79	0.61	0.16	0.17	0.14	0.21	-
		F stat	1.09	0.92	2.57	0.07	0.27	2.17	2.06	2.59	1.76	-
	Site origin	P value	0.71	0.94	0.96	0.88	0.26	0.13	0.21	**0.025**	0.93	-
		F stat	0.35	0.06	0.04	0.13	1.51	2.44	1.74	**5.39**	0.07	-
	Interaction	P value	0.15	0.18	0.38	0.13	0.63	0.74	0.32	0.96	0.15	-
		F stat	2.23	1.99	1.05	2.4	0.48	0.31	1.26	0.046	2.22	-
30-45	Afforestation	P value	0.18	0.39	0.29	0.39	0.46	0.99	0.86	0.14	0.70	-
		F stat	2.03	0.77	1.22	0.79	0.61	0.0001	0.03	2.3	0.15	-
	Site origin	P value	0.59	0.99	0.95	0.93	0.66	0.23	0.71	0.70	0.81	-
		F stat	0.56	0.01	0.05	0.08	0.45	1.66	0.34	0.36	0.21	-
	Interaction	P value	0.09	0.45	0.45	0.16	0.99	0.64	0.48	0.18	0.39	-
		F stat	2.97	0.86	0.84	2.08	0.005	0.47	0.77	1.18	1.02	-

P: Phosphorus; K: Potassium; Ca: Calcium; Mg: Magnesium; SOC: Soil Organic Carbon; N: Nitrogen; Bd: Bulk density

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