Université de Montréal

La dominance mycorhizienne en tant que facteur local déterminant des processus écologiques forestiers

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Thèse présentée

en vue de l'obtention du grade de *Philosophiae Doctor* (Ph.D.)

en sciences biologiques

Septembre 2020

Université de Montréal

Unité académique : Département de sciences biologiques, Faculté des arts et des sciences

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Cette thèse intitulée

La dominance mycorhizienne en tant que facteur local déterminant des processus écologiques forestiers

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Résumé

L'association mycorhizienne implique nombre de plantes et de champignons, étant sans doute la symbiose mutualiste la plus importante et la plus répandue au sein des écosystèmes terrestres. Étant donné que la plupart des arbres forment des mycorhizes arbusculaires ou des ectomycorhizes qui se distinguent par leur écophysiologie, il est judicieux de caractériser les forêts en fonction de leur dominance mycorhizienne afin d'en mesurer les impacts sur les processus écologiques. Ainsi, l'objectif de cette thèse est de quantifier les influences de la dominance mycorhizienne en forêt sur les propriétés abiotiques et biotiques du sol ayant un impact à l'échelle locale sur deux processus associés : la décomposition de la matière organique et la régulation de la diversité végétale. Les forêts étudiées, de dominance mycorhizienne très contrastée, présentent des propriétés physico-chimiques et des communautés microbiennes distinctes au niveau du sol, mais des patrons de distribution verticale des microorganismes du sol d'une similarité inattendue. Dans ces forêts nordiques décidues, la décomposition de la matière organique est favorisée dans les couches supérieures du sol, notamment grâce à la présence du réseau fongique et d'autant plus lorsque les ectomycorhizes prédominent, ce qui prouve l'aspect déterminant du contexte local. L'établissement d'arbres mycorhiziens arbusculaires peut être limité par la combinaison des conditions abiotiques et biotiques édaphiques de la forêt boréale, qui est dominée par les ectomycorhizes, contrairement aux forêts à dominance partagée entre mycorhize arbusculaire et ectomycorhize, où la diversité est favorisée à l'échelle de la communauté. Cette thèse démontre le rôle déterminant, au niveau local, exercé par la dominance mycorhizienne sur les processus écologiques, et soulève l'importance de l'hétérogénéité biotique et abiotique du sol pour mieux saisir le fonctionnement des écosystèmes terrestres.

Mots-clés : Interactions plantes-sols, biodiversité microbienne, champignons saprotrophes, forêt tempérée nordique de feuillus, écotone tempéré-boréal, érable à sucre, hêtre à grandes feuilles, forêt boréale, cycle du carbone, changement climatique.

Abstract

Mycorrhizas, which involve plants and fungi, are probably the most important and widespread mutual symbioses in terrestrial ecosystems. Since most trees form arbuscular mycorrhizas or ectomycorrhizas that are ecophysiologically distinct from each other, it is useful to characterize forests according to their mycorrhizal dominance in order to measure their respective impacts on ecological processes. The objective of this thesis is to quantify the impacts of forest mycorrhizal dominance on the abiotic and biotic properties of the soil, which influence at the local scale two associated processes: the decomposition of organic matter and the maintenance of plant diversity. The forests studied have opposite mycorrhizal dominance exhibit distinct soil physico-chemical properties and microbial communities, but more similar vertical distribution patterns of microorganisms than expected. Decomposition is favored by organic matter in the upper soil layers, but also by the presence of the fungal network, especially when ectomycorrhizas predominate, illustrating the importance of the local environmental context. Establishment of arbuscular mycorrhizal tree may be limited by the combination of abiotic and biotic edaphic factors of the boreal forest, which is ectomycorrhizal-dominated, in contrast to forests with shared dominance between arbuscular mycorrhizas and ectomycorrhizas, where tree species diversity is favored at the community level. This thesis demonstrates the decisive role, at the local scale, played by mycorrhizal dominance on ecological processes, and raises the importance of soil biotic and abiotic heterogeneity to better understand the functioning of terrestrial ecosystems.

Keywords: Plant-soil interactions, microbial biodiversity, saprotrophic fungi, northern broadleaf temperate forest, temperate-boreal ecotone, sugar maple, American beech, boreal forest, carbon cycle, climate change.

Table des matières

Liste des tableaux

Liste des figures

INTRODUCTION

CHAPITRE 1

CHAPITRE 2

CHAPITRE 3

Liste des abréviations

(Les caractères italiques indiquent les termes en anglais)

AIC	*Akaike information criterion* | critère d'information d'Akaike
Al	*aluminium* | aluminium
AM	*arbuscular mycorrhizal* | mycorhize arbusculaire
ANOVA	*analysis of variance* | analyse de variance
asl	*above sea level* | au-dessus du niveau de la mer
ASV	*amplicon sequence variant* | variante de la séquence d'amplicon
Ba	*barium* | baryum
bp	*base pairs* | paires de bases
C	*carbon* | carbone
CI	*credible interval* | intervalle de crédibilité
Cl	*chlorine* | chlore
CV	*coefficient of variation* | coefficient de variation
DBH	*diameter at breast height* | diamètre à hauteur de poitrine
DF	*degrees of freedom* | degrés de liberté
DNA	*deoxyribonucleic acid* | acide désoxyribonucléique
ECEC	*effective cation exchange capacity* | capacité d'échange cationique effective
EcM	*ectomycorrhizal* | ectomycorhize
EDTA	*ethylenediaminetetraacetic acid* | acide éthylènediaminetétraacétique

ErM	*ericoid mycorrhizal* | mycorhize éricoïde
F	*fragmented* | fragmenté
Fe	*iron* | fer
H	*humus* | humus
ITS	*internal transcribed spacer* | espaceur interne transcrit
L	*litter* | litière
Mg	*magnesium* | magnésium
N	*nitrogen* | azote
Na	*sodium* | sodium
NMDS	*non-metric multidimensional scaling* | positionnement multidimensionnel non métrique
P	*phosphorus* | phosphore
PCR	*polymerase chain reaction* | réaction en chaîne par polymérase
PERMANOVA	*permutational multivariate analysis of variance* | analyse permutationnelle multivariée de la variance
Po	*organic phosphorus* | phosphore organique
pRDA	*partial redundancy analysis* | analyse de redondance partielle
PVC	*polyvinyl chloride* | polychlorure de vinyle
RDA	*redundancy analysis* | analyse de redondance
SD	*standard deviation* | écart-type
TEB	*total exchangeable bases* | total des bases échangeables

« *Comme nous, plus que nous, l'arbre a une patrie, un sol natal, et il supporte mal l'exil. Comme chez les humains, l'arbre soutient son frère dans la forêt; mais les arbres se livrent aussi parfois des luttes fratricides et la forêt est pleine d'implacables suppressions, de silencieux triomphes du fort sur le faible. Enfin, comme nous aussi, l'arbre ayant atteint le nombre de ses jours, disparaît et retourne à la terre, pendant que folle de sève, la génération suivante monte vers le soleil. L'arbre est donc bien pour nous un grand frère muet, impuissant à nous dire, cependant le poème de sa vie intérieure et formidable. Nous l'aimons tel quel, ce frère muet, venu de plus loin que nous dans les abîmes du passé, mûri dans son immobilité et son silence. S'il ne peut nous initier au mystère de son origine et de sa vie limitée, il peut, en revanche, sans rompre son auguste silence, nous apprendre à nous tenir droit, à chercher les hauteurs, à raciner profondément, à purifier le monde, à offrir généreusement à tous l'ombre et l'abri.* » [1]

Frère Marie-Victorin.

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[1] Transcription d'un extrait du Frère Marie-Victorin (12 octobre 1943). L'arbre : méditation [chronique radiophonique]. Dans *La cité des plantes*. Radio-Collège, Radio-Canada. http://www.disten.com/radiocollege/sonores.php.

Remerciements

Il aura fallu tout un village pour réaliser cette thèse, qui est avant tout un travail d'équipe. Je souhaite donc remercier sincèrement toutes les personnes qui ont participé à cette aventure de près ou de loin. J'ai été choyé de pouvoir compter sur des gens passionnés et dévoués qui m'ont permis de présenter ce travail aujourd'hui et en particulier des stagiaires pour l'aide sur le terrain et en laboratoire, mais aussi des personnes de soutien scientifique et administratif au Centre sur la biodiversité, à l'Institut de recherche en biologie végétale et au Département de sciences biologiques de l'Université de Montréal.

Mon parcours a été riche de personnes passionnées et passionnantes, depuis l'éducation que j'ai reçue en Guadeloupe jusqu'à aujourd'hui au Québec, qui ont fait grandir le scientifique en moi. Les derniers en date sont Etienne Laliberté et Mark Vellend, que je remercie chaleureusement pour la direction de cette thèse avec confiance, patience, excellence et bien plus encore. Cette thèse a été rendu possible par leurs implications directes dans la conception et la réalisation des différentes études présentées, mais aussi en tant que mentors et experts dont j'essaye de m'inspirer et d'apprendre depuis maintenant plus de quatre ans.

J'ai aussi eu l'aubaine de profiter des conseils d'autres chercheurs et chercheuses chevronnés dont Pierre-Luc Chagnon, Simon Joly, Mélanie Roy et Ben Turner que je souhaite remercier sincèrement. Je remercie également Nicolas Fanin et David Rivest d'avoir bien voulu faire partie du jury de cette thèse.

Impossible *de passer au travers* sans le soutien continu et les innombrables discussions avec de formidables collègues dont Marie Beigas, Vanessa Grenier, Vlad Parasquive, Nicolas Pinceloup, Julian Wittische, ainsi que Andrew Blackney, Alizée Girard et Simon Morvan que je remercie tout particulièrement pour leurs commentaires sur cette thèse. Je tiens aussi à remercier chaleureusement Mila Bathurt pour la révision de cette thèse.

Je remercie sincèrement toutes les personnes qui ont et qui continuent de développer des plateformes libres, et la communauté fédérée autour du partage des connaissances et des données, permettant à la science d'avancer de façon plus libre et ouverte.

Cette thèse n'aurait pas pu être réalisée sans le financement qui m'a été attribué par Etienne en premier lieu, puis par le Fonds québécois de la recherche sur la nature et les technologies, et aussi par le Département de sciences biologiques, les Études supérieurs et postdoctorales de l'Université de Montréal, ainsi que l'Institut de recherche en biologie végétale. J'ai aussi eu l'occasion de participer et de présenter les résultats de cette thèse lors de conférences au Québec et à l'étranger grâce à de généreux financements octroyés par le Centre sur la science de la biodiversité au Québec, du Centre d'études sur la forêt et de l'Institut de recherche en biologie végétale.

Finalement, je tiens à remercier ma famille qui m'a offert un support inconditionnel.

J'ai été choyé par mon village, ***merci***.

Érablière, Station de biologie des Laurentides, St-Hippolyte.

INTRODUCTION

1. Plantes, sols et microbes : des interactions souterraines aux origines de processus écologiques

Les végétaux façonnent la vie sur Terre et sont à la base de notre monde. La grande majorité des plantes terrestres, dont l'ensemble des arbres, interagissent de façon continue avec le sol. Le sol est composé d'éléments organiques et minéraux que l'on retrouve naturellement à la surface de la Terre, sous forme non-consolidée, et qui permet la croissance des plantes (Groupe de travail sur la classification des sols, 1998). C'est un milieu très complexe, hétérogène, présentant de forts gradients horizontaux et verticaux au niveau des propriétés chimiques et physiques, mais également biologiques. De par ses propriétés, le sol influence donc grandement les plantes, de l'échelle individuelle à celle de la communauté végétale (Ricklefs & Miller, 2005). À leur tour, les plantes, modifient profondément le sol et les processus écologiques souterrains tels que les cycles biogéochimiques, donnant ainsi lieu à des rétroactions entre plantes et sols (Hobbie, 1992; van der Putten *et al.*, 2013; Bardgett *et al.*, 2014). L'importance des facteurs abiotiques souterrains pour l'assemblage des communautés végétales, visibles au niveau aérien, est bien reconnue et ces paramètres ont donc déjà été largement étudiés (Ehrenfeld *et al.*, 2005). En revanche, on connaît moins bien le rôle que jouent les microorganismes présents dans le compartiment souterrain des écosystèmes, bien que son importance soit désormais admise par le plus grand nombre (Watkinson, 1998; van der Heijden *et al.*, 2008). En définitive, le sol et les plantes sont en constante interaction dans un système complexe d'interdépendance entre composantes chimiques, physiques et biologiques, contrôlé largement par les organismes vivants (Bardgett & Wardle, 2010). L'étude de ces interactions souterraines est décisive dans la compréhension des processus écologiques permettant le fonctionnement des écosystèmes terrestres et notamment ceux dominés par les plantes, comme c'est le cas avec la décomposition de la matière organique dans les sols de forêt.

L'étude de l'écologie des écosystèmes a toujours largement sous-estimé l'importance des facteurs biotiques souterrains tels que les interactions entre les plantes et les microorganismes (Bardgett & Wardle, 2010). Ceux-ci sont certes invisibles, mais ils dominent la biomasse du sol (van der Heijden *et al.*, 2008) et ont une influence déterminante sur la composition, la structure et la dynamique des communautés végétales (Mangan *et al.*, 2010; van der Putten *et al.*, 2013). Parmi ces microorganismes, les champignons mycorhiziens sont des acteurs importants des écosystèmes terrestres de par la symbiose qu'ils forment avec les racines des plantes (Smith & Read, 2008).

Cette symbiose mycorhizienne créée avec les plantes est « [...] incontestablement la symbiose mutualiste la plus courante et la plus importante dans les écosystèmes terrestres » [2] (Martin *et al.*, 2018). La symbiose mycorhizienne est déterminée par l'interaction étroite et prolongée entre le champignon (mycobionte) et la plante (phytobionte) et un environnement spécifique (Fig. 1). L'importance de cette symbiose s'illustre par sa prévalence puisque le mode de vie mycorhizien est présent depuis les milieux tropicaux jusque dans la toundra et impliquerait jusqu'à 95 % des plantes sur Terre (Tedersoo *et al.*, 2010; van der Heijden *et al.*, 2015; Davison *et al.*, 2015; Brundrett, 2017).

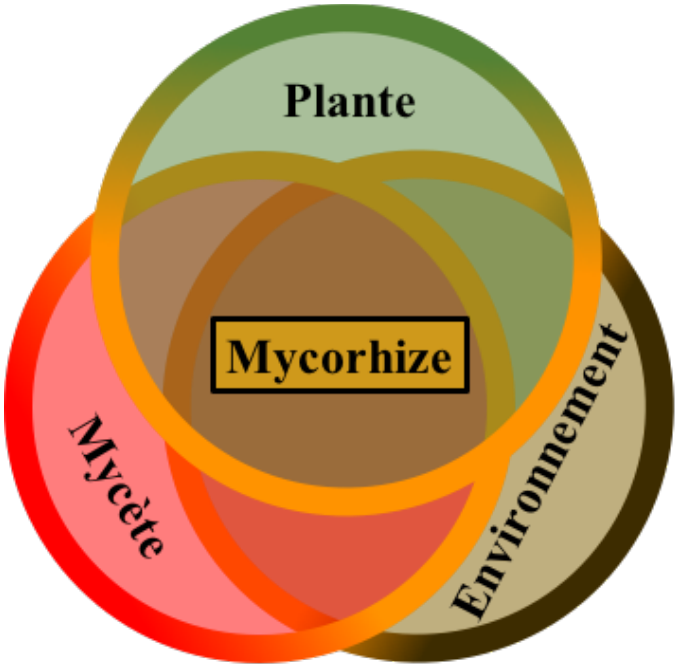

Figure 1. L'association mycorhizienne résulte d'une interaction tripartite entre mycobionte (mycète ou champignon) et phytobionte (plante) au sein d'un environnement donné. Inspirée de Brundrett (1991).

[2] Traduction libre d'un extrait de Martin *et al.* (2018).

La symbiose mycorhizienne s'est développée de façon indépendante à de nombreuses reprises et il en existe plusieurs types, dont les plus répandues sont les mycorhizes arbusculaires (abréviée AM par la suite; 200 000 espèces de plantes et 300-1600 taxons fongiques), les ectomycorhizes (EcM; 6000 espèces de plantes et 20 000 taxons fongiques), les mycorhizes éricoïdes (ErM, 20 000-35 000 espèces de plantes et 25 000 taxons fongiques) et les mycorhizes des orchidées (3900 espèces de plantes et plus de 150 taxons fongiques), selon van der Heijden *et al.* (2015). Les AM sont d'anciennes associations qui ont probablement été initiées entre les premières plantes qui ont colonisé la terre ferme et les ancêtres des champignons des groupes des Glomeromycètes et des Mucoromycètes, il y au moins 400 millions d'années (Taylor *et al.*, 1995; Brundrett, 2002; Parniske, 2008). Les premières EcM se seraient développées plus tard, il y a environ 190 millions d'années, par l'association entre des Gymnospermes et des champignons saprotrophes des groupes des Basidiomycètes, des Ascomycètes et des Mucoromycètes (Skrede *et al.*, 2011; Floudas *et al.*, 2012; Desirò *et al.*, 2017). La mycorhize est une symbiose de type mutualiste, reconnue notamment pour sa capacité à améliorer la nutrition minérale et la protection des phytobiontes contre les pathogènes en échange de carbone sous forme de sucres délivrés aux mycobiontes (détaillé en section 3; Smith & Read, 2008; Hodge, 2017). Cette association symbiotique est indispensable à la survie des mycobiontes, qui sont pour la plupart des symbiotrophes obligatoires, et permettrait aux phytobiontes une meilleure performance, voire même d'élargir leurs niches écologiques (Smith & Read, 2008; Gerz *et al.*, 2018). Il est à noter que la symbiose mycorhizienne peut être très couteuse pour les plantes, voir même de type parasitique dans certains cas (Johnson *et al.*, 1997). La symbiose mycorhizienne contribue donc considérablement à la valeur sélective de la plupart des plantes, mais elle contribue aussi plus largement à la dynamique des communautés végétales et aux processus écologiques locaux (Aerts, 2003; Bardgett & Wardle, 2010).

Les champignons mycorhiziens sont situés dans l'interface entre le sol et les plantes et y agissent comme des régulateurs des interactions entre plantes et sol. Ainsi, les champignons mycorhiziens ont le potentiel d'influencer de façon considérable le fonctionnement des écosystèmes terrestres. En effet, en raison des bénéfices amenés aux plantes (Smith & Read, 2008) et de la grande biomasse fongique mycorhizienne dans le sol (Leake *et al.*, 2004), la présence et le type de mycorhize font partie des principaux déterminants des processus écologiques au sein des écosystèmes terrestres

(van der Heijden *et al.*, 2015). Ces processus écologiques peuvent être définis comme des mécanismes qui évoluent au sein d'un écosystème, liant les organismes et leur environnement, tels que le cycle des éléments nutritifs, la succession des espèces et les interactions biotiques. Il est par exemple bien reconnu que la symbiose mycorhizienne est l'un des principaux moteurs des cycles des nutriments et du carbone (détaillé en section 3; Read & Perez-Moreno, 2003; Phillips *et al.*, 2013; Steidinger *et al.*, 2019). Bien que l'action de la symbiose mycorhizienne se situe à l'échelle du micron (p. ex. accès et transfert des nutriments entre mycobionte et phytobionte), les impacts liés au type de mycorhize peuvent se mesurer à l'échelle globale (Averill *et al.*, 2014; Steidinger *et al.*, 2019; Soudzilovskaia *et al.*, 2019). Il est donc primordial de connaître la variabilité, la distribution et la succession des communautés mycorhiziennes et microbiennes du sol, afin de pouvoir en tenir compte dans les modèles du système terrestre et dans les prévisions écologiques.

Les difficultés liées à l'identification taxonomique des microorganismes tels que les champignons mycorhiziens, ont longtemps constitué un obstacle majeur à la description de leur distribution, à l'étude de leurs interactions et à la compréhension de leurs impacts sur l'environnement (Dickie & John, 2016; Bálint *et al.*, 2016). Des outils tels que des biomarqueurs spécifiques peuvent être utilisés pour quantifier la biomasse de différents types de champignons dans les sols (Tedersoo & Bahram, 2019), mais ces marqueurs ne permettent pas de déterminer précisément la composition en espèces des communautés fongiques et microbiennes. Le séquençage d'amplicons à haut débit a par la suite rendu possible le profilage taxonomique des communautés microbiennes, notamment celle des champignons, à partir de matériel génétique environnemental (Lindahl *et al.*, 2007; Dickie & John, 2016; Nilsson *et al.*, 2019). Ainsi, il est maintenant reconnu que les communautés microbiennes du sol varient de façon marquée sur de grandes échelles spatiales, sous l'effet de changements des propriétés édaphiques et climatiques (Talbot *et al.*, 2014; Tedersoo *et al.*, 2014). Toutefois, les mécanismes qui façonnent la distribution de communautés fongiques et microbiennes à de fines échelles spatiales restent pour l'instant relativement peu étudiés (Wolfe *et al.*, 2009; Bahram *et al.*, 2015; Lembrechts *et al.*, 2020).

2. Distribution des mycorhizes : hypothèses quant aux variations, causes et conséquences en forêt

Afin d'améliorer notre compréhension de l'écologie des mycorhizes et de leur rôle au sein des écosystèmes, il est important d'en définir les composantes qui déterminent leurs distributions. Dans un environnement donné, la distribution des mycorhizes dépend par définition de la présence conjointe du phytobionte et du mycobionte. La présence combinée de ces partenaires symbiotiques est un prérequis à toute interaction. Au-delà de ce pré-requis, la mesure de l'abondance mycorhizienne peut être divisée en trois composantes: l'abondance des hyphes fongiques extra-radicaux du mycobionte, l'abondance des racines fines du phytobionte, et l'intensité de la colonisation des racines du phytobionte par le mycobionte (Soudzilovskaia *et al.*, 2017). La distribution au niveau horizontal est souvent estimée en fonction de la présence ou l'abondance des phytobiontes, qui sont facilement observables et relativement bien connus. Mais outre la distribution spatiale au niveau horizontal, il est aussi important de considérer la dimension verticale des mycorhizes (Bahram *et al.*, 2015). Ainsi, le manque de connaissances concernant la distribution à travers les différents horizons d'un profil de sol limite notre compréhension de la répartition des mycorhizes et de l'influence exercée par les facteurs physico-chimiques (Dickie *et al.*, 2002; Bahram *et al.*, 2015). Plus généralement, il est possible d'établir la dominance mycorhizienne d'une forêt en fonction des stratégies mycorhiziennes des arbres présents dans une zone donnée. Ainsi, il est par exemple admis que la forêt boréale est dominée par les EcM, car les arbres qui la composent forment majoritairement des associations avec des champignons ectomycorhiziens (Read & Perez-Moreno, 2003). De plus, il est possible de déterminer un degré de dominance de manière plus précise et quantitative en utilisant la surface terrière du peuplement forestier étudié. Le diamètre à hauteur de poitrine (DHP) est une mesure souvent effectuée lors des relevés forestiers et à partir de laquelle il est possible de calculer la surface terrière. Cette approche permet de quantifier la proportion ou la dominance mycorhizienne forestière à l'échelle locale (p. ex. parcelle forestière) ainsi qu'à l'échelle mondiale (Fig. 2). La stratégie mycorhizienne dominante (qualitatif) et la proportion mycorhizienne en général (quantitatif) peuvent être intégrées comme facteurs pour expliquer le rôle des mycorhizes dans les processus écologiques, mais aussi pour mieux comprendre l'impact des facteurs environnementaux sur la distribution des mycorhizes.

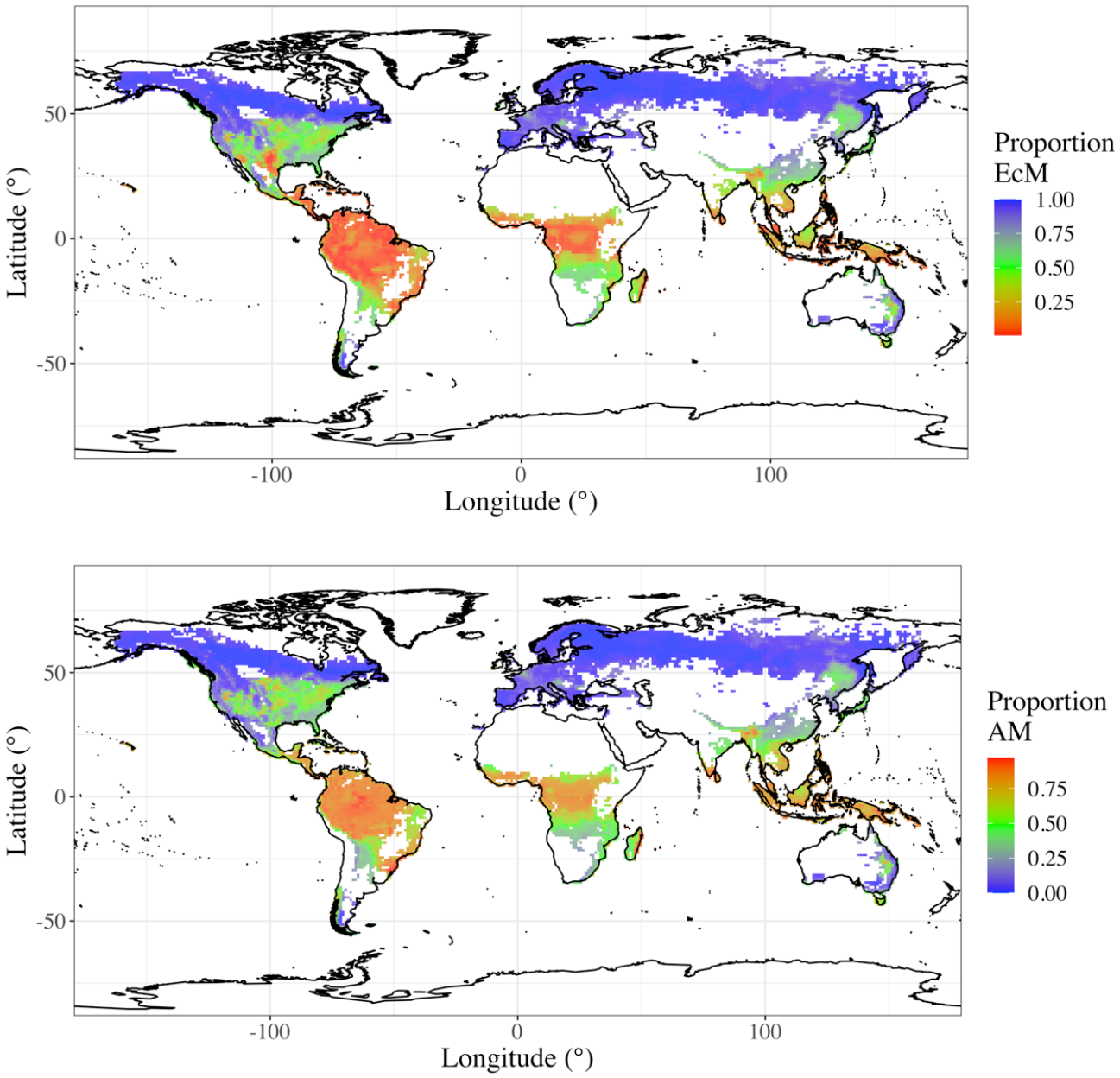

Figure 2. Répartition mondiale des deux types mycorhiziens les plus répandus, à savoir les ectomycorhizes (EcM, carte du haut) et les mycorhizes arbusculaires (AM, carte du bas), estimée à partir de la surface terrière de projections affichées à une échelle de 1° par 1° de latitude et longitude. Pour un grand nombre de cas, la somme de la surface terrière des EcM et AM est proche de 1. Données disponibles sur une intervalle de]0-1] pour les EcM et [0-1[pour les AM (voir Steidinger *et al.*, 2019), et en accès libre à l'adresse suivante : https://doi.org/10.1038/s41586-019-1128-0.

Les patrons de dominance des mycorhizes au niveau du biome coïncident avec des gradients distincts des propriétés du sol (Read, 1991). Ces grands patrons biogéographiques semblent être stabilisés par des traits mycorhiziens, probablement par le biais de rétroactions locales entre plantes, champignons et environnement (Read & Perez-Moreno, 2003; Soudzilovskaia *et al.*, 2019). Dans sa proposition initiale, Read (1991) a divisé grossièrement la Terre en biomes dominés par les plantes à AM (p. ex. les prairies tempérées), par les plantes à EcM (p. ex. la forêt boréale), par les plantes à ErM (p. ex. la toundra) et les zones « mixtes », conjointement dominées par plus d'un type de stratégie mycorhizienne (p. ex. la végétation méditerranéenne). Ainsi, les plantes à AM se retrouveraient dans des écosystèmes où les sols sont davantage minéraux, tandis que ce serait dans des sols plus organiques pour les plantes à EcM et à ErM. Des efforts récents d'unification de bases de données de parcelles présentes sur tous les continents ont permis de mieux estimer la répartition mondiale des mycorhizes (Fig. 2; Crowther *et al.*, 2019; Soudzilovskaia *et al.*, 2019), mais aussi de réviser le statut mycorhizien de nombreuses espèces (Brundrett & Tedersoo, 2020), ce qui pourrait s'avérer important en fonction des études (Tedersoo *et al.*, 2019). Ces études confirment les patrons généraux initialement décrits et mettent par ailleurs en lumière la grande variabilité de la dominance mycorhizienne au sein même de biomes considérés auparavant comme homogènes. Par exemple, la forêt tempérée à l'est de l'Amérique du Nord est conjointement dominée par les AM et les EcM (Phillips *et al.*, 2013). En revanche, la forêt boréale est nettement dominée par des EcM. Il est possible de supposer qu'une forte abondance de plantes à EcM et une faible présence de plantes à AM soit une conséquence des quantités élevées de matière organique dans le sol. L'effet du climat sur la décomposition de la matière organique serait donc un moteur principal de la répartition de la symbiose mycorhizienne en forêt (Steidinger *et al.*, 2019). Cependant, des études tendent à montrer que les partenaires symbiotiques (mycobionte et phytobionte) qui forment les EcM pourraient être les principaux moteurs de l'accumulation en surface de carbone dans le sol (Soudzilovskaia *et al.*, 2019), et non le climat. Cela serait causé par les champignons à EcM qui limiteraient l'azote directement accessible aux plantes et renforceraient donc l'avantage concurrentiel des plantes à EcM dans les systèmes déjà dominés par celles-ci (détaillé en section 3; Näsholm *et al.*, 2013; Corrales *et al.*, 2016; Truong *et al.*, 2019). Néanmoins, ce mécanisme reste à vérifier pour les diverses forêts EcM sur la planète.

Les forêts sont des écosystèmes complexes dans lesquels les arbres sont la forme de vie prédominante. De façon générale, les arbres dominent la végétation dans les habitats où ils ne sont

pas exclus par des perturbations ou des conditions environnementales défavorables. Par conséquent, les écosystèmes forestiers recouvrent une grande partie de la surface terrestre et ils représentent un réservoir pour la biodiversité essentiel à la vie sur Terre. Les forêts constituent également le plus grand réservoir de carbone terrestre au monde (Dixon *et al.*, 1994; Baldrian, 2017). Une grande partie de ce carbone est contenu dans le compartiment souterrain, en particulier pour les forêts des hautes latitudes comme la forêt boréale (Lal, 2005; Crowther *et al.*, 2019). Le stockage du carbone dans les sols est contrôlé par de nombreux facteurs, notamment le climat, la végétation, la topographie et la disponibilité des nutriments (Carvalhais *et al.*, 2014; Wiesmeier *et al.*, 2019). Cependant, les facteurs biotiques souterrains sont également cruciaux pour le cycle du carbone (Schimel & Schaeffer, 2012). C'est le cas des champignons mycorhiziens qui sont reconnus comme jouant un rôle majeur dans le cycle du carbone des forêts. Ils peuvent notamment constituer une source de nécromasse récalcitrante qui se décompose lentement, mais ils sont également en mesure de produire des enzymes extracellulaires qui favorisent en retour la décomposition de la matière organique (Kubartová *et al.*, 2008; Orwin *et al.*, 2011; Frey, 2019).

La grande majorité des arbres en forêt s'associent avec des champignons à AM ou à EcM (Fig. 2; Crowther *et al.*, 2019) et il est estimé que plus de 50% des individus d'espèces d'arbres sur Terre formeraient des EcM (Steidinger *et al.*, 2019). Pour mieux comprendre l'impact de la dominance mycorhizienne sur le cycle du carbone et, plus largement, le fonctionnement des forêts, il est indispensable de prendre en considération les différents types de champignons mycorhiziens et de comparer leurs impacts simultanément (Dickie *et al.*, 2014; Fernandez & Kennedy, 2016; Tedersoo *et al.*, 2020). À l'échelle de la communauté forestière qui nous intéresse ici, il existe un gradient mycorhizien complet, mais une grande partie des communautés n'est dominée que par un seul type de mycorhize (Fig. 3). Des mécanismes de rétroactions positives à l'échelle locale seraient à l'origine du maintien de cette dominance con-mycorhizienne (c.à.d. du même type mycorhizien). L'étude de parcelles forestières voisines dominées par des stratégies mycorhizienne différentes représente une approche prometteuse pour mieux comprendre l'impact des différences clés entre mycorhizes sur le fonctionnement des écosystèmes et la dynamique végétale à l'échelle locale (Phillips *et al.*, 2013; Bahram *et al.*, 2015; Tedersoo *et al.*, 2020). Cette approche semble plus appropriée et précise que celle consistant à comparer des biomes qui présentent de grandes différences climatiques et édaphiques.

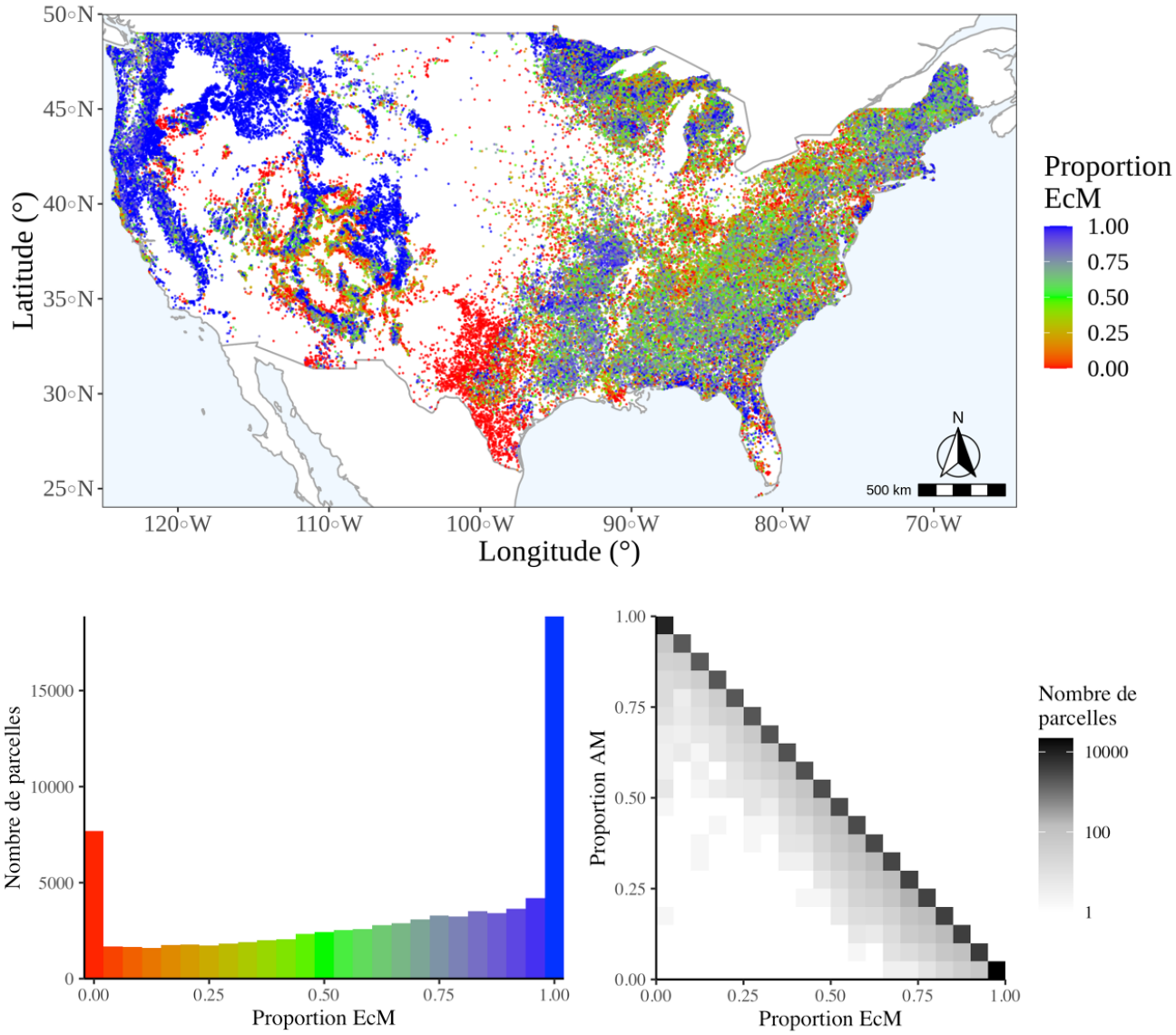

Figure 3. Proportion d'arbres à EcM dans le réseau de parcelles forestières des États-Unis d'Amérique permettant de constater une répartition géographique hétérogène (en haut), en fonction du nombre de parcelles (en bas à gauche) et de la correspondance avec la proportion d'arbres à AM au sein des mêmes parcelles (en bas à droite). Il est possible de voir que la majeure partie des parcelles sont dominées par les EcM et/ou AM, le reste étant des arbres à ErM ou non-mycorhiziens. Ces proportions sont basées sur la surface terrière des arbres ayant un diamètre à hauteur de poitrine supérieur à 12,7 cm. Les parcelles sont composées de quatre sous-parcelles d'environ 168 m^2 et espacées de 36,6 m (voir Burrill *et al.*, 2018). Données disponibles à l'adresse suivante : https://apps.fs.usda.gov/fia/datamart/.

De manière générale, les champignons mycorhiziens ont la capacité d'assurer une meilleure performance à leur phytobionte grâce à leurs hyphes qui améliorent l'exploration du sol et protègent les racines. Les deux guildes les plus courantes de symbiotes de racines d'arbres sont les champignons à AM et les champignons à EcM. Ces guildes impactent profondément la biologie et la dynamique végétale ainsi que les processus du sol, mais elles le font de manière différente (Tedersoo & Bahram, 2019; Frey, 2019; Tedersoo *et al.*, 2020). Certaines différences au niveau éco-physiologique entre champignons à AM et EcM sont cruciales pour comprendre leurs distributions et leurs impacts fonctionnels au sein d'écosystèmes dominés par différents types de mycorhizes (différences détaillées dans la section suivante). Dans l'ensemble, la capacité d'accéder aux nutriments, notamment aux formes organiques complexes, est plus grande chez les champignons à EcM que chez les champignons à AM. Cependant, en raison du coût d'entretien vraisemblablement plus élevé des champignons à EcM pour le phytobionte, les bénéfices nets entre les deux types de mycorhizes seraient similaires (Tedersoo & Bahram, 2019). Les différentes histoires évolutives entre AM et EcM ont abouti à des modes d'acquisition des nutriments distincts. Ces différences ont des impacts sur leurs distributions respectives, mais aussi sur les taux de recyclage des nutriments et de stockage de la matière organique qui peuvent varier grandement en fonction du type dominance mycorhizienne (Frey, 2019).

3. Différences clés entre mycorhizes arbusculaires et ectomycorhizes

Les champignons mycorhiziens exhibent, en général, une grande variabilité spatiale au niveau horizontal (p. ex. Tedersoo *et al.*, 2014), mais aussi vertical (p. ex. Dickie *et al.*, 2002; Jumpponen *et al.*, 2010). Ainsi, la diversité des champignons mycorhiziens peut être très forte, même à de petites échelles spatiales, et le partitionnement vertical de la niche en serait l'un des mécanismes responsables (Bruns, 1995). C'est pourquoi une première étape vers la compréhension des interactions entre champignons mycorhiziens et autres microorganismes du sol, ainsi que des conséquences fonctionnelles qui en résultent, consiste à identifier leurs patrons de cooccurrence dans les sols (p. ex. Peršoh *et al.*, 2018). Plusieurs études ont démontré que les groupes et taxons fongiques diffèrent dans leur distribution verticale, en particulier dans les sols très stratifiés (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Lindahl *et al.*, 2007). Dans les forêts boréales, où les sols sont bien stratifiés, une forte ségrégation verticale des guildes de champignons se produit dans le profil de sol, où la couche de litière est dominée par les champignons saprotrophes, alors que les couches

plus anciennes et plus profondes sont davantage dominées par les champignons mycorhiziens (Lindahl *et al.*, 2007; McGuire *et al.*, 2013; Santalahti *et al.*, 2016). Cependant, différents groupes de champignons peuvent se faire concurrence autour des ressources du sol, en raison de niches qui se chevauchent (Mujic *et al.*, 2016; Fernandez & Kennedy, 2016; Bödeker *et al.*, 2016). Les champignons à EcM bénéficient d'un accès plus direct aux nutriments sous forme organique, tandis que les champignons à AM dépendent indirectement des microorganismes saprotrophes pour l'assimilation des nutriments organiques (Lindahl & Tunlid, 2015; Brzostek *et al.*, 2015; Hodge, 2017). Par conséquent, il reste à discerner si la séparation spatiale des champignons observée dans les sols, notamment les sols de forêt boréale, est davantage causée par la différenciation de niche ou par l'exclusion compétitive dans les horizons organiques des champignons saprotrophes par les champignons à EcM (Fernandez & Kennedy, 2016; Bödeker *et al.*, 2016). Les interactions compétitives pour les nutriments entre ces deux groupes de champignons peuvent largement influencer certains processus écologiques tels que le stockage du carbone (Clemmensen *et al.*, 2013; Baskaran *et al.*, 2017; Kyaschenko *et al.*, 2017). Étant donné que la compétition entre les champignons à AM et les saprotrophes devrait être plus faible, le patron vertical de distribution pourrait s'avérer être moins différencié dans les forêts dominées par les AM. Cependant, les données disponibles sur la distribution verticale des champignons dans les écosystèmes dominés par des plantes à AM proviennent largement de prairies ou de systèmes de culture (Oehl *et al.*, 2005; Montero Sommerfeld *et al.*, 2013; Higo *et al.*, 2013) et non de forêts, où les AM peuvent être tout aussi dominantes (Fig. 3).

Une hypothèse générale sur la ségrégation verticale parmi les différents types mycorhiziens suggère que, lorsqu'ils sont présents en même temps, les champignons à EcM prédominent dans les horizons et les sols généralement organiques, tandis que les champignons à AM occupent principalement les horizons et les sols minéraux (Read, 1991; Smith & Read, 2008). Ce point de vue est étayé par des études basées sur des observations de colonisation racinaire avec la présence de différents types mycorhiziens (p. ex. Moyersoen *et al.*, 1998; Neville *et al.*, 2002), sur des mesures indirectes liées à la nutrition des plantes (Fig. 4; Smith & Read, 2008), et sur des patrons globaux de distribution (Fig. 2; Read, 1991; Allen *et al.*, 1995). Toutefois, cette hypothèse sur la distribution verticale des types mycorhiziens à travers les divers horizons n'a pas été appuyée par des analyses détaillées des communautés fongiques. Peu d'études ont été portées sur la distribution verticale à de fines échelles spatiales, et un nombre encore plus restreint d'entre elles l'ont fait en

examinant différents types mycorhiziens concomitants, et ce notamment en raison de limitations techniques (détaillées en section 1). Par conséquent, on ne sait toujours pas avec certitude si les champignons à EcM et à AM présentent des niches verticales différentes (Smith & Read, 2008), ce qui limite notre compréhension de leurs interactions avec les organismes saprotrophes.

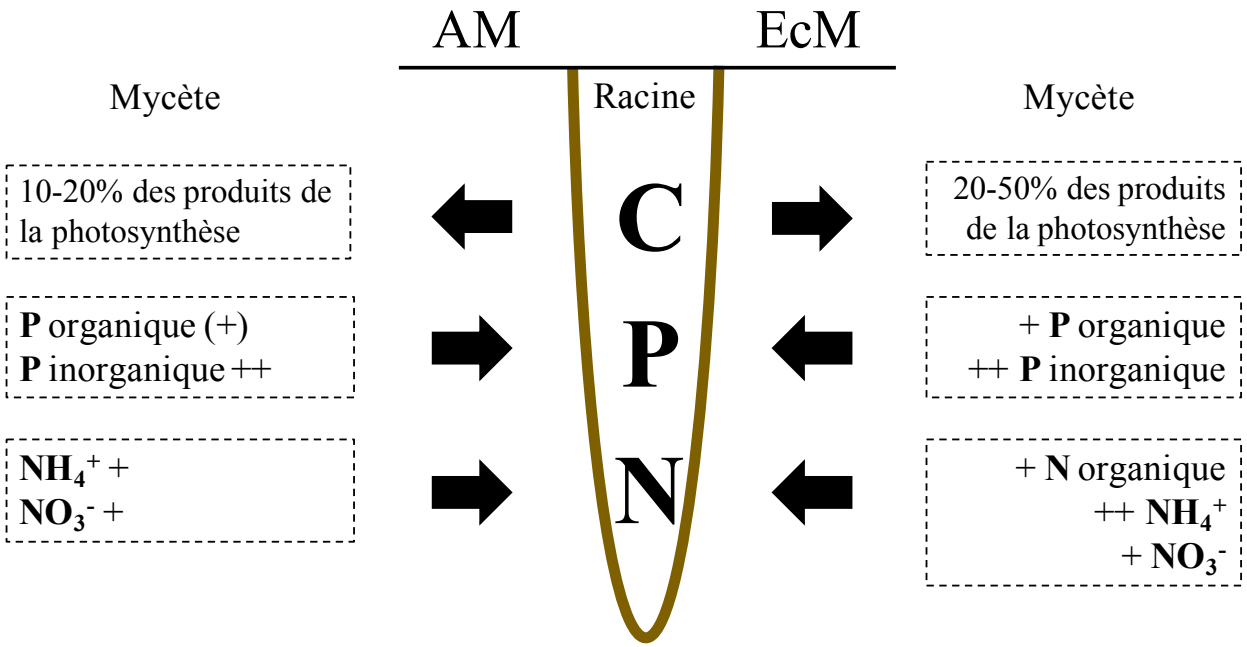

Figure 4. Schéma conceptuel des effets des deux types majeurs mycorhiziens sur la nutrition des partenaires symbiotiques en carbone (C; Hobbie & Hobbie, 2008; van der Heijden *et al.*, 2015), en phosphore (P; Smith & Smith, 2011; Cairney, 2011) et en azote (N; Hodge & Storer, 2015; Hodge, 2017). Les flèches pointent vers le partenaire mycorhizien qui reçoit l'élément. Le symbole + représente la capacité du mycobionte à acquérir directement l'élément et à le transférer au phytobionte.

L'interaction entre champignons mycorhiziens et saprotrophes est d'une importance potentiellement considérable pour la prédiction des cycles globaux tels que ceux du carbone et de l'azote (Terrer *et al.*, 2016; Brzostek *et al.*, 2017; Frey, 2019). Il a été démontré que les écosystèmes qui diffèrent de par leurs types mycorhiziens sont associés à des modèles de cycles biogéochimiques locaux significativement différents (Read & Perez-Moreno, 2003; Phillips *et al.*, 2013; Netherway *et al.*, 2020). L'accumulation de carbone serait par exemple plus importante dans les écosystèmes dominés par les EcM que dans ceux dominés par les AM (Averill *et al.*, 2014;

Crowther *et al.*, 2019; Soudzilovskaia *et al.*, 2019). Une hypothèse de longue date suggère que les champignons à EcM ralentissent la décomposition de la litière, en raison de leur compétition avec les organismes saprotrophes libres du sol pour les nutriments organiques (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016). Comme les champignons à EcM acquièrent leur carbone par le biais des phytobiontes, ils laisseraient derrière eux une matière organique riche en carbone, favorisant ainsi l'accumulation de carbone dans le sol. D'autre part, certains champignons à EcM ont la capacité d'oxyder la matière organique, limitant ainsi la disponibilité des ressources pour les organismes saprotrophes (Lindahl & Tunlid, 2015; Verbruggen *et al.*, 2017). Les champignons saprotrophes pourraient également être influencés par les champignons à EcM, et ce par le biais de mycoparasitisme, d'antibiose et de l'altération des conditions abiotiques vers des sols plus acides et moins propices à la croissance des organismes libres du sol (Fernandez & Kennedy, 2016; Bahram *et al.*, 2020). Cependant, l'hypothèse suggérant le ralentissement de la décomposition de par la présence de champignons à EcM dépend de certains éléments du contexte tels que la qualité de la litière (Smith & Wan, 2019) et du taux d'humidité (Koide & Wu, 2003). De plus, cette hypothèse n'a été appuyée que par quelques études concentrées en surface du sol et sur un seul type mycorhizien, rendant difficile la distinction des effets à différentes profondeurs des AM et EcM sur la décomposition de la matière organique.

Les champignons à AM n'ont pas la capacité de produire des enzymes extracellulaires qui décomposent efficacement la matière organique (Tisserant *et al.*, 2013; Tedersoo & Bahram, 2019). Par conséquent, un ralentissement de la décomposition de la matière organique n'est pas prévu à court terme dans les forêts dominées par les AM, mais cela reste à vérifier de manière spécifique (Fernandez & Kennedy, 2016; Frey, 2019). Dans certains cas, les champignons à AM pourraient même favoriser la décomposition en stimulant l'activité des saprotrophes libres dans le sol (Hodge, 2017; Frey, 2019). De plus, il sembleraient que les champignons à AM produisent une moins grande biomasse de mycélium, qui est aussi potentiellement moins récalcitrante que celle des champignons à EcM (Leake *et al.*, 2004). En comparaison des champignons à AM ou des racines, les champignons à EcM ont une meilleure capacité à extraire l'azote des sols qui n'en contiennent que de faibles quantités, et en immobilisant cet azote dans leur propre biomasse, ils limitent la croissance d'autres microorganismes tels que les saprotrophes (Terrer *et al.*, 2018; Tedersoo & Bahram, 2019).

Les différences observées dans le cycle des nutriments entre les systèmes AM et EcM pourraient aussi être dues à des différences au niveau des taux de décomposition de la litière (Read, 1991). En effet, les plantes à AM ont tendance à produire une litière de haute qualité qui se décompose plus rapidement que celle des plantes à EcM, notamment en raison de rapports C/N et lignine/N plus faibles (Read & Perez-Moreno, 2003; Lin *et al.*, 2017; Keller & Phillips, 2019). Les systèmes dominés par les AM ont donc tendance à avoir une litière qui est rapidement décomposée par les saprotrophes, ce qui entraîne une minéralisation élevée du carbone, des transformations de l'azote organique en azote inorganique et une respiration plus élevée au niveau du sol (Phillips *et al.*, 2013; Taylor *et al.*, 2016). Ainsi, les systèmes EcM sont en général composé d'une plus grande biomasse fongique qui est dominée par les champignons ectomycorhiziens, au contraire des systèmes AM où les bactéries, les saprotrophes et les pathogènes seraient plus abondants (Netherway *et al.*, 2020). Parmi la faune du sol, les herbivores, les prédateurs et les vers de terre tendraient aussi à être plus abondants dans les systèmes AM. En effet, la plus grande présence de bactéries par rapport aux champignons et la moins bonne protection des racines devraient favoriser une plus grande densité d'invertébrés herbivores, de protistes et de nématodes bactérivores, ainsi qu'une plus grande densité de leurs prédateurs et pathogènes associés (Antunes & Koyama, 2017; Netherway *et al.*, 2020). Les systèmes dominés par les AM possèdent une économie dite inorganique, où le recyclage des nutriments est plutôt rapide et dans lesquels les champignons AM recherchent les nutriments inorganiques libérés de la matière organique par d'autres organismes du sol. Cela contraste au niveau de l'utilisation des nutriments avec les systèmes dominés par les EcM qui sont basés davantage sur les champignons et une économie organique avec un recyclage des nutriments plutôt lent et conservateur. En résumé, les différences clés entre AM et EcM sont nombreuses et influencent de façon majeure les processus écologiques au sein des forêts. Une meilleure compréhension des dynamiques mycorhiziennes permettrait de relier les processus végétaux et microbiens, couplant ainsi les cycles du carbone et des nutriments (Brzostek *et al.*, 2017).

4. Quel impact local de la dominance mycorhizienne sur la réponse des communautés forestières aux conditions environnementales ?

La plupart des arbres s'associent à l'un des deux types majeurs de champignons mycorhiziens (AM ou EcM) qui ont des influences distinctes et non-négligeables sur les processus écologiques (Tedersoo & Bahram, 2019). Il peut donc être utile de définir les forêts en fonction de la dominance

mycorhizienne, afin de pouvoir faire des prédictions sur les processus écologiques au sein de différents écosystèmes forestiers. Dans ce sens, une classification des forêts basée sur l'association mycorhizienne a été proposée afin de comparer leur sensibilité face aux changements environnementaux (Phillips *et al.*, 2013; Terrer *et al.*, 2016). Cependant, du fait que les forêts, selon qu'elles sont dominées par des AM ou par des EcM, diffèrent significativement en termes de propriétés physico-chimiques du sol, il est difficile de distinguer l'impact direct des propriétés locales de nature abiotiques de celles qui sont de nature biotiques ainsi que leurs interactions sur les processus écologiques (Bennett & Klironomos, 2019). En influençant les interactions entre sol et plante, les mutualistes tels que les champignons mycorhiziens peuvent être des facteurs importants de la répartition des plantes, notamment dans les contextes de succession végétale (Nara, 2006), d'expansion de l'aire de répartition (Richardson *et al.*, 2000), de maintien des communautés végétales riches en espèces (van der Heijden, 2004), mais aussi des réponses aux changements environnementaux globaux (Jo *et al.*, 2019).

L'association mycorhizienne est un prédicteur important de la répartition des espèces végétales (Pringle *et al.*, 2009; Klironomos *et al.*, 2011; Gerz *et al.*, 2018). En effet, l'absence ou la présence de symbiontes mycorhiziens a été un facteur majeur de la propagation de certaines plantes introduites (Nuñez *et al.*, 2009; Dickie *et al.*, 2010). Le stade juvénile est d'ailleurs particulièrement sensible et dépendant de la symbiose mycorhizienne (van der Heijden, 2004; Nara, 2006), mais c'est aussi un stade crucial pour l'établissement des plantes. On peut distinguer deux facteurs importants liés aux mycorhizes pour l'établissement d'une plante hors de son aire de répartition : le type de stratégie de la plante concernée et la dominance mycorhizienne de l'écosystème « receveur ». Il y a un intérêt pressant quant à la compréhension de l'impact du réchauffement climatique sur la dynamique des communautés végétales, afin de pouvoir faire des prédictions sur la végétation future et les rétroactions possibles sur le cycle du carbone (Zhu *et al.*, 2012; Corlett & Westcott, 2013). Le réchauffement de la température moyenne prédit par exemple un déplacement de l'aire de distribution de nombreuses espèces de plantes vers le nord (Talluto *et al.*, 2017). Bien qu'ils aient été moins étudiés, les facteurs non-climatiques sont quant à eux reconnus comme ayant un fort potentiel d'influencer la régénération des espèces méridionales dans les écosystèmes plus nordiques, comme c'est le cas pour la migration des espèces de la forêt tempérée vers la zone boréale (Lafleur *et al.*, 2010; Brown & Vellend, 2014). Étant une zone de fortes variations environnementales, l'écotone tempéré-boréal a pour sa part fait l'objet de nombreuses études

portant sur la dynamique de la végétation (par ex. Savage & Vellend, 2015; Evans & Brown, 2017; Brice *et al.*, 2019). Plus précisément, la forêt boréale est dominée par les EcM alors que la forêt tempérée comprend davantage d'arbres formant des AM, faisant ainsi de la transition tempérée-boréale une zone de choix pour étudier l'influence de la dominance mycorhizienne sur la dynamique de la végétation. La dominance mycorhizienne pourrait donc directement impacter l'établissement de plantes hors de leur aire de répartition, influençant de ce fait leurs futures distributions, mais aussi le maintien de la diversité végétale de façon générale.

Les champignons mycorhiziens sont reconnus pour leur aptitude à façonner les communautés végétales et notamment pour ce qui est de la diversité des espèces (van der Heijden *et al.*, 1998; Revilla *et al.*, 2012). En effet, il a été démontré expérimentalement que les champignons à AM peuvent augmenter ou diminuer cette diversité en balançant la performance des espèces dominantes (Lin *et al.*, 2015). Cependant, il reste à déterminer l'impact des différents types mycorhiziens sur la diversité végétale à l'échelle de la communauté forestière. Une grande partie des recherches a toujours été menée sur les champignons et les plantes à AM, notamment pour des raisons techniques car les herbacées, majoritairement associées à des champignons à AM, sont plus faciles à utiliser en approche expérimentale (Kernaghan, 2005; Lin *et al.*, 2015; Tedersoo *et al.*, 2020). Or, il n'est pas possible de généraliser les effets des AM aux autres types de mycorhizes en raison de leurs grandes différences éco-physiologiques. Dans une démarche plus globale, mais limitée à l'observation, certaines études ont permis de constater que les grands patrons de dominance des mycorhizes au niveau du biome, qui correspondent à des gradients distincts des propriétés du sol, semblent aussi correspondre à des gradients de richesse végétale (Connell & Lowman, 1989; Brundrett, 1991; Allen *et al.*, 1995; Tedersoo *et al.*, 2020). Les observations historiques de la dominance mycorhizienne au niveau du biome suggèrent que les communautés végétales plus riches sont dominées par les AM, contrairement aux EcM (Brundrett, 1991; Allen *et al.*, 1995; Tedersoo *et al.*, 2020). Cette idée est appuyée par des exemples de grande richesse végétale dans les forêts néo-tropicales, qui sont souvent dominées par des arbres à AM (Wilson *et al.*, 2012) et où, à l'opposé, il subsiste pourtant des peuplements mono-spécifiques d'arbres à EcM (Connell & Lowman, 1989; Peh *et al.*, 2011). Plusieurs mécanismes imputés aux EcM seraient responsables de l'amoindrissement de la diversité végétale dans les forêts dominées par ce type de mycorhize. En effet, les champignons à EcM sont connus pour : (i) protéger les plantes contre les pathogènes du sol, favorisant ainsi la concentration des congénères (Bagchi *et al.*, 2014; Laliberté *et al.*, 2015;

Bennett *et al.*, 2017), (ii) diminuer l'accès direct des plantes aux nutriments inorganiques en modifiant leur disponibilité dans le sol (Read & Perez-Moreno, 2003; Tedersoo & Bahram, 2019), et (iii) favoriser l'accumulation de composés organiques et allélopathiques pouvant entraver l'établissement des semis et des organismes symbiotiques non EcM (Corrales *et al.*, 2016; Fernandez & Kennedy, 2016; Tedersoo *et al.*, 2020). En définitive, grâce à ces nombreux mécanismes qui se mettent en place à l'échelle de l'individu, de façon concomitante et en interaction, les plantes qui s'associent aux champignons à EcM ont potentiellement tendance à être impliquées dans des rétroactions plante-sol plutôt positives, tandis que les plantes à AM bénéficient de leurs symbiotes fongiques dans une moindre mesure (Bennett *et al.*, 2017; Teste *et al.*, 2017). Les observations de patrons de richesse à l'échelle mondiale ont conduit à proposer l'hypothèse générale selon laquelle la dominance des EcM réduirait la diversité végétale. Néanmoins, cela reste à tester à l'échelle plus fine de la communauté forestière, d'autant que certains éléments du contexte local, tels que la disponibilité en eau, peuvent fortement impacter les effets des mycorhizes sur les écosystèmes (Koide & Wu, 2003; Bennett & Klironomos, 2018). Une échelle spatiale plus réduite pourrait également permettre de dissocier le(s) effet(s) des mycorhizes sur la diversité des plantes le long de larges gradients environnementaux. De plus, pour mieux appréhender le rôle des mycorhizes dans la structuration des communautés végétales, les écologistes auraient avantage à s'intéresser aux systèmes dans lesquels différents types de mycorhizes sont bien représentés, tels que les forêts tempérées à feuilles caduques, les maquis méditerranéens et les forêts tropicales de montagne (Brundrett, 1991; Tedersoo *et al.*, 2020).

5. Cadre conceptuel et objectifs de la thèse

Dans le cadre de cette thèse, je me suis appliqué à décrire et à comprendre l'impact au niveau local de la dominance mycorhizienne sur les processus écologiques dans le but de mieux comprendre le fonctionnement des écosystèmes forestiers (Fig. 5). L'action de la symbiose mycorhizienne se situe à l'échelle du micron, que ce soit pour la protection face aux pathogènes, les réactions enzymatiques liées à l'accès aux nutriments ou leurs transferts. Pourtant, les impacts de la symbiose mycorhizienne peuvent avoir une incidence à plus grande échelle, jusqu'au niveau de la biosphère terrestre et du climat. Étant donné que la majorité des arbres forment des AM ou des EcM, et que ces types mycorhiziens ont une influence distincte sur les processus écologiques, il peut être pertinent de définir les forêts par rapport à leur dominance mycorhizienne (Fig. 5). Les variations

de dominance mycorhizienne affectent l'identité et la distribution des partenaires symbiotiques, mais également l'environnement dans lesquels ils évoluent et *vice-versa*, créant ainsi une boucle de rétroactions (Fig. 5). Mieux comprendre les patrons de distribution des mycorhizes et les interactions entre plante-mycète-environnement permet de mieux définir le rôle des mycorhizes dans les processus écologiques. À terme, et en raison de leur impact, il serait d'ailleurs nécessaire d'inclure les mycorhizes dans les modèles globaux de biosphère terrestre. Ainsi, cette thèse s'articule autour de quatre objectifs, chacun étant traité dans les différents chapitres faisant suite à l'Introduction et qui ont fait l'objet de publications scientifiques sous forme d'articles revus par des pairs, ou de manuscrits qui seront soumis à cette occasion. Il s'en suit une conclusion générale pour synthétiser les résultats présentés et pour ouvrir la discussion

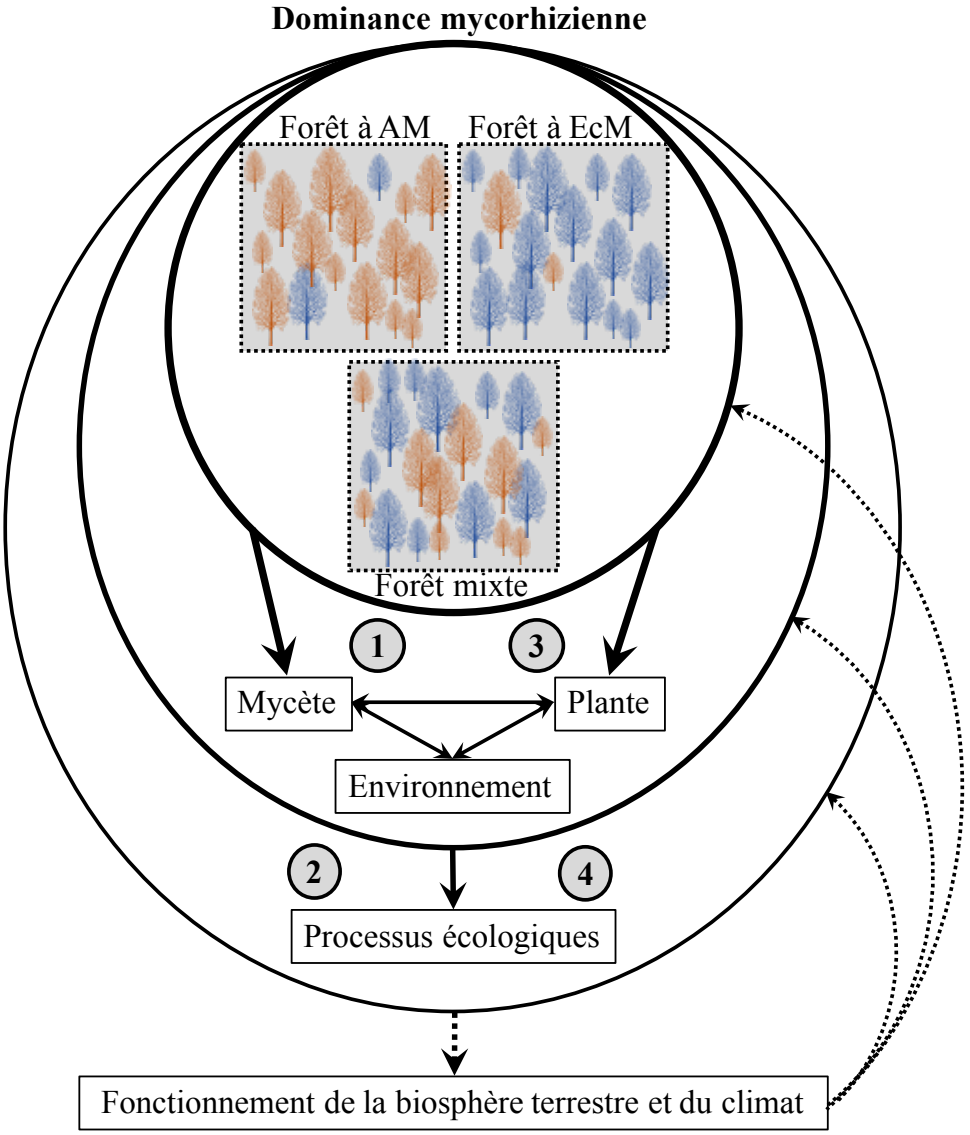

Figure 5. Schéma conceptuel illustrant la structure de la présente thèse (les chiffres encerclés correspondant aux chapitres) dans les différents contextes de dominance par les mycorhizes arbusculaires (AM, en rouge), par les ectomycorhizes (EcM, en bleu), ou d'une dominance partagée entre AM et EcM (mixte). Cette thèse met en avant l'impact de la dominance mycorhizienne (intérieur de la première ellipse) sur les organismes associés à la symbiose mycorhizienne et leur environnement (intérieur de la deuxième ellipse, sujet principalement investigué dans les chapitres 1 et 3), le tout étant déterminant dans la modulation des processus écologiques (intérieur de la troisième ellipse, sujet principalement investigué dans les chapitres 2 et 4). Finalement, l'ensemble des impacts la dominance mycorhizienne influence le fonctionnement de la biosphère et le climat (en dehors des ellipses). Ces facteurs à larges échelles peuvent, à leur tour, directement impacter les processus écologiques, mais aussi la symbiose mycorhizienne et même sa distribution, notamment dans un contexte de changements climatiques et de diminution de la biodiversité. Les flèches pleines indiquent les effets testés dans cette thèse et les flèches en pointillés indiquent des effets non testés.

Étant donné que la distribution des partenaires symbiotiques peut être influencée par les propriétés abiotiques du sol mais aussi par d'autres organismes libres présents dans celui-ci, il est important d'identifier les interactions potentielles et d'en mesurer les impacts de façon distincte. Ainsi, l'objectif du **Chapitre 1** est de mieux comprendre de quelle manière la dominance mycorhizienne et la chimie du sol influencent la distribution verticale entre les différentes guildes de champignons (notamment les champignons saprotrophes et mycorhiziens) à une fine échelle spatiale, afin de mieux appréhender les effets de leurs interactions biotiques. L'hypothèse principale est que le changement de dominance au niveau vertical, des champignons saprotrophes aux champignons mycorhiziens, se produit plus profondément dans le sol des forêts à AM que dans les forêts à EcM, et à une profondeur intermédiaire dans les forêts mixtes avec les champignons à EcM préférentiellement dans les horizons organiques et les champignons AM dans les horizons minéraux. Cela serait dû à des niches potentiellement plus similaires entre EcM et saprotrophes, et à des propriétés physico-chimiques divergentes selon le type mycorhizien qui prédomine dans les différentes forêts.

Ces interactions souterraines et complexes entre mycorhizes, microorganismes et facteurs abiotiques peuvent engendrer des effets importants sur d'autres processus écologiques des

écosystèmes forestiers tels que les cycles des nutriments et du carbone. Ainsi, l'objectif du **Chapitre 2** est de quantifier l'impact des différents acteurs impliqués dans la décomposition de la matière organique du sol et l'impact de la qualité de la matière organique selon qu'on se trouve dans une forêt dominée par les AM ou par les EcM, l'hypothèse étant que la décomposition de la matière organique serait différente en fonction du type de dominance mycorhizienne. Selon cette hypothèse, la décomposition serait plus lente en cas de dominance par les EcM en raison de l'inhibition des microorganismes saprotrophes. Néanmoins, ce ralentissement pourrait s'avérer être plus marqué dans l'horizon fragmenté où coïncident à la fois matière organique issue de la litière, organismes saprotrophes, champignons mycorhiziens et racines fines.

La symbiose mycorhizienne est essentielle aux plantes dans leur acquisition des éléments nutritifs du sol et influence aussi plus largement les cycles biogéochimiques des forêts. Elle a donc un fort potentiel d'influence sur la rétroaction des arbres avec le sol. Ainsi, l'objectif du **Chapitre 3** est de comprendre de quelle manière les facteurs abiotiques et biotiques au sein de forêts dominées par différents types de mycorhizes, selon un gradient d'élévation et de dominance mycorhizienne, peuvent influencer l'établissement de semis. L'hypothèse principale consiste à dire que les propriétés édaphiques abiotiques telles que la disponibilité en nutriments, mais aussi les propriétés biotiques telles que la colonisation par les champignons à AM, limitent la performance des semis d'érable à sucre dans les sols en dehors de leur aire de répartition.

La dominance mycorhizienne a un fort potentiel d'influence sur la dynamique des communautés végétales forestières à long terme, et ce de façon persistante au sein d'environnements très variés. Elle affecte la survie et la croissance des arbres (*cf.* Chapitre 3), mais elle agit aussi en tant que facteur local déterminant des processus écologiques des sols tels que la décomposition de la matière organique (*cf.* Chapitre 2) et les interactions biotiques entre champignons (*cf.* Chapitre 1). Ainsi, l'objectif du **Chapitre 4** est de déterminer comment la dominance mycorhizienne module la diversité des arbres en forêt, l'hypothèse étant que la diversité globale des arbres diminue à mesure que la proportion des arbres s'associant aux EcM augmente dans la communauté forestière. Cette hypothèse se base sur le fait que les plantes à EcM ont tendance à être impliquées dans des rétroactions plantes-sol plus positives que les plantes à AM. Étant donné que les patrons de dominance mycorhizienne sont liés aux facteurs environnementaux, les conditions climatiques, topographiques et physiographiques devraient elles aussi influencer la diversité locale des arbres.

Hêtre à grandes feuilles et érable à sucre, tronc à tronc, St-Hippolyte.

CHAPITRE 1 – Les forêts tempérées dominées par des champignons mycorhiziens à arbuscules ou ectomycorhiziens sont caractérisées par un fort changement des champignons saprotrophes vers les champignons mycorhiziens plus en profondeur dans le sol

Temperate forests dominated by arbuscular or ectomycorrhizal fungi are characterized by strong shifts from saprotrophic to mycorrhizal fungi with increasing soil depth

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Keywords: Fungal guilds; Soil physico-chemistry; Podzolic soil; Vertical segregation; *Acer saccharum*; *Fagus grandifolia*.

Published in: *Microbial Ecology*

DOI: https://doi.org/10.1007/s00248-020-01540-7

Abstract

In temperate and boreal forests, competition for soil resources between free-living saprotrophs and ectomycorrhizal (EcM) fungi has been suggested to restrict saprotrophic fungal dominance to the most superficial organic soil horizons in forests dominated by EcM trees. By contrast, lower niche overlap with arbuscular mycorrhizal (AM) fungi could allow fungal saprotrophs to maintain this dominance into deeper soil horizons in AM-dominated forests.

Here we used a natural gradient of adjacent forest patches that were dominated by either AM or EcM trees, or a mixture of both to determine how fungal communities characterized with high-throughput amplicon sequencing change across organic and mineral soil horizons.

We found a general shift from saprotrophic to mycorrhizal fungal dominance with increasing soil depth in all forest mycorrhizal types, especially in organic horizons. Vertical changes in soil chemistry, including pH, organic matter, exchangeable cations, and extractable phosphorus, coincided with shifts in fungal community composition.

Although fungal communities and soil chemistry differed among adjacent forest mycorrhizal types, variations were stronger within a given soil profile, pointing to the importance of considering horizons when characterizing soil fungal communities. Our results also suggest that in temperate forests, vertical shifts from saprotrophic to mycorrhizal fungi within organic and mineral horizons occur similarly in both ectomycorrhizal and arbuscular mycorrhizal forests.

Introduction

Soil fungi drive the biogeochemical cycling of carbon (C) and nutrients in terrestrial ecosystems. Free-living saprotrophic fungi are major decomposers of soil organic matter, but mycorrhizal fungi also play an important role (Kubartová *et al.*, 2008; Crowther *et al.*, 2019; Frey, 2019). In northern temperate forests, there are two major types of root-associated fungi: arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungi (Brundrett, 2017; Steidinger *et al.*, 2019). Mycorrhizal fungi acquire C via plant hosts and many EcM fungi possess the enzymatic capacity to directly degrade organic matter, potentially competing with free-living saprotrophs for organic nutrients such as nitrogen (N), which promote soil C accumulation (Dickie *et al.*, 2014; Fernandez & Kennedy, 2016; Verbruggen *et al.*, 2017). By contrast, AM fungi have limited degrading abilities and therefore might compete less strongly with saprotrophic fungi for nutrients (Smith & Smith, 2011; Phillips *et al.*, 2013; Hodge, 2017). Such interactions among saprotrophic and mycorrhizal fungi could have far-reaching implications for the C cycle, especially in northern forests where a large fraction of global soil C is stored (Dixon *et al.*, 1994; Scharlemann *et al.*, 2014; Crowther *et al.*, 2019). In particular, it has been suggested that these interactions might help to explain differences in the amount and vertical distributions of soil C between ectomycorrhizal- and arbuscular mycorrhizal-dominated forests (Averill *et al.*, 2014; Fernandez & Kennedy, 2016; Craig *et al.*, 2018).

A first step toward understanding of interactions among saprotrophic and mycorrhizal fungi and their functional consequences is to identify their co-occurrence patterns in soils (e.g. Peršoh *et al.*, 2018). Different groups of fungi can compete with each other for soil resources because of overlapping niches (Mujic *et al.*, 2016; Fernandez & Kennedy, 2016; Bödeker *et al.*, 2016; Peršoh *et al.*, 2018). In particular, fungal types and taxa differ in their vertical distribution, especially in well-stratified soil (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Lindahl *et al.*, 2007). In EcM-dominated ecosystems such as boreal forests, strong vertical segregation of fungal guilds occurs in the soil profile, where the litter layer is dominated by saprotrophic fungi and in older and deeper layers are increasingly dominated by EcM fungi (Lindahl *et al.*, 2007; McGuire *et al.*, 2013; Santalahti *et al.*, 2016). However, it remains unclear whether this spatial separation reflects niche differentiation or competitive exclusion of saprotrophic fungi by EcM fungi (Fernandez & Kennedy, 2016; Bödeker *et al.*, 2016). Competitive interactions for nutrients among these fungal groups could promote organic matter accumulation (Clemmensen *et al.*, 2013; Baskaran *et al.*,

2017; Kyaschenko *et al.*, 2017). In AM-dominated forests, interactions and distribution patterns may be different because AM fungi might not compete as strongly with saprotrophic fungi than EcM fungi. However, studies of fungal vertical distribution in AM-dominated ecosystems have largely focused on grasslands and crop systems (Oehl *et al.*, 2005; Montero Sommerfeld *et al.*, 2013; Higo *et al.*, 2013) but not forests. To better understand the impacts of global and land use changes on forest functioning, there is a crucial need to take different mycorrhizal types fungi into consideration simultaneously (Dickie *et al.*, 2014; Fernandez & Kennedy, 2016; Tedersoo *et al.*, 2020), especially the AM strategy given its importance in temperate forests (Phillips *et al.*, 2013).

A general hypothesis on vertical segregation among mycorrhizal types suggests that, when they co-occur, EcM fungi and ericoid mycorrhizal (ErM) will dominate organic horizons while AM fungi will predominantly occupy mineral horizons or soils (Read, 1991; Smith & Read, 2008). This view is supported by studies based on: (i) root colonization patterns in environments where mycorrhizal types co-occur (e.g. Moyersoen *et al.*, 1998), (ii) root patterns and isotopic measurements of plants of different mycorrhizal types (Schulze *et al.*, 1994; e.g. Smith & Read, 2008), (iii) root colonization patterns in "dual mycorrhizal" plants (Reddell & Malajczuk, 1984; Neville *et al.*, 2002; Teste *et al.*, 2020), (iv) the different nutritional benefits of fungal symbionts and their enzymatic capacity (Read, 1991; Smith & Read, 2008) and (v) global patterns of mycorrhizal distribution (Read, 1991; Allen *et al.*, 1995). However, to our knowledge this hypothesis about vertical distribution of distinct mycorrhizal types (e.g. EcM and AM) across horizons has not been supported by detailed fungal community analyses. For example, mycorrhizal fungal distribution does not always follow root distribution (e.g. presence of AM fungi in the litter horizon (Bunn *et al.*, 2019)), and to focus on roots or rhizosphere sampling overlooks at long extraradical hyphae of mycorrhizal fungi that penetrate far from root surfaces. Few studies have studied vertical distribution at spatial scales that are fine (i.e. cm) and functional (i.e. by horizons). To our knowledge, the vertical distribution of soil fungi in neighboring forest stands dominated by different mycorrhizal types has not been reported. Therefore, it is not clear whether EcM or AM fungi show similar vertical niches (Smith & Read, 2008).

The difficulties associated with identifying the microorganisms directly involved in soil biogeochemical cycling such as fungal saprotrophs and mycorrhizal fungi though their extraradical hyphae has been a major obstacle to understand their impacts and the importance of their

interactions. Specific biomarkers can be used as proxy to quantify fungal biomass in soils such as phospholipid fatty acid (e.g. Teste *et al.*, 2016), but they are common in many fungal groups and cannot discriminate between free-living saprotrophic fungi and EcM fungal lineages because EcM symbiosis has arisen independently and persisted numerous times in the Basidiomycetes, Ascomycetes, and Zygomycetes (Tedersoo *et al.*, 2010). Also, the mycelia of some fungi does not contain ergosterol (Weete & Gandhi, 1999). With advances in high-throughput amplicon sequencing (Lindahl *et al.*, 2013), we are able to identify community members and their corresponding guilds (Dickie & John, 2016; Nguyen *et al.*, 2016; Nilsson *et al.*, 2019). Determining the taxonomic composition of fungal communities is important because different species within the same fungal guild can vary in their effects on C and nutrient cycling (e.g. Lindahl & Tunlid, 2015; Sterkenburg *et al.*, 2018). Using such sequencing methods, fungal community composition has been found to vary markedly across large spatial scales, driven by broad-scale changes in climate and soil properties (Talbot *et al.*, 2014; Tedersoo *et al.*, 2014). However, the mechanisms shaping distribution of fungal community and fungal groups such as free-living and root-associated at small spatial scales remain comparatively little studied, and high-throughput amplicon sequencing will allow to understand their potential impact on ecosystem functioning (Dickie *et al.*, 2002; Bahram *et al.*, 2015; Zak *et al.*, 2019).

To determine the vertical distribution of fungal communities and guilds among temperate forests, we characterized soil fungi and chemistry in adjacent forest patches dominated by trees that form AM or EcM or a mixture of both strategies. Specifically, we used the natural co-occurring distribution of *Acer saccharum* and *Fagus grandifolia* that associates exclusively with AM and EcM fungal symbionts respectively (Brundrett *et al.*, 1990). These two co-occurring tree species share similar ecological strategies that they are both deciduous, shade-tolerant and can dominate the canopy in adjacent forest patches in northeastern North America (Poulson & Platt, 1996; Duchesne *et al.*, 2005). Their natural co-occurrence patterns provide an opportunity to compare vertical distribution of fungal community composition in different forest mycorrhizal types, under similar environmental conditions, thus minimizing variation in other important factors such as climate, parent material, or topography. Using this natural experimental design, we assessed how the fungal community, guilds, and root colonization vary across soil horizons along an AM-EcM gradient, and determined to which extent this variability was linked with changes in soil chemical properties. We expected the shift from saprotrophic to mycorrhizal fungi to occur deeper in AM

forests compared to EcM forests, and at an intermediate depth in forests containing a mixture of both strategies.

Material and Methods

Study area

The study was conducted at the University of Montréal's field station (Station de biologie des Laurentides, Saint-Hippolyte, Québec, Canada). The field station is representative of temperate forests of the Lower Laurentians and the Canadian Shield. The soil has a sandy loam texture derived from well-drained rocky glacial till on a bedrock of Precambrian anorthosite (Bélanger *et al.*, 2004; Courchesne *et al.*, 2005). The soils are ferro-humic and gleyed humo-ferric podzols with moder humus forming the forest floor (Courchesne & Hendershot, 1988; Côté *et al.*, 1998; Courchesne *et al.*, 2005). The mean annual temperature is 4.3 °C and total annual precipitation is 1195 mm, with ~ 25% falling as snow (based on 1981–2010 data, meteorological station no. 7037310, Saint-Hippolyte). The study area is located within the sugar maple-yellow birch domain (Saucier *et al.*, 2011). Most of the forest regrew following a major fire that occurred around 1923 (Savage, 2001). Mesic sites are composed mostly of a mosaic of *Acer saccharum* and *Fagus grandifolia,* with *Betula alleghaniensis*, *Populus grandidendata* and *Acer rubrum* also common (Courchesne *et al.*, 2005). The understory comprised various small tree species (e.g. *Acer pensylvanicum*) and shrubs (e.g *Vaccinium* spp., *Viburnum* spp.).

Selection of forest plots

Plots were selected based on the dominance of different mycorrhizal tree types: AM-dominated stands (>80% relative basal area by AM trees; mainly *Acer saccharum*) and EcM-dominated stands (generally >80% relative basal area by EcM trees except one plot at 63%; mainly *Fagus grandifolia*), and mixed stands (approximately equal basal area of AM and EcM trees, mainly *A. saccharum maple* and *F. grandifolia*). Tree basal area was based on all trees ≥5 cm diameter at breast height (DBH) within a plot. Plots were 20 m × 20 m in size. We selected five blocks, each containing one plot of each corresponding to one of the three mycorrhizal types (i.e. EcM, AM, mixed), for a total of 15 plots (Fig. S1). Plots were selected as to minimize variation in environmental conditions (i.e. altitude, slope, aspect, total basal area; Table S1) among plots within

a block, and to be as close as possible from each other (<400 m). For each plot, precise geographic coordinates, altitude, topographic location, slope and orientation were measured (Table S1).

Soil sampling

Soil sampling was conducted in July and August 2015. In each plot, 10 samples were taken along two oriented north-south transects (five samples per transect). Samples were collected to 20 cm depth using PVC cores (7.5 cm in diameter). Samples were kept in coolers with ice and transported to the laboratory to be processed within 96 h of sampling. The PVC cores were split open to measure horizon thickness then separated by: litter (L), where original structures are easily distinguishable, fragmented (F), where there had been partial decomposition where structures were difficult to recognize, and humus (H), comprised of highly decomposed organic matter, where original structures are indistinguishable (see Fig. S2). The mineral horizons were Ae, as characterized by leaching/eluviation of clay, Fe, Al or organic matter; and B, as characterized by illuviation/enrichment in organic matter (Groupe de travail sur la classification des sols, 1998). The 10 samples per plot were pooled by horizon. One sub-sample per horizon per plot was immediately frozen for subsequent DNA extraction. Fine roots (< 2 mm in diameter) were set aside for mycorrhizal colonization analyses and a sub-sample of soil was air-dried for chemical analyses.

Soil analysis

Air-dried soils were analyzed for pH, total carbon (C), total nitrogen (N), total phosphorus (P), organic P, inorganic P and labile P. The pH was determined in 10 mM $CaCl_2$ in a 1:2 soil to solution ratio with a glass electrode. Total C and N were determined simultaneously by automated combustion and gas chromatography with thermal conductivity detection on a Flash EA112 analyzer (CE Elantech, New Jersey, USA). After NaOH-EDTA extraction, inorganic P in the extraction material was determined by molybdate colorimetry at 880 nm with a 1-cm path length. Total P in the NaOH-EDTA extracts was determined by molybdate colorimetry at 880 nm with a 1-cm path length, following acid-persulfate digestion at 80 °C overnight in sealed glass tubes. Organic P was calculated as the difference between NaOH-EDTA total P and NaOH-EDTA P_i. Labile (plant-available) P was determined by Bray-1 extraction, with phosphate detected using automated molybdate colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO). Exchangeable cations were determined by extraction in 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio) and detection by inductively-coupled plasma optical-emission spectrometry (ICP–OES) with

an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA). Total exchangeable bases (TEB) was calculated as the sum of the charge equivalents of Ca, K, Mg and Na. Effective cation exchange capacity (ECEC) was calculated as the sum of the charge equivalents of Al, Ca, Fe, K, Mg, Mn and Na. Base saturation was determined as TEB / ECEC ×100.

Root colonization by fungi

Fungal colonization was determined on fine roots (< 2 mm diameter) of F, H, Ae and B horizons (no roots in the L). Roots were cleared in 10% w/v KOH, then stained in an ink and vinegar solution for 5 min at 90 °C (Brundrett *et al.*, 1996; Vierheilig *et al.*, 1998, 2005). Roots were then rinsed in slightly acidified tap water for 30–40 min to remove excess ink, after which they were placed in a 50% (v/v) lacto-glycerol solution for storage until colonization could be evaluated. The gridline intersection method was performed under stereomicroscope to quantify the length of roots colonized by AM and EcM fungi (Tennant, 1975; Brundrett *et al.*, 1996). Due to magnification limits, some structures of ericoid mycorrhizal fungi might have been included in the AM colonization percentage.

Fungal community characterization

The fungal community was characterized by amplicon sequencing. Soil DNA was extracted using the PowerSoil DNA Isolation Kit (no. 12888-100 - Mo-Bio Laboratories Inc., Carlsbad, USA) following the instructions of the manufacturer. Around 100 mg of soil for organic horizons (L, F and H), and 200 mg for mineral horizons (Ae and B) were used for the extraction.

Soil amplification of the Internal Transcribed Spacer of the ribosomal RNA was performed by Genome Québec (Montréal, Canada) with the ITS3_KYO2 and ITS4 primer pair (Toju *et al.*, 2012). This pair of primer limits coverage bias toward Ascomycetes or Basidiomycetes and is also known to amplify Glomeromycetes (e.g. Toju *et al.*, 2014). The final reaction mix contained 0.02 U μl^{-1} Taq Roche HiFi polymerase, 1 × Buffer 10 × with 18 mM MgCl2, 5% DMSO, 0.2mM of each dNTP and 0.5 μM of each primer and DNA sample diluted at 1/100. Thermal cycling was done in an Eppendorf Mastercycler Gradient (Eppendorf, Hamburg, Germany) with the following cycling conditions: 2 min initial denaturation at 94 °C; 40 cycles of 30 s denaturation at 94 °C, 30 s annealing at 55 °C and 30 s elongation at 72 °C; and a 7 min final elongation at 72 °C. The PCR products were loaded on 1% agarose gels with 1× sodium borate buffer run at 220 V, and visualized after ethidium bromide staining (1 μg ml^{-1}).

Soil amplicon sequencing was performed by using the MiSeq Illumina technology by Genome Québec (Montréal, Canada). The final concentration of the reaction mix contained 0.025 U μl^{-1} Taq Roche HiFi polymerase, 1 × Buffer 10 ×, 1.8mM of $MgCl_2$, and 5% DMSO. Sequencing was done in an MiSeq Illumina with the following conditions: 10 min initial denaturation at 95 °C; 15 cycles of 15 s denaturation at 95 °C, 30 s annealing at 60 °C and 1 min elongation at 72 °C; and a 3 min final elongation.

Bioinformatics

The fungal community was determined by filtering, denoising and assigning taxonomy to paired amplicons using a customized script (https://github.com/alexiscarter/Fungal_com_SBL/tree/master/dada2) adapted from the DADA2 pipeline (Callahan *et al.*, 2016). In brief, using the *filterAndTrim* function, reads were truncated at 280 bp and discarded if they had more than three expected errors or a quality score lower than six. Then, amplicon sequence variants (ASV) were inferred for each sample with the *dada* function. Forward and reverse reads were merged using the *mergePairs* function with a minimum overlap of 12 bp. Potentially chimeric sequences were identified by the pooled method of the *removeBimeras* function. The amplicon sequence variant approach was used instead of the classical operational taxonomic as proposed by Callahan *et al.* (2017) and others (Thompson *et al.*, 2017). This method does not use a particular threshold for classifying sequences into operational taxonomic units, as no threshold appears to be universally applicable for fungi (Nilsson *et al.*, 2008). Instead, it used the divisive amplicon denoising algorithm aimed at finding ASV that refer back to original biological sequences (Rosen *et al.*, 2012; Callahan *et al.*, 2016). The taxonomy of the ASV was assigned with the UNITE database, version 7.2 (Abarenkov *et al.*, 2010). ASV that belong to the same species were grouped together. The functional information for ASV was obtained from the online FUNGuild database (Nguyen *et al.*, 2016).

Statistical analyses

To describe the fungal community and assess the effects of environmental parameters we used ordination approaches and multivariate analyses of variance. The shifted log transformation was applied to normalize the raw sequence count data. The community matrix was composed of the number of sequences per ASV of 75 soil samples from five soil horizons in each of 15 plots (one sample of L horizon in an EcM plot was excluded due to poor amplification). Due to some inherent

limitations of the approach, either biological (e.g. varying number of DNA copies per organism) or technical (varying sequencing depth, extraction and amplification biases among samples), the number of sequence reads is not a direct measure of taxa abundance in the environment, but comparisons among samples remain useful as they can be considered semi-quantitative (Nguyen *et al.*, 2015; Pauvert *et al.*, 2019). Explanatory variables for each sample were classified into three groups: (i) soil chemistry, (ii) soil horizon (L, F, H, Ae or B), and (iii) forest type (AM, EcM or mixed).

Differences in soil properties, root colonization, guild abundance, and richness among horizons and forest type were tested using linear mixed-effect models; block was treated as random factor. Model assumptions were assessed by visual inspections of residuals. Comparisons were determined using post-hoc Tukey tests which were used to determine significant differences.

In β-diversity analyses, we used the Bray-Curtis dissimilarity index for the community structure and its binary version, the Sørensen index for the community composition (Legendre & Legendre, 2012). These asymmetrical coefficients do not consider double zeroes and can therefore be used with raw abundances or counts (Legendre & Legendre, 2012).

To visualize differences in fungal community composition and abundance among samples, we used non-metric multidimensional scaling (NMDS). To test for differences between samples across horizons and forest types, we used permutational multivariate analysis of variance (PERMANOVA). *P*-values for pairwise tests were adjusted using the Benjamini-Hochberg method (Benjamini & Hochberg, 1995). Because the PERMANOVA method is sensitive to differences in multivariate dispersions among groups, the homogeneity of dispersion was tested to assess differences and tested for significance by permutations (Anderson, 2006).

Distance-based redundancy analysis (RDA) was used to quantify the extent to which changes in fungal community structure were related to soil chemistry, horizon and forest type (Legendre & Legendre, 2012). Soil chemistry data were standardized and linear dependencies were explored using variance inflation factors and avoided if >10 (Borcard *et al.*, 2018). To test how much variance was independently explained by the explanatory matrices, variation partitioning was performed using partial RDA (pRDA, Borcard *et al.*, 1992). In RDA and pRDA, coefficients of determination were adjusted (i.e. adjusted-R^2 values) to take into account the number of explanatory variables in the model (Peres-Neto *et al.*, 2006; Legendre *et al.*, 2011).

Analyses were performed and visualized using the R software (R Core Team, 2018) with the following main packages: *dada2* (Callahan *et al.*, 2016, p. 2), *dplyr* (Wickham *et al.*, 2017), *emmeans* (Lenth, 2019), *ggplot2* (Wickham, 2016), *ggpubr (Kassambara, 2018), nlme* (Pinheiro *et al.*, 2012), *phyloseq* (McMurdie & Holmes, 2013) and *vegan* (Oksanen *et al.*, 2017). Code for bioinformatical and statistical analyses are available at: https://doi.org/10.5281/zenodo.3631982. Sequence and chemistry data can be accessed at https://doi.org/10.5281/zenodo.3631861.

Results

Soil chemistry variation across horizons and forest types

All soil chemical properties varied significantly across horizons (Fig. 1), and these differences were consistent across forest types (soil horizon × forest type interaction, $P > 0.05$; except for pH where P-value = 0.026). The pH of the L horizon declined from pH ~4 (in 0.01 M $CaCl_2$) to ~3.25 in the H horizon, but this decline was not as pronounced for AM forests than for EcM or mixed forests (Fig. 1a). The pH then increased from the H to the B horizon in all forests. Effective cation exchange capacity and base saturation declined with increasing depth (Figs. 1b-c), except for ECEC in the Ae horizon. Organic C generally declined with depth, but AM forests tended to have lower organic C concentration in the H horizons than EcM or mixed forests (Fig. 1d). By contrast, total N increased from the L to the Ae horizon and then declined in the B horizon (Fig. 1e). As a result, the C:N ratio decreased with increasing depth from the L to the Ae horizon (Fig. 1f). Inorganic and organic P increased in deeper horizons while labile (Bray) P decreased (Fig. 1g-i).

Forest types differed significantly in their pH, C:N ratio, NaOH-EDTA total P, NaOH-EDTA organic and inorganic P concentrations (P-value < 0.05). AM-dominated forest plots tended to have higher pH, total P, inorganic P and organic P but lower C:N ratio compared to EcM-dominated forest plots.

Root colonization by mycorrhizal fungi

Colonization of fine roots by AM and EcM fungi was significantly different among mycorrhizal type (P-value < 0.0001, Fig. 2) but only differ across horizons in the EcM-dominated forest (P-value = 0.007). Fine roots in AM forest were more strongly colonized by AM fungi than those from mixed and EcM forests (P-value < 0.05, Fig. 2a). By contrast, fine roots in EcM forests were more strongly colonized by EcM fungi compared to those from AM forests (P-value < 0.05, Fig. 2b).

Root colonization by EcM fungi tended to decrease with soil depth in EcM forest down to ~20% in the B horizon (Fig. 2b). In mixed and AM forests, EcM colonization was highest in the H or Ae horizons but always lower than 30.

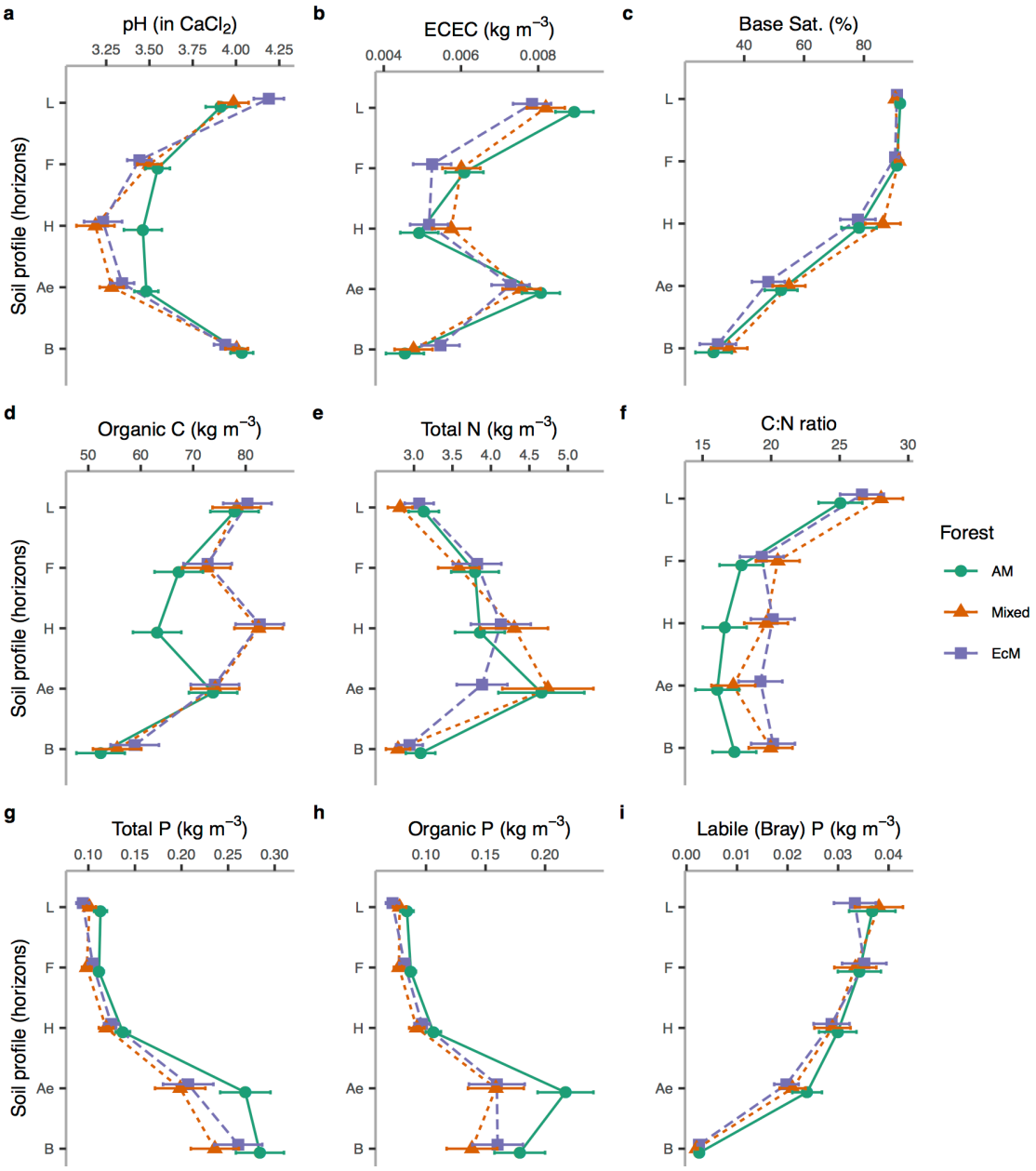

Figure 1. Soil physico-chemical characteristics from organic-to-mineral horizons (L, F, H, Ae, B) in each mycorrhizal forest type (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; Mixed, mixture of AM and EcM): (a) pH (in $CaCl_2$), (b) effective cation exchange capacity, (c) base saturation, (d) organic carbon, (e) total nitrogen, (f) carbon over nitrogen ratio, (f) total phosphorus, (g) organic phosphorus, and (h) labile (Bray) phosphorus. All data are means ± 1 SE (n = 5).

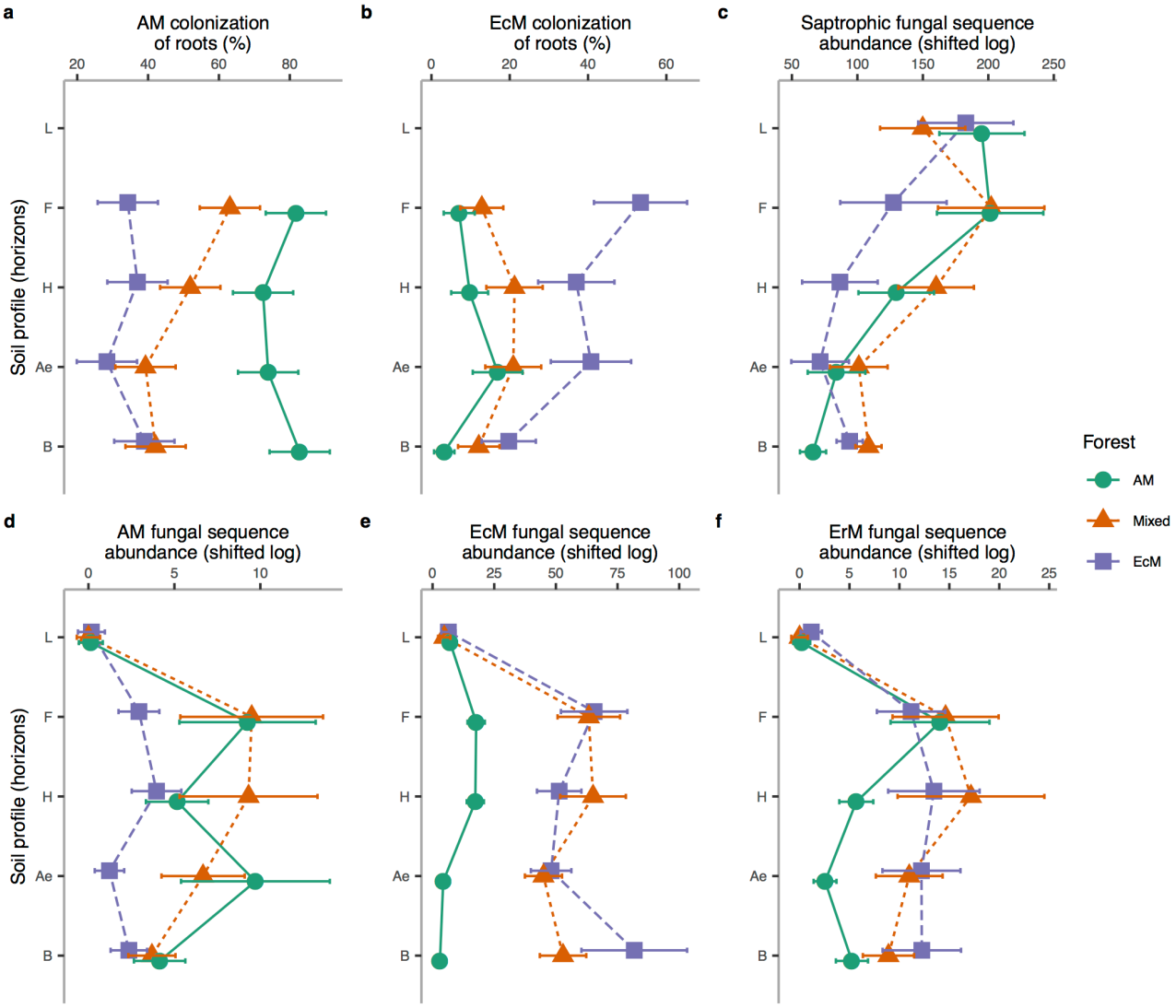

Figure 2. Soil profiles from organic-to-mineral horizons (L, F, H, Ae, B) on each mycorrhizal forest type (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; Mixed, mixture of AM and EcM) showing variations in: root colonized by (a) AM fungi, (b) EcM fungi, and abundances (on shifted log data) of sequences belonging to (c) saprotrophic fungi, (d) AM fungi, (e) EcM fungi, and (d) ericoid mycorrhizal (ErM) fungi. Upper organic horizon (L) had no roots so colonization was set to zero. All data are means ± 1 SE (n = 5, except n = 4 for the L horizon in EcM forest).

Overall fungal community

We found 781 fungal taxa (at the species level or below) from a total of 2521 ASV detected using high-throughput amplicon sequencing across all horizons and plots. Fungal ASV richness tended

to decrease with soil depth regardless of the forest type (Fig. S3). The highest fungal ASV richness was found in L horizons of the AM forests.

Fungal guilds

Saprotrophic and symbiotrophic (EcM, AM, and ErM) guilds showed distinct vertical distributions among horizons and across forest types (Fig. 2c-f). Saprotrophic fungal taxa dominated the upper horizons (especially L and F; Fig. 2c), and mycorrhizal fungi were almost absent in the L horizon (Fig. 2d-f). Fungal taxa assigned to the saprotrophic guild were slightly more abundant in the organic horizons of the AM and mixed forests compared to EcM forest (Fig. 2c). Abundance of saprotrophic fungi was significantly different among forest types (P-value = 0.031) but differences were not significant across horizons of different forest types (soil horizon × forest type, P-value = 0.325). In deeper horizons, sequences attributed to mycorrhizal fungi were more abundant (Fig. 2d-f). Sequences of AM (i.e. Glomeromycetes) fungi were much more abundant in the AM forest (Fig. 2d), and the opposite was true for EcM fungi (Fig. 2f). Both AM and EcM taxa were well represented in the mixed forests (Fig. 2d-e). Sequences of ericoid mycorrhizal (ErM) fungi were less abundant in AM forest except for the F horizon where their abundance was high in all forests (Fig. 2f). Richness patterns of fungal guilds tended to follow abundance data (Fig. S4). Saprotrophic fungi had the higher number of taxa followed by EcM, ErM, and AM fungi. Saprotrophic fungal richness was highest in the upper horizons and decreased with depth. There was a higher richness of EcM fungi in EcM and mixed forests and very few EcM taxa in the L horizon.

Fungal community structure

Soil horizons had the strongest influence over fungal community structure (includes abundance data) in the three forest types, as shown by the NMDS ordination (Fig. 3). The composition (based on presence-absence data) of the fungal community showed similar patterns (Fig. S5), suggesting that results primarily reflected changes in ASV composition rather than relative abundance. Differences in multivariate dispersions with Bray-Curtis and Sørensen measures were not significant among forest types (P-value > 0.05) but were significant among horizons (P-value < 0.05), with the L horizon showing the lowest multivariate dispersions. In other words, fungal communities from the L horizons were more similar to each other than fungal communities from the other horizons. Fungal community composition and abundance significantly differed among all

horizons but also among forest types (*P*-value < 0.001, Table S2). However, the differences among horizons did not depend on forest type and vice-versa (soil horizon × forest type interaction not significant; Table S2). Pairwise comparisons revealed that fungal community composition and abundance in AM and EcM forests significantly differed from each other, but not from mixed forests (Fig. 3).

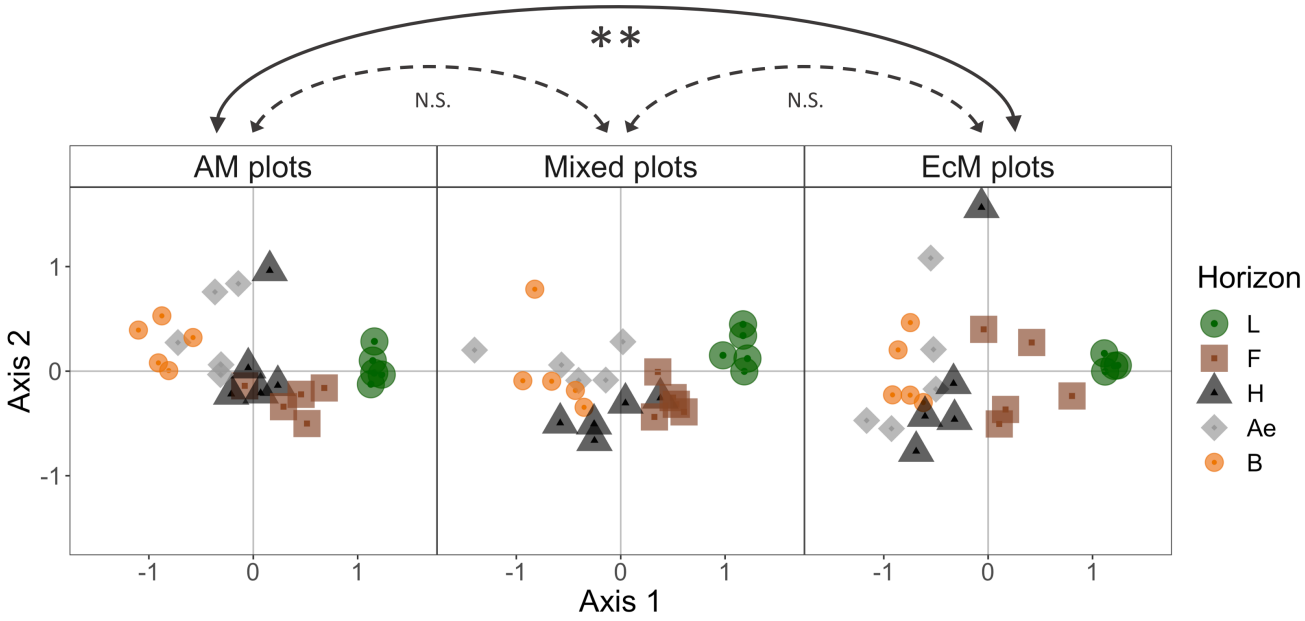

Figure 3. Ordination of the fungal community composition (Bray-Curtis dissimilarities) plotted in the different forest types using a non-metric multidimensional scaling with two dimensions and a stress of 0.17. ** indicates difference in fungal community structure between arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) plots (*P*-value ≤ 0.01), N.S. indicates non-significant differences (see Table S2 for details).

Edaphic drivers of fungal community structure

Variation in soil chemistry explained a large fraction of the total variation in fungal community structure (adjusted-R^2 = 23.3%, *P*-value = 0.001, see Table S3 for results of the constrained ordinations). In the L horizons, fungal communities were associated with higher pH, ECEC, labile L and C:N ratio (Fig. 4). Fungal communities in mineral horizons (Ae and B) were associated with high organic and inorganic P but low labile P (Fig. 4). Between L and mineral horizons, fungal communities were associated with low pH (H horizon) and high labile P (F horizon).

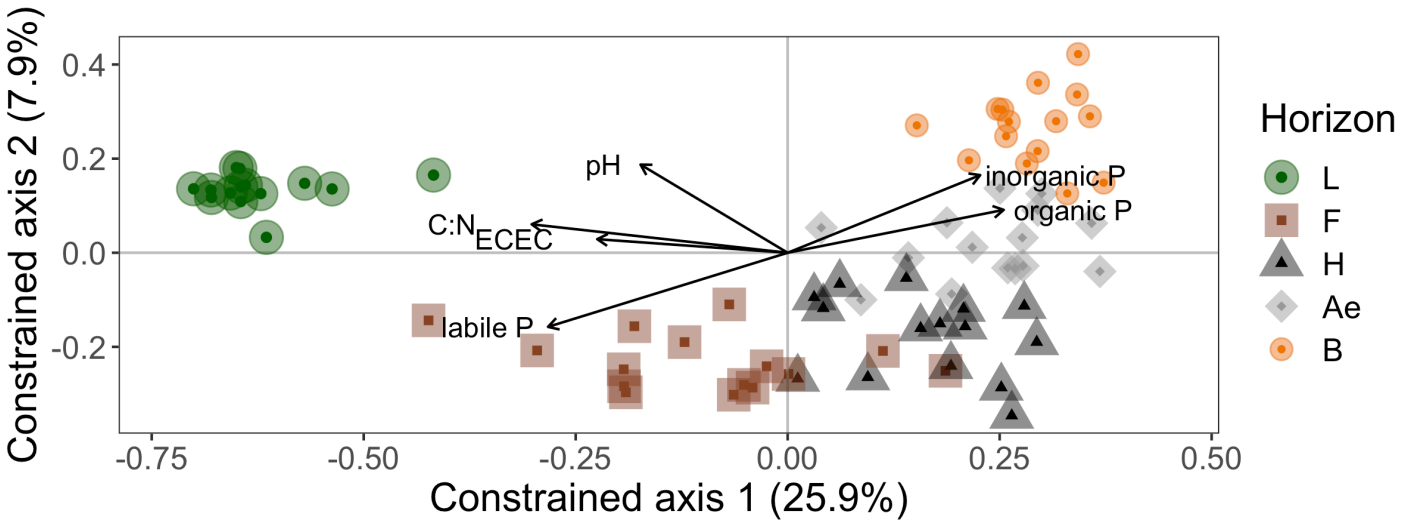

Figure 4. Constrained ordination of the overall fungal community by soil chemistry variables using a distance-based redundancy analysis with Bray-Curtis dissimilarities. Horizons are shown in different shape and colors. The two first constrained axes explaining most variation are drawn. Adjusted-R^2 = 23.3 %, *P*-value = 0.001.

Forest mycorrhizal type explained a lower but still significant amount of variation (adjusted-R^2 = 2.7%, *P*-value = 0.006). There was a clear difference in the fungal community structure of AM and EcM forests, whereas the mixed forests were intermediate or more similar to EcM forest (Fig. 5).

Abiotic and biotic variables together explained ~35% (*P*-value = 0.001) of the total variation in the fungal community structure. Variation in fungal community structure depended on horizons and forest mycorrhizal types, and was also influenced by soil chemistry (Fig. 6). Within forest types, fungal communities were not significantly different among blocks. Horizon, forest type, and soil chemistry still explained a significant fraction of the variation in the fungal community structure when considering the effects of the other variables (Table S3). Most of the explained variation was shared between soil chemistry and horizon (Fig. 6). However, forest type still had a unique and significant impact on the variation of the fungal community. A small fraction of variation was shared between soil chemistry and forest type (Fig. 6).

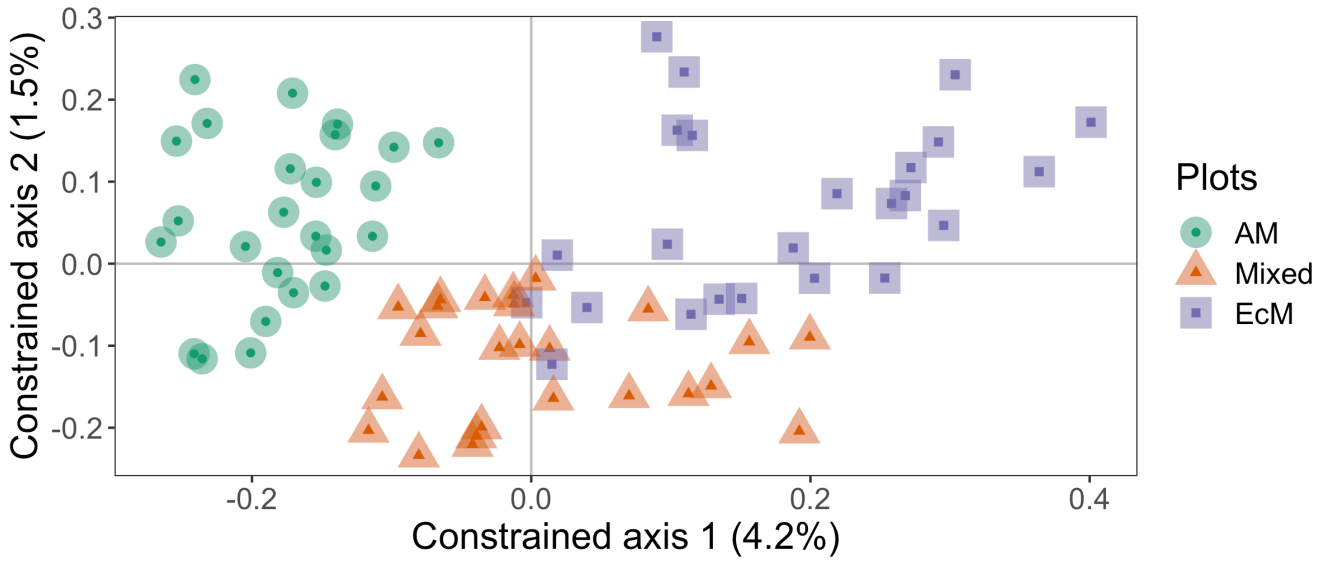

Figure 5. Constrained ordination of the fungal community structure depending on the forest mycorrhizal type (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; Mixed, mixture of AM and EcM) using a distance-based redundancy analysis with Bray-Curtis dissimilarities. Forest types are shown in different shapes and colors. The two constrained axes are shown. Adjusted-R^2 = 2.7 %, *P*-value = 0.006.

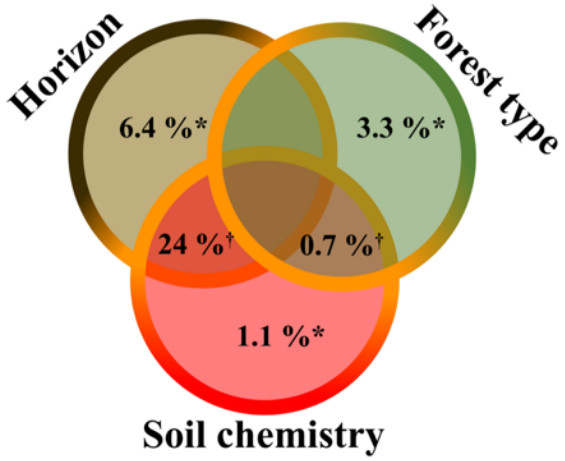

Figure 6. Venn diagram displaying the amount of variation (i.e. adjusted-R^2) of the fungal community explained by horizon, soil chemistry, and forest mycorrhizal type or a combination of them. Values < 0.1 % are not shown. Ellipses are not drawn to scale. Only variables with significant redundancy analysis (RDA) results were tested for partial-RDA and included in this diagram. Overall adjusted-R^2 = 34.8 %, * indicates *P*-value < 0.05 and † indicates non-testable portion. For more details see Table S3.

Discussion

In this study, we determined vertical shifts in soil fungal community composition across soil horizons and forest mycorrhizal types (AM, EcM, and mixed AM/EcM) and compared how saprotrophic fungal dominance extends to deeper horizons in AM vs. EcM forests. Although there was a tendency for lower abundance of saprotrophic fungi in organic F and H horizons in EcM forests than in AM or mixed forests, all three forest types showed a similar saprotrophic-to-mycorrhizal shift in fungal composition with increasing soil depth. This shift in fungal dominance was most pronounced in organic horizons. Moreover, we found that changes in fungal community composition were largely driven by differences in soil chemistry, which were far stronger across horizons (i.e. depth) within a single forest than across forest mycorrhizal types for the same horizon. Our results highlight the importance of considering soil vertical structure and associated changes in chemistry when characterizing soil fungal communities. They also suggest that, at least in northern forests, AM fungi are not being restricted where inorganic nutrients predominate and might have more similar edaphic vertical niches with EcM fungi than what has been suggested in the literature (Read, 1991; Neville *et al.*, 2002; Smith & Read, 2008).

Fungal communities were strongly stratified with depth along the soil profile, being most distinct in the L horizon (composed of recently-fallen leaves). Litter of the EcM, AM and mixed forests had high fungal richness and distinct fungal communities that were dominated by saprotrophic fungi. This has also been observed in forests of tropical, temperate and boreal biomes dominated by EcM trees (Dickie *et al.*, 2002; O'Brien *et al.*, 2005; Lindahl *et al.*, 2007; McGuire *et al.*, 2013; Voříšková *et al.*, 2014). Dominance by saprotrophic fungi in the most superficial litter layer has also been observed in other AM-dominated ecosystems (Oehl *et al.*, 2005; Schlatter *et al.*, 2018), as we have found in this northern temperate forest. Our results therefore provide further evidence of this general pattern whereby the L horizon possesses a distinct fungal community dominated by fungal saprotrophs, compared to deeper horizons in which mycorrhizal fungi are more abundant.

As suggested by Bahram *et al.* (2015), studies that have reported weak vertical segregation of fungal communities have often excluded the most superficial L horizon from their analyses (e.g. Talbot *et al.*, 2014; Peršoh *et al.*, 2018). The L horizon of the EcM, AM, and mixed forests tended to have higher C:N ratio, pH, concentration of cations and labile P than deeper horizons. While this pattern seems generalizable for pH (e.g. Lindahl *et al.*, 2007; Voříšková *et al.*, 2014), it remains

uncertain or unexplored for the other chemical variables. Our results suggest that the L horizon which is characterized by the presence of organic matter in which the original structures can be visually distinguished (Groupe de travail sur la classification des sols, 1998) should be considered separately in future studies of fungal community composition, given its chemical, microbial and functional distinctiveness.

From the F to the B horizon, fungal communities showed strong turnover across soil horizons, with distinct fungal communities in each horizon. The fungal composition, abundance, and guilds tended to progressively change among horizons in the soil profile but these changes were less pronounced than with the L. This was also observed in other study systems (Lindahl *et al.*, 2007; Voříšková *et al.*, 2014; Nagati *et al.*, 2018). There are reports of evenly distributed guilds among the organic and mineral horizons (e.g. Peršoh *et al.*, 2018), but vertical segregation of fungi and especially root-associated fungi is often strongly impacted by determinant factors such as soil chemistry and host plants (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Bahram *et al.*, 2015). In our study, there was major variation in the vertical distribution of soil fungi that was largely driven by soil chemical characteristics, with these changes being observed in all three forest mycorrhizal types. Our results further support those of other studies that have found the vertical variability of mycorrhizal and saprotrophic fungal communities across different soil horizons to be much larger than horizontal or temporal variability (Jumpponen *et al.*, 2010; Bahram *et al.*, 2015). Studies that focus on ecosystem topsoil processes in terrestrial environments should consider the strong physical, chemical and biological heterogeneity that occurs within the first few centimeters, by sampling distinct soil horizons separately.

We showed that underground fungal community structure varied significantly between neighboring forest dominated by AM or EcM trees. As expected, AM forests showed higher abundance of AM fungi, whereas EcM forests showed higher abundance of EcM fungi. Direct observation of fungal colonization in roots confirmed these patterns. Forests with a mix of both strategies supported intermediate communities between the two extremes of the gradient, as reported in a study focusing on ecosystem processes (e.g. Cheeke *et al.*, 2016). It is worth noting that fungal saprotrophs tended to be more abundant in organic horizons of mixed and AM forests compared to EcM forests. Together with higher pH and lower organic C in these AM forests, this result might indicate a tendency toward a more “inorganic nutrient economy” compared to the

studied forests dominated by EcM fungi. The latter would represent a more "organic nutrient economy", associated with a slower turnover of plant-derived C due to lower abundance of free-living saprotrophs (Phillips *et al.*, 2013). These small differences observed at local scale may be responsible for observed patterns found at the ecosystem scale (Averill *et al.*, 2014). It has been found elsewhere that forests dominated by different species of broadleaf trees of the same mycorrhizal strategy can also show differences in fungal community structure (Bahnmann *et al.*, 2018). However, in our study, fungal composition, abundance and guilds tended to differ between EcM and AM forests. Such a distinction has previously been reported in a study comparing very distinctive EcM forests of broadleaf trees vs. conifers (Awad *et al.*, 2019), the effect of mycorrhizal type was relatively small but nonetheless present, and could also be linked to differences in nutrient availability.

Our study design provides a useful system for exploring the relative importance of mycorrhizal type on soil biogeochemical cycling. The soil profile in these northern temperate forests have low vertical mixing, resulting in podzols with high stratification, as commonly encountered in boreal soils. Soil horizons were easily identifiable mainly through their color and such sampling may allow for better association between DNA sequences and soil chemistry as well as more valuable comparison across sites (Dickie *et al.*, 2018). Variation in important factors such as parent material, topography and regional climate were minimized but other factors (e.g. productivity, soil texture) could still co-vary with mycorrhizal dominance at the plot scale. Importantly, this study system allowed us to study different mycorrhizal types within the same site (Bahram *et al.*, 2015; Fernandez & Kennedy, 2016; Tedersoo *et al.*, 2020) and across a gradient of mycorrhizal dominance (Craig *et al.*, 2018). The observed differences in soil chemistry among forests could be linked with dominant mycorrhizal strategies. Higher saprotrophic fungal diversity has been observed in the upper soil layers of AM-dominated tropical forests compared to EcM forests (McGuire *et al.*, 2010). Our study provides further evidence that, in a temperate system, host plants are an important factor controlling mycorrhizal community composition (Bahram *et al.*, 2015; van der Linde *et al.*, 2018). To some extent, this was expected given that AM and EcM fungi are obligate symbionts with their host plants (Smith & Read, 2008). As such, considering tree mycorrhizal strategies and their interactions with saprotrophs may help to better predict carbon storage at small and global scale (Verbruggen *et al.*, 2017).

Our use of high-throughput amplicon sequencing approach allowed us to assess the distribution of the soil fungal community and to discriminate among AM, EcM and saprotrophic fungi. However, result from high-throughput sequencing approaches need to be interpreted with caution because of unavoidable biases at different levels (Lindahl *et al.*, 2013; Hart *et al.*, 2015). For example, how to adequately normalize for taxa abundance among samples remains unresolved (McMurdie & Holmes, 2014; Weiss *et al.*, 2017). Furthermore, although we acknowledge that soil and root compartments might host different fungal communities (e.g. Gao *et al.*, 2019), sampling bulk soil allows to capture the potential free-living saprotrophs as well as root-associated fungi and their extraradical hyphae. Finally, our choice of the primers might have resulted in an under-representation of some fungal groups such as Glomeromycetes, but comparisons in taxa abundance between samples remain relevant (Pauvert *et al.*, 2019).Using specific primers targeting Glomeromycetes (Krüger *et al.*, 2009; Öpik *et al.*, 2013), and plants using DNA from the root tissue (Kress & Erickson, 2007; Toju *et al.*, 2014) would certainly allow to further understand the importance of these underground interactions and the vertical segregation among root and fungi of different mycorrhizal types.

Our results show that fungal communities in horizons vertically separated by a few centimeters are very different from each other in terms of composition and abundance. This contributes to high fungal and functional diversity in the topsoil. Moreover, our work suggests that the forest mycorrhizal type influences the overall and saprotrophic fungal community, advancing our current understanding of the potential impacts of mycorrhizal strategies on the distribution of key organisms for ecosystem functioning such as C and nutrient cycling (Phillips *et al.*, 2013). We also reported for the first time that broad patterns of vertical fungal distribution across the upper five horizons in AM-dominated northern forest are comparable to neighboring EcM-dominated or mixed forests. This result challenges the traditional view that AM fungi have a more restricted niche toward mineral soils compared to EcM fungi due to their incapability to directly decompose organic matter (Read, 1991). Our study suggests that the ecological and functional roles of AM fungi in organic horizons of temperate forests, including recently deposited litter, deserve more attention (Bunn *et al.*, 2019).

Acknowledgements

We are grateful to two anonymous reviewers for the suggestions that improved the manuscript. We would like to thank Dayana Agudo, William Barrette, Aleksandra Bielnicka, Sarah Dupont, Paola Escobar, Caroline Fink-Mercier, Audren Jiquel and David Poissant for the field and the laboratory assistance. We also thank the staff from the Station de biologie des Laurentides (SBL) of Université de Montréal for facilitating the field work. Funding, including scholarships to AC, was provided by Discovery Grants to EL (RGPIN-2014-06106, RGPIN-2019-04537) by the Natural Sciences and Engineering Research Council of Canada (NSERC) as well as a "Nouveau Chercheur" grant (2016-NC-188823) by the Fonds de recherche du Québec sur la Nature et technologies (FRQNT). AC would like to sincerely thank the Institut de recherche en biologie végétale, Centre d'étude de la forêt, Centre de la science de la biodiversité du Québec, Université de Montréal, and the FRQNT for providing generous financial support.

Authors' contributions

EL and AC conceived the ideas and designed methodology; AC, BT, SJ and MB collected the data; AC analyzed the data; AC and EL interpreted the results; AC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Code and data availability

Sequence and chemistry data can be accessed at: https://doi.org/10.5281/zenodo.3631861.
Custom code for bioinformatical and statistical analyses are available at:
https://doi.org/10.5281/zenodo.3631982.

Supplementary information

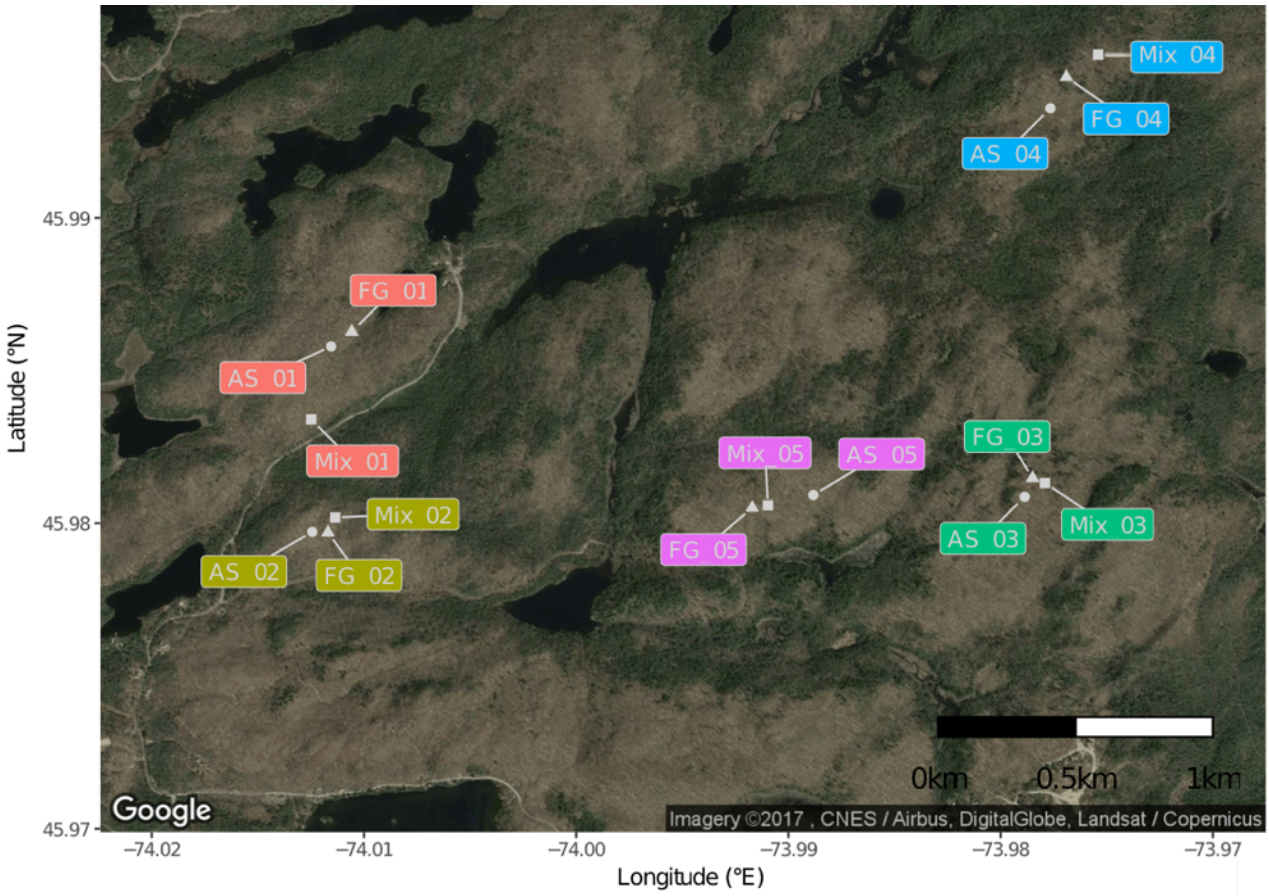

Figure S1. Map showing the 15 plots grouped in five blocks (different colors) at the University of Montréal's field station (Québec, Montréal). The characteristics of each plots are listed in Table S1.

Figure S2. Picture of a soil core of approximately 25 cm deep, sampled with a rectangular auger, representing a typical profile in the studied sites. The five horizons can easily be distinguished with entire leaves at the top (L), then partially decomposed materials (F) and black humus (H), followed by grey Ae and brown B.

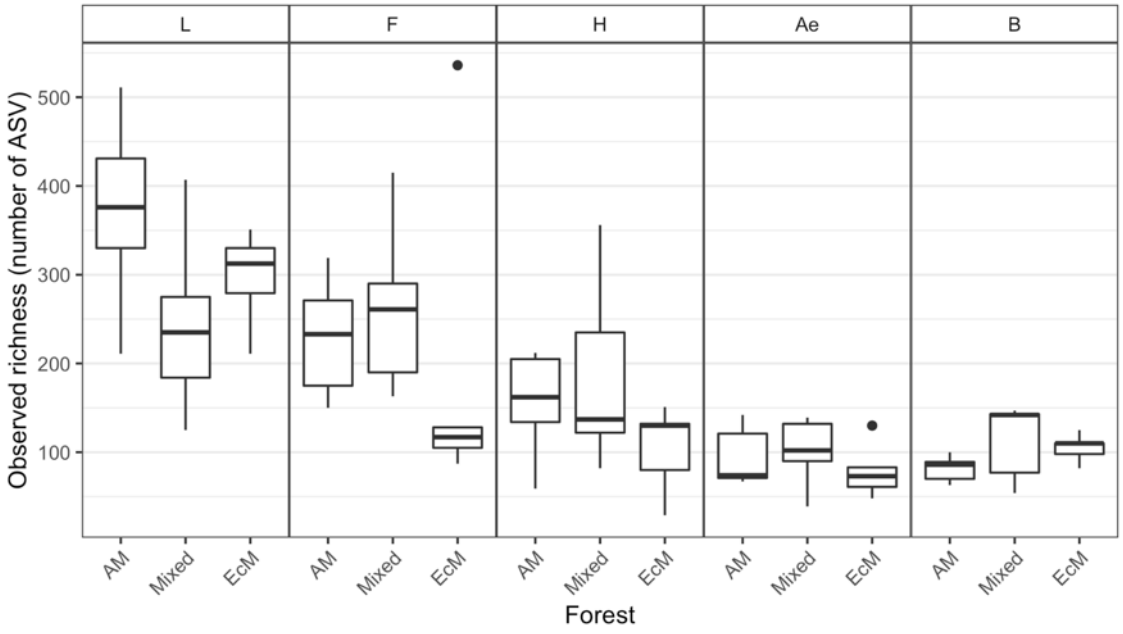

Figure S3. Boxplots illustrating differences in the number of amplicon sequence variant (ASV) by horizon (L to B, from left to right). Singletons and doubletons were excluded. Bold horizontal lines represent median values; box margins 25th and 75th percentile; vertical lines represent largest and lowest value within 1.5 times interquartile range above 75th and below 25th percentile respectively; dots represent outliers that fall outside of that range.

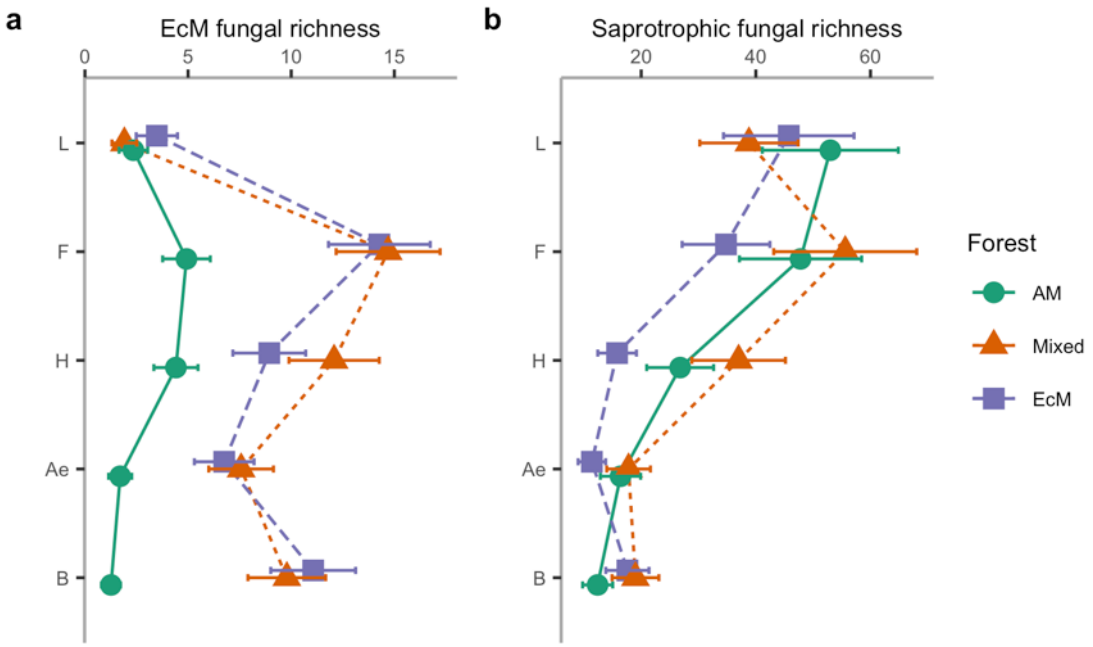

Figure S4. Soil profiles from organic-to-mineral horizons (L, F, H, Ae, B) on each mycorrhizal forest type (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; Mixed, mixture of AM and EcM) showing variations in richness of (a) EcM fungi and (b) saprotrophic fungi. All data are means ± 1 SE (n = 5, except n = 4 for the L horizon in EcM forest). Note: Due to low value, richness of AM and ErM guilds were not modeled.

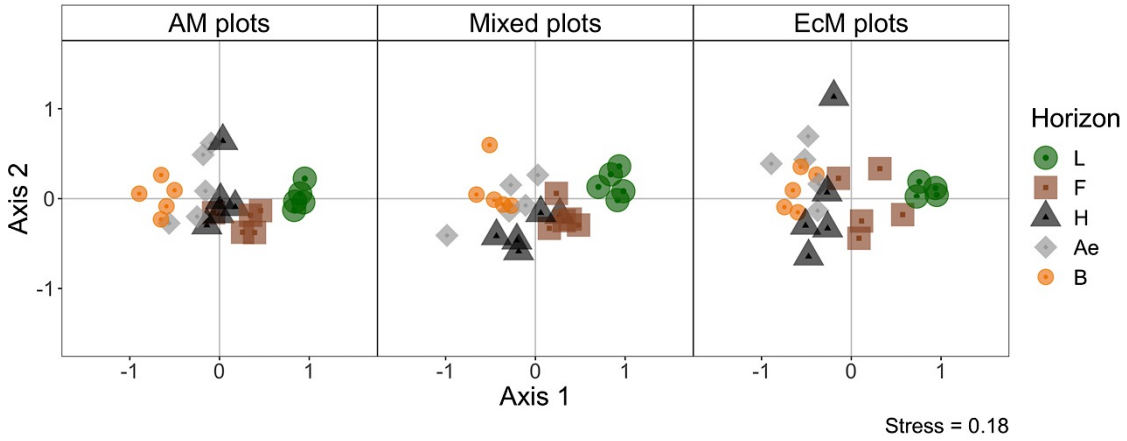

Figure S5. Ordination of the fungal community composition (Sørensen distances) of the different forest type on two axes using a non-metric multidimensional scaling with two dimensions and a stress of 0.18. To visually assess the impact of Sørensen distance, the scale is kept identical to the one of Fig. 1.

Table S1. Characteristics of each plot under study. Plots in the same block were selected to have homogenous environmental conditions.

Plot ID	Block	Altitude (m)	Slope (%)	Aspect (°)	Total basal area (m^2 ha^{-1})	EcM tree basal area (% of total)	AM tree basal area (% of total)	Dominant canopy species	Mycorrhizal dominance
AS_01	1	403	10	95	23.2	7.5	92.5	AS	AM
FG_01	1	381	20	103	37.4	81.6	18.4	FG	EcM
Mix_01	1	383	18	160	36.1	53.4	46.6	AS and FG	Mixed
AS_02	2	398	13	140	30.9	8.4	91.6	AS	AM
FG_02	2	391	9	105	40.4	95.8	4.2	FG	EcM
Mix_02	2	381	10	110	41.9	57.4	42.6	AS and FG	Mixed
AS_03	3	374	9	140	33.3	8.4	91.6	AS	AM
FG_03	3	388	0	0	29.9	79.7	20.3	FG	EcM
Mix_03	3	396	0	0	37.0	43.9	56.1	AS and FG	Mixed
AS_04	4	376	16	220	38.9	8.3	91.7	AS	AM
FG_04	4	395	14	120	39.1	62.8	37.2	FG	EcM
Mix_04	4	375	18	180	27.8	55.5	44.5	AS and FG	Mixed
AS_05	5	366	15	140	40.2	6.4	93.6	AS	AM
FG_05	5	365	9	150	36.3	89.7	10.3	FG	EcM
Mix_05	5	366	20	190	30.8	56.1	43.9	AS and FG	Mixed

Acronyms: AS = *Acer saccharum*, FG = *Fagus grandifolia*, AM = arbuscular mycorrhiza, EcM = ectomycorrhiza.

Table S2. Multivariate analyses of differences in structure (Bray-Curtis dissimilarities) and composition (Sørensen distances) among different types of fungal communities. Analyzed using permutational multivariate analysis of variance (PERMANOVA). *P*-values were determined using 9999 permutations. * $P \leq 0.05$; ** $P \leq 0.01$, *** $P \leq 0.001$. Df stands for degree of freedom.

Fungal Community	Dissimilarity measure	*P*-Value	Df	Fungal Community	*P*-Value
Among forest types	Structure	0.00014***	2	AM vs Mixed	0.0935
				AM vs EcM	0.0039**
				Mixed vs EcM	0.0935
	Composition	0.00074***	2	AM vs Mixed	0.118
				AM vs EcM	0.026*
				Mixed vs EcM	0.089
Among horizons	Structure	0.00001***	4	L vs F	0.00001***
				F vs H	0.00001***
				H vs Ae	0.0023**
				Ae vs B	0.00007***
	Composition	0.00001***	4	L vs F	0.00001***
				F vs H	0.0001***
				H vs Ae	0.0118*
				Ae vs B	0.0022**
Forest × Horizon	Structure	0.11718	8	-	-
	Composition	0.15424	8	-	-

Note: Only PERMANOVA results with *P*-value ≤ 0.05 were considered for multiple comparisons. L vs H, L vs Ae, L vs B, F vs Ae, F vs B, H vs B not included but *P*-values < 0.0001.

Table S3. Partition of variation of the fungal community due to soil chemistry (Chemistry), experimental blocking design (Block), soil layers (Horizon) and forest mycorrhizal type (Forest) using distance-based redundancy analysis (RDA) and partial-RDA analyses. *P*-values were determined using 999 permutations. ** *P*-values ≤ 0.01; *** *P*-values ≤ 0.001. In the formula Y is the fungal community matrix, X is the explained matrix and Z is the conditional matrix which is partialed out. Only significant RDA results were tested for partial-RDA.

Model	Formula (Y~X | Z)	adjusted-R^2 (%)	*P*-value
Overall RDA	Y~ Chemistry + Block + Horizon + Forest	34.8	0.001***
Single RDA	Y ~ Chemistry	23.3	0.001***
	Y~ Block	0.3	0.372
	Y~ Horizon	27.8	0.001***
	Y~ Forest	2.7	0.006**
partial-RDA	Y~ Chemistry | Block + Horizon + Forest	1.1	0.036*
	Y~ Horizon | Chemistry + Block + Forest	6.4	0.001***
	Y~ Forest | Chemistry + Block + Horizon	3.3	0.001***

Décomposition en action, St-Hippolyte.

CHAPITRE 2 – Les ectomycorhizes accélèrent la décomposition dans une plus grande mesure que les mycorhizes à arbuscules dans une forêt de feuillus nordique

Ectomycorrhizas accelerate decomposition to a greater extent than arbuscular mycorrhizas in a northern deciduous forest

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Keywords: Organic matter decomposition; carbon cycle, nitrogen cycle, temperate forest, vertical segregation; Gadgil effect; mycorrhizal fungi; *Acer saccharum*; *Fagus grandifolia.*

Abstract

It has been proposed that ectomycorrhizal (EcM) fungi slow down decomposition by competing with free-living saprotrophs for resources (known as the 'Gadgil effect'), therefore increasing soil carbon sequestration. As such, this Gadgil effect should depend on soil organic matter age and quality (i.e. across soil organic horizons), but this remains unstudied. In addition, the Gadgil effect is not expected to occur in arbuscular mycorrhizal (AM) forests since AM fungi cannot access directly nutrients from soil organic matter, yet few direct comparisons between EcM and AM forests have been made. We performed a two-year reciprocal decomposition experiment of soil organic horizons (litter - L, fragmented - F, humic - H) in adjacent deciduous forests dominated by EcM or AM trees. Litterbags were made of different mesh sizes allowing or excluding ingrowth of mycorrhizal fungal hyphae. As expected, soil carbon stocks to 20 cm depth were higher in EcM forests than in AM forests, and organic matter originating from deeper horizons and EcM forests was of lower quality and decomposed more slowly. However, contrary to the Gadgil effect, organic matter exposed to mycorrhizal fungi actually decomposed faster in both forest types, and this effect was strongest in EcM forests, particularly in the F horizon. Unexpectedly, organic matter decomposition was faster in EcM than in AM forests, regardless of organic matter origin (i.e. collected from EcM or AM forests). Our study shows that the local fungal network, including mycorrhizal hyphae, speed up rather than slow down organic matter decomposition in this deciduous forest. In addition, our results suggest that decomposer communities from EcM forests can be more efficient at degrading organic matter than those of adjacent AM forests, despite EcM forests showing higher soil C accumulation. Resolving this apparent paradox will require further investigation into other processes regulating soil C accumulation, notably above- and belowground litter production, as well as studying other components of the decomposer food web. Overall, our study reinforces the view that forest mycorrhizal strategy is an important factor to consider in global soil C models.

Introduction

Forests cover much of the land surface, and represent the largest terrestrial carbon (C) pool globally (Dixon *et al.*, 1994; Baldrian, 2017). A majority of that C is stored in forest soils, especially in northern forests (Lal, 2005; Crowther *et al.*, 2019). Soil C storage is controlled by many abiotic and biotic factors such as climate, vegetation, topography and nutrient availability that interact together (Averill *et al.*, 2014; Carvalhais *et al.*, 2014; Wiesmeier *et al.*, 2019). However, belowground biotic factors, such as microorganisms, also play an important role, directly influencing soil C inputs (i.e. litter quantity and quality) and outputs (i.e. decomposition) (Schimel & Schaeffer, 2012). For example, soil microorganisms such as fungi can produce recalcitrant organic matter that decomposes slowly or they can produce extracellular enzymes that break down organic matter (Frey, 2019). As a result, soil fungi play a major role in forest C cycling (Kubartová *et al.*, 2008; Bardgett & Wardle, 2010; Orwin *et al.*, 2011).

A long-standing hypothesis about the effects of fungi on the soil C cycle is the 'Gagdil effect' (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016). This hypothesis suggests ectomycorrhizal (EcM) fungi slow down litter decomposition, potentially due to competition between EcM fungi and free-living saprotrophs for organic nutrients. Because EcM fungi acquire their C in highly labile form via plant hosts (Smith & Read, 2008) in exchange for nutrients such as nitrogen and phosphorus, they would leave behind C-rich but nutrient-poor organic matter, potentially favoring soil C accumulation (Read *et al.*, 2004; Averill *et al.*, 2014). On the other hand, some EcM fungi have the capacity to oxidize organic matter, directly influencing decomposition and indirectly influencing saprotrophic organisms (Lindahl & Tunlid, 2015; Verbruggen *et al.*, 2017). Saprotrophic fungi could also be impacted by EcM fungi through mycoparatism, antibiosis and alteration of abiotic conditions (Fernandez & Kennedy, 2016; Zak *et al.*, 2019). The Gagdil effect has only been supported by a few studies but seems to be largely context dependent, for example to litter quality (Smith & Wan, 2019) and moisture level (Koide & Wu, 2003). Compared to EcM fungi, it is thought that arbuscular mycorrhizal (AM) fungi lack the capacity to produce enzymes that break down organic matter (Tisserant *et al.*, 2013; Tedersoo & Bahram, 2019). Therefore, it is expected that decomposition would be quicker in AM forests compared to EcM forests, but this still remains an open question (Fernandez & Kennedy, 2016; Frey, 2019). For example, AM fungi may even enhance organic matter decomposition in some cases via a 'priming effect', by promoting

the activity of free-living saprotrophs (Hodge, 2017; Frey, 2019). A better understanding of the roles that different mycorrhizal types play in organic matter decomposition is thus needed.

Because fungal types and taxa differ strongly in their vertical distribution, especially in well-stratified soil such as podzols (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Bahram *et al.*, 2015), the strength and direction of the Gadgil effect could vary across soil organic horizons, yet most previous studies have only considered the uppermost litter layer. Strong vertical segregation of fungal guilds occurs across podzol profile: saprotrophic fungi dominate the litter horizon, and can still be abundant in upper organic horizons where mycorrhizal fungi increasingly dominate (Lindahl *et al.*, 2007; Clemmensen *et al.*, 2015; Santalahti *et al.*, 2016). It is recognized that overlapping niches between different groups of fungi can generate competition for soil resources (Mujic *et al.*, 2016; Bödeker *et al.*, 2016). Therefore, the greatest potential for mycorrhizal fungi to inhibit saprotrophs and thus slow down organic matter decomposition is just below the layer of fresh litter. It has been suggested that these interactions might help to explain differences in the amount and vertical distributions of soil C in EcM systems (Clemmensen *et al.*, 2013; Kyaschenko *et al.*, 2017) and between EcM- and AM-dominated forests at different depth or horizons (Phillips *et al.*, 2013; Soudzilovskaia *et al.*, 2015b; Craig *et al.*, 2018). By competing with saprotrophs for organic nutrients, EcM fungi may promote C accumulation more than AM fungi that cannot directly access these resources. These vertically segregated interactions among fungal guilds need to be better understood because they play an important role in regulating organic matter accumulation (Frey, 2019).

Competition between microbial guilds could also be influenced by litter quality and its origin. In fact, plant litter decomposition may be quicker in its native environment due to decomposer's adaptations driving higher efficiency (Austin *et al.*, 2014). Specifically, because EcM litter tends to be more recalcitrant (Keller & Phillips, 2019), it could be expected that EcM litter decays faster in EcM forest with decomposers better adapted to break down recalcitrant organic matter. Furthermore, decomposers in EcM soils may be very specialized, and therefore less adapted to quickly decompose high-quality litter from AM soils, showing a so-called 'home-field advantage' (Gholz *et al.*, 2000; van der Wal *et al.*, 2013). Using published data on mass loss from 125 reciprocal litter transplants, Veen *et al.* (2015) have shown that HFA increases decomposition rates by 7.5% on average. However, HFA depends largely on the context such as plant identity, litter

quality and moisture level (Veen *et al.*, 2015; Wang *et al.*, 2020). There are some evidences suggesting that AM litter shows higher home-field advantage (HFA) than ECM litter (Midgley *et al.*, 2015; Jacobs *et al.*, 2018). However, further investigation is needed to better understand the effect of microbial decomposers driving the HFA depending on the litter type, the stage of litter decomposition (Lin *et al.*, 2020; Li *et al.*, 2020), and the mycorrhizal type.

The main objective of our study was to assess the impact of EcM and AM strategies on the decomposition of soil organic matter in organic horizons in northern forests. First, we determined stocks of C and nutrients in the upper 20 cm of soil in adjacent forest plots dominated by AM or EcM trees. Then, we performed a litterbag experiment using a reciprocal transplant of AM and EcM forest soil enabling us to isolate site *vs.* litter quality effects on decomposition. To assess the direct impact of mycorrhizas on decomposition, litterbags were composed of different mesh size that allowed or excluded ingrowth of fungal hyphae. Decomposition of the three upper organic horizons (litter - L, fragmented - F, humic - H) was followed by measuring changes in soil mass, and changes in C and nitrogen (N) over two years. In addition, the fate of C fractions was followed in decomposing L samples and potential access of N by mycorrhiza in the F samples. We hypothesized that the impact of mycorrhizas on organic matter decomposition would differ between AM and EcM forests. More specifically, we expected based on the Gadgil hypothesis that EcM forests would sequester a higher amount of C in the topsoil and show slower organic matter decomposition due to the inhibition of saprotrophs by EcM fungi and the lower litter quality, whereas this effect would not occur in AM forests. In addition, we hypothesized that the slowing down of C cycle by EcM fungi would be strongest in the fragmented (F) horizon where litter-derived organic materials, free-living saprotrophs, mycorrhizal fungi and roots coincide (Clemmensen *et al.*, 2013; Cotrufo *et al.*, 2015; Carteron *et al.*, 2020). Due to microbial adaptations, we also hypothesized that litter would decompose fastest in their “home” forests relative to “away” forests (Veen *et al.*, 2015). Specifically, mass loss of organic matter from AM soil would be highest when incubated in AM forest and mass loss of EcM organic matter highest in EcM forest.

Material and methods

Study area and site selection

Our study was conducted in a northern temperate forest at the Université de Montréal's field station (Station de biologie des Laurentides, Saint-Hippolyte, Québec, Canada). The mean annual temperature is 4.3 °C and total annual precipitation is 1195 mm, with ~25% falling as snow (based on 1981–2010 data, meteorological station #7037310, Saint-Hippolyte). Soils consist of podzols with moder humus formed from Precambrian anorthosite (Bélanger *et al.*, 2004; Courchesne *et al.*, 2005). We selected ten 20 m × 20 m plots from Carteron *et al.* (2020), either dominated by EcM or AM trees (see Table S1), and grouped into five clusters or "blocks" (n = 5 blocks, each containing one plot of each of the two mycorrhizal types, EcM and AM). These pairs of EcM-AM sites were clustered together to minimize variation in environmental conditions (e.g. slope, aspect, elevation) within each block. Previous root colonization and molecular analyses on the same sites showed that forests dominated by EcM trees had the highest EcM fungal abundances while forests dominated by AM trees had the highest AM fungal abundances. Carteron *et al.* (2020) also found strong shifts from saprotrophic to mycorrhizal fungal dominance with increasing soil depth in both forest types, especially across surface organic horizons.

Soil carbon and nutrient stocks

Carbon and nutrient stocks were quantified by measuring C, N, phosphorus (P) concentrations and thickness for all horizons in the upper 20 cm of soil, as reported in Carteron *et al.* (2020). Soil bulk density was measured simultaneously for the five horizons in three randomly-positioned locations replicates per plot using an auger, and values from these locations were averaged across sites. The horizons considered were litter (L), fragmented (F), humic (H), and mineral horizons Ae and B.

Organic matter collection

In each plot, organic matter samples were collected separately from the three organic horizons, namely: L, F and young H (i.e. most recent layer) from two pits. Samples were homogenized by horizon within each plot. Samples were collected in July 2016. A subsample from each horizon by plot was preserved at 4 °C as inoculum (see below). Another subsample was oven-dried at 60 °C for 72 h and ground for chemical analyses. The rest of the organic matter was air-dried for filling the bags.

Litterbag design

Litterbags were 15 cm × 15 cm in size and designed to have three compartments (L, F, H; in the same order in which they occur through the soil profile) separated by 44-µm polyethylene mesh (PETEX® 07-40/12; Sefar Inc., Buffalo, NY, USA). Our use of 44-µm mesh ensured that hyphae could grow across compartments within each bag, an important process for decomposition (i.e. to allow for translocation of nutrients and C across horizons), while still keeping L, F, and H horizons separate for later retrieval. The outer mesh of the litterbags was made with either the same 44-µm polyethylene mesh described above or 1-µm mesh from the same material (PETEX® 07-1/2; Sefar Inc., Buffalo, NY, USA). The 44-µm mesh size excludes fine roots but not fungal hyphae, thus allowing us to study decomposition in the presence of mycorrhizal hyphae (and other saprotrophic fungi located outside of the bag). By contrast, the 1-µm mesh prevents most external fungal hyphae to grow through the litterbag (Teste *et al.*, 2006). Because most mycorrhizal hyphae cannot grow within the bag (as mycorrhizal fungi are obligate biotrophs), this bag design allows us to study organic matter decomposition without the effect of mycorrhizal fungi. Litterbags of 50 µm-pore size mesh have been found to allow mycorrhizal fungi ingrowth (i.e. Teste *et al.*, 2006; Sterkenburg *et al.*, 2018). Polyethylene mesh was selected over nylon mesh (e.g. NITEX®, Sefar Inc. Buffalo, NY, USA) because it is much more resistant to degradation when buried in soil (Colin *et al.*, 1981), yet still allows water to cross the mesh easily to the sample within the bag by capillary action. In total, 160 litterbags were used (Fig. S1). Each bag was stored within a 1-mm mesh nylon bag to provide additional physical protection for the less robust 44- or 1-µm PETEX® mesh.

Litterbag preparation and collection

Weighed air-dry organic matter was transferred to litterbags (2.85 g for L and 4.75 g for F and H horizons). Bags of 1 and 44 µm-pore size mesh might have somewhat decreased the potential for outside free-living saprotrophs to colonize organic matter inside the bags, therefore horizon specific fresh inoculum (~5 % of dry-weight equivalent) was added to each horizon from the receiving plot to ensure that plot-specific microbial biota, including free-living saprotrophic fungi, could colonize each litterbag. Water content was determined from oven-dried sub-samples at 60 °C for dry-mass inoculum conversion. Filled litterbags were put back in situ October 2016, directly on top of the H horizon (with L horizon facing up) and covered by a thin layer of fresh litter (< 1 cm). Litterbags were secured on the ground with small stakes and tied together with nylon fishing

line to a central stake to facilitate retrieval of bags. Two spatial replicates within each plot were installed. A total of 160 bags were collected after one and two years of residence (i.e. field incubation) for 480 samples analyzed (Fig. S1).

Soil analysis

Initial subsamples of ground horizons L, F and H were weighed (5.0, 6.0 and 7.0 mg ± 0.2 respectively) and analyzed to estimate C and N contents by dry combustion in a CN analyzer (Vario Micro Cube; Elementar, New-Jersey, United States, dx.doi.org/10.17504/protocols.io.udces2w). The concentrations of soluble cell contents (e.g. non-structural carbohydrates), hemicellulose, cellulose and lignin (% dry weight) were also determined on these initial samples by sequential digestion (Fiber Analyzer 200; ANKOM technology, dx.doi.org/10.17504/protocols.io.yinfude). After one and two years, organic matter samples were retrieved from litterbags, oven-dried at 60 °C for at least 72 h and then weighed to estimate mass loss percentage. These samples were then ground with a cyclone mill (Cyclone Sample Mills, UDY Corporation, Colorado, United States), using a 2-mm screen. Concentrations of C and N were also determined using the method described above. Thirty subsamples of the initial horizons, and all the F horizons after two years of residence were analyzed for $\delta^{15}N$ with a Micromass model Isoprime 100 isotope ratio mass spectrometer coupled to an Elementar Vario MicroCube elemental analyser in continuous flow mode.

Statistical analyses

Differences in organic matter stocks among forest types were evaluated using a linear mixed-effects model with forest type (AM or EcM as soil provenance) as a fixed factor and block as a random factor. Horizon was added as fixed factor for the modeling of initial soil chemistry. To predict the changes in mass (within the litterbags), linear mixed-effects models were also used by adding as fixed factors outside fungal hyphae (i.e. size of mesh pore) excluded (1 µm) or not (44 µm). Finally, forest of residence (AM or EcM forest) and time (one or two years) were added as fixed factors to compare decomposition in the two forest types including relevant interactions among fixed factors (see Table S2 for more details). Models were compared using the Akaike information criterion corrected for small sample size (AIC_c). Validation of the models was done by visual inspection of the residuals. Spatial replicates within one plot were averaged prior to analyses. Eleven bags with damaged mesh were removed from the analysis. Statistical analyses were performed using the R software (R Core Team, 2018) and the following packages *dplyr*

(Wickham *et al.*, 2017), *emmeans* (Lenth, 2019), *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2018), *nlme* (Pinheiro *et al.*, 2012). Data and R scripts can be found at https://github.com/alexiscarter/decompo_myco.

Results

Organic matter stocks

Stocks of C were higher in EcM forest stands compared to AM stand within the upper 20 cm of soil (one-way analysis of variance, *P*-value < 0.001; Fig S2) as observed in the organic horizons (Table 1). Stands dominated by EcM trees stored 14% more C than AM stands in surface soils. The soil C:N ratio also differed among forest types, with higher values in EcM stands (*P*-value = 0.024; Fig. S3). By contrast, there were no differences in soil C:P ratio among forest types (Fig. S4).

Initial soil chemistry

Soil C, cellulose and hemicellulose concentrations decreased from L to H horizons in both forest types, while lignin was highest in the F horizon and in EcM stands overall (23% in AM forest and 26 % in EcM forest; Table S3). By contrast, soil total [N] increased slightly with soil depth in both forest types (Table S3). As a result, soil C:N and lignin:N ratios were higher in EcM forest for the three organic horizons compared to AM forest (Table S3). $\delta^{15}N$ values showed similar increases from L to H horizons in both forest types but the F horizon in EcM forest was slightly enriched (but not significantly, *P*-value = 0.224; Table 1). Horizons tended to be thicker in EcM forest (Table 1).

Effect of residence on decomposition: AM vs. EcM forests

In AM and EcM stands, older (i.e. deeper) horizons decomposed more slowly than younger ones (Fig. 1). Organic matter loss was slower in the litterbags of 1 µm-pore size mesh in all horizons of both types of forests. However, the slowing down of decomposition due to mycorrhizal fungal exclusion was only statistically significant in the F horizons in stands dominated by AM (-3.7 %, *P*-value = 0.02; Fig. 1a) and EcM (-4.4 %, *P*-value = 0.019; Fig. 1b). Differences in the effects of the mycorrhizal exclusion treatments among forest types increased between one and two years of incubation (Fig. 2). Overall, decomposition was slower in AM compared to EcM stands, ranging from -0.8% (*P*-value > 0.05) of mass loss after one year to -3% (*P*-value < 0.001) after two years

of incubation. After two years, decomposition of organic matter originating from EcM and AM soils was higher in EcM stands (Fig. 2).

Table 1. Initial soil chemistry characteristics: C:N ratio, lignin:N ratio, $\delta^{15}N$, thickness and carbon stocks of the upper three horizons (litter - L, fragmented - F, humic - H) of arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) forest. Means and standard deviation are shown (n = 5).

	Horizon	AM-dominated forest	Standard deviation	EcM-dominated forest	Standard deviation
C:N ratio	L	22.71	2.53	27.36	1.81
	F	20.50	1.01	22.32	1.36
	H	18.41	0.85	20.09	1.48
lignin:N ratio	L	9.68	1.40	13.05	1.74
	F	10.70	1.69	12.57	0.99
	H	8.62	1.30	10.50	1.50
$\delta^{15}N$ (‰)	L	-3.26	0.36	-3.16	0.63
	F	-2.48	0.40	-1.96	0.48
	H	-0.72	0.59	-0.74	0.36
Thickness (cm)	L	0.71	0.22	0.81	0.30
	F	2.36	0.68	3.44	0.65
	H	4.21	0.95	7.19	2.73
Carbon stock (kg m^2)	L	0.89	0.28	1.05	0.43
	F	2.68	0.76	4.24	0.86
	H	2.97	0.67	6.99	4.00

Effect of provenance: AM vs. EcM forests

Litter originating from AM stands decomposed more quickly than EcM litter after one year but this was no longer the case after two years (P-value > 0.05; Fig. S5). While changes in the litter C:N ratio remained similarly low for both soil origins (~1, Fig. S6), the EcM litter showed a clear increase (~1.2) suggesting a lower loss in N compared to C. Similarly, changes in lignin:N ratio were also stronger for EcM litter (Fig. S7).

Effect of provenance and residence on C fractions and N

Mycorrhizal exclusion did not affect concentrations of soluble contents nor hemicellulose in litter incubated in AM and EcM stands. Compared to EcM stands, decomposition was slower in AM stands for litter cellulose (-4.12 %, *P*-value = 0.001; Fig. S8) and lignin (-6.56 but *P*-value > 0.05; Fig. S9). Mycorrhizal exclusion slowed down decomposition of cellulose (-3.79 %, *P*-value = 0.003) and lignin (-5.13% but *P*-value > 0.05). Overall, N loss was reduced by mycorrhizal exclusion (-2.83 %, *P*-value < 0.001) and reduced in AM stands (+2.7 %, *P*-value < 0.001). After two years, ^{15}N enrichment was higher in EcM stands (F horizons only, *P*-value = 0.046) but effect of mycorrhizal exclusion was rather low (Fig. S10).

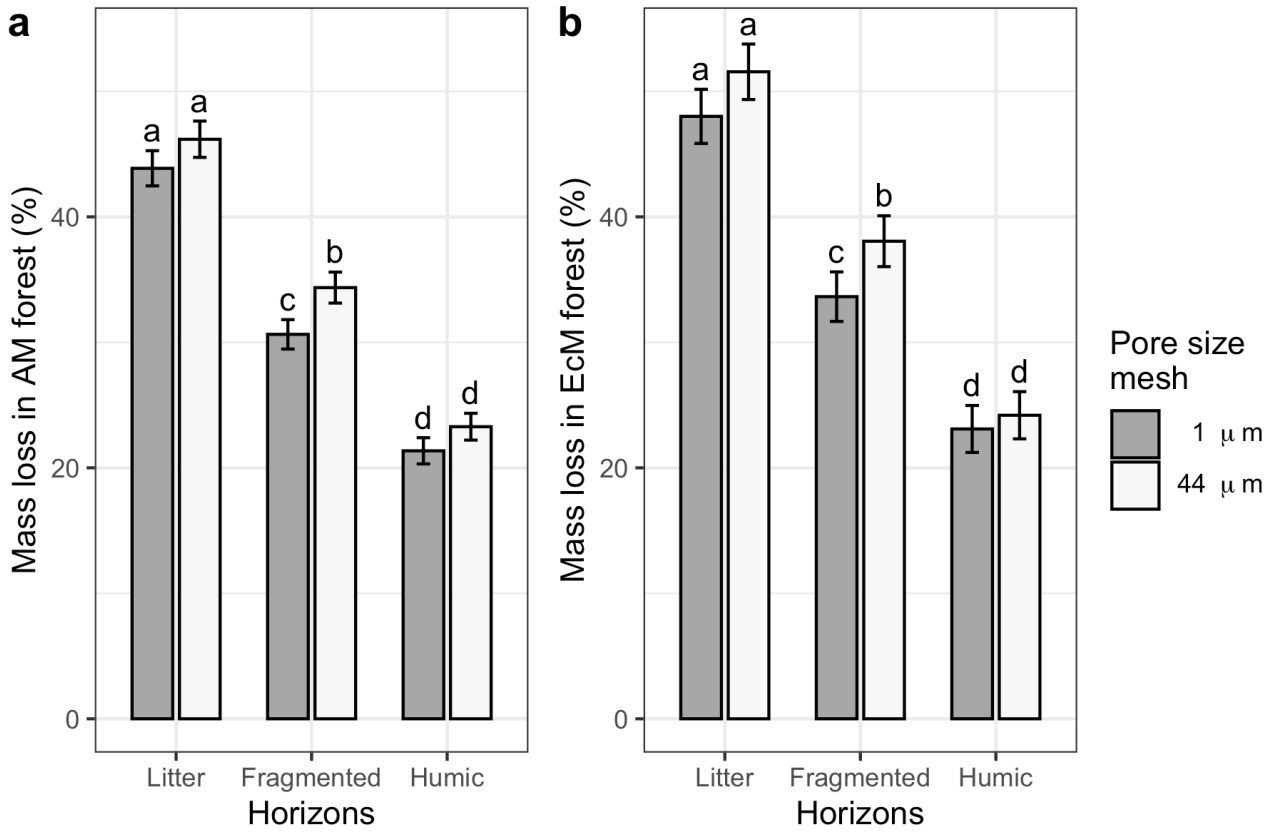

Figure 1. Percentage of mass loss of the three upper horizons incubated for two years in forests dominated by (a) arbuscular mycorrhiza (AM) or (b) ectomycorrhiza (EcM) in litterbags with pore mesh size of 1 µm (grey bars) and 44 µm (white bars). Means ± 1 SE are shown (*n* = 20). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters within each panel indicates significant differences (*P*-value < 0.05).

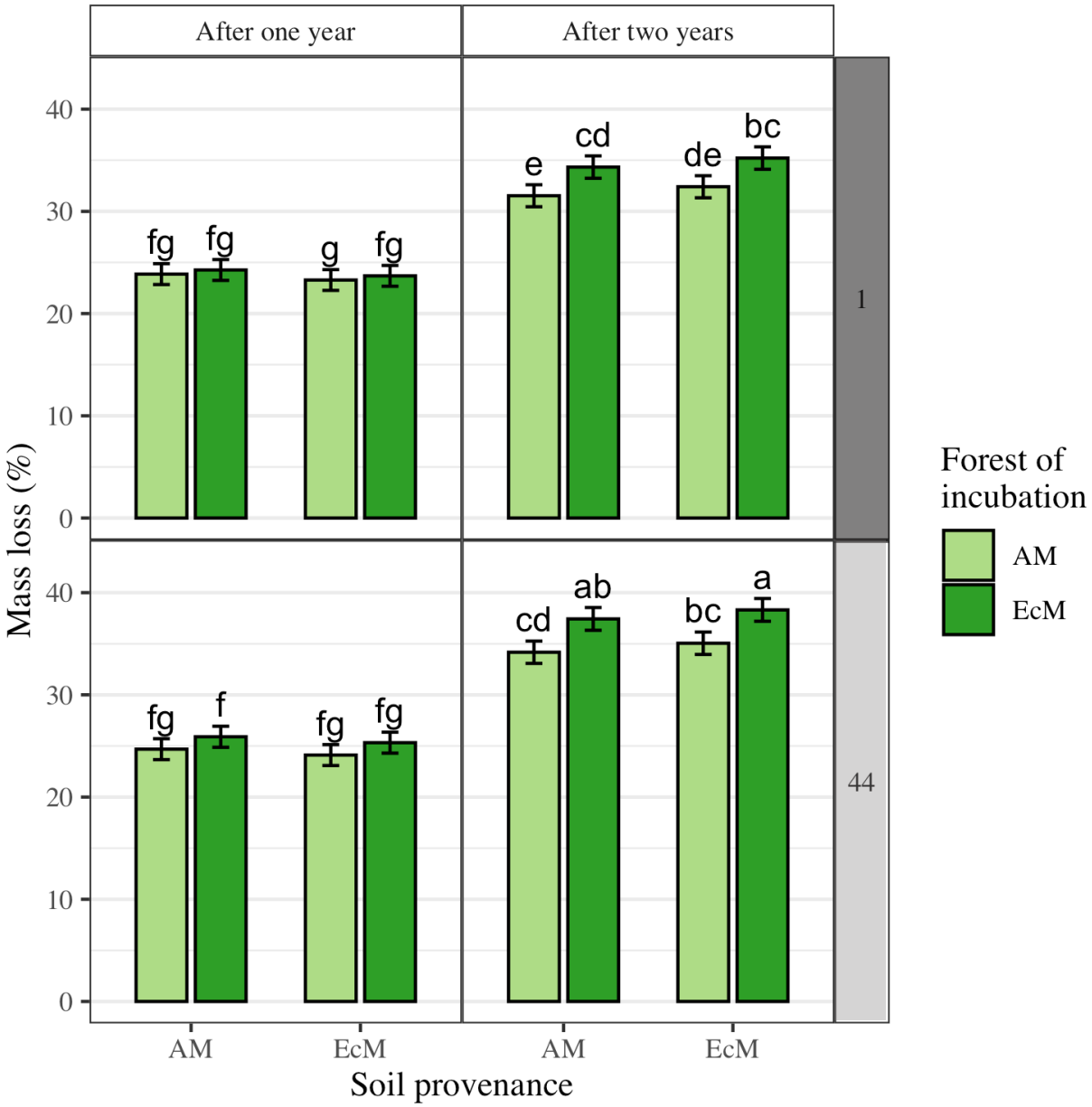

Figure 2. Percentage of mass loss after one and two years of incubation in forests dominated by arbuscular mycorrhiza (AM) or ectomycorrhiza (EcM) in litterbags with pore size mesh of 1 µm (top panels) and 44 µm (bottom panels) and organic matter provenance from AM and EcM. Means ± 1 SE are shown ($n = 30$). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

Discussion

No evidence of a Gadgil effect in either forest mycorrhizal type was observed. In fact, the opposite effect was observed, in that decomposition was faster in the presence of EcM or AM fungi than in their absence. Contrary to our hypothesis, decomposition was faster in EcM- than in AM-dominated forests, but C stocks within the upper 20 cm of soil were greater in EcM stands compared to neighboring AM stands. As predicted, decomposition was higher in upper horizons (i.e. 'younger' soil), and the net effect of the broader fungal network on decomposition was significant in the fragmented (F) horizons. The F horizon is located just below the litter (L), where most decomposition studies tend to focus. Our results suggest that the Gadgil effect is not a universal pattern in EcM forests, and that mycorrhizal fungi may actually accelerate rather than slow down decomposition (Frey, 2019). In agreement with these results, we found that decomposition was quicker in EcM forests regardless of organic matter origin, suggesting an HFA in EcM but not AM systems.

Several abiotic and biotic factors can impact litter decomposition, such as climate and soil fauna (Hättenschwiler *et al.*, 2005; Steidinger *et al.*, 2019). However, given the importance of fungi in soil decomposition processes, there has been much interest in exploring the potential effects of interguild fungal interactions over C and nutrient dynamics (Dighton *et al.*, 1987; Verbruggen *et al.*, 2017). Mycorrhizal fungi can inhibit saprotrophs by competing for nutrients, resulting in slower organic matter decomposition and promotion of C accumulation (Frey, 2019). We took advantage of a natural experiment of co-occurring patches of AM and EcM trees under similar environmental conditions but distinct fungal communities and soil chemistry (Carteron *et al.*, 2020) to test if contrasting mycorrhizal strategies exerted different control on organic matter decomposition (Phillips *et al.*, 2013; Dickie *et al.*, 2014). However, contrary to the Gadgil effect hypothesis, our results showed that both EcM and AM fungi accelerate organic matter decomposition in this northern deciduous forest. This might occur if the overall positive effect of mycorrhizal hyphae and other outside fungi on decomposition was greater than any potential negative impacts of competition with saprotrophs. In addition, mycorrhizal fungi combined with their local microbial community in EcM forests tended to degrade cellulose and lignin more quickly compared to AM forests. By isolating the effect of mycorrhizas, microbial communities and local environmental conditions, our study shows that decomposition tends to be higher in EcM than AM forests regardless of soil origin and incubation time. Our results challenge the view that EcM fungi slow

down litter and soil decomposition compared to AM fungi (Tedersoo & Bahram, 2019 and references therein). They also suggest that more attention should be paid to priming *vs.* inhibitory effects of different mycorrhizal types on the decomposition of organic matter (Kuzyakov, 2010).

Ectomycorrhizal fungi have traditionally been suggested to slow down litter decomposition via their negative competitive effects on free-living saprotrophs (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016). In our field experiment, we have found that EcM fungi in fact accelerated the decomposition across the three upper organic horizons over two years, particularly in the fragmented (F) horizon. Fernandez & Kennedy (2016) suggested a number of important environmental factors that could modulate the inhibiting impact of EcM fungi on free-living saprotrophs, which might help to explain our results. First, organic matter recalcitrance was relatively low in this broadleaf forest, with lignin:N ratios below 20. Similarly, the C:N ratio was below 30, making N less limiting for saprotrophs compared to other studies where a Gadgil effect was observed (Smith & Wan, 2019). Secondly, the studied podzols were well-stratified and exhibited a strong vertical segregation with distinct fungal communities with strong shifts from saprotrophic to mycorrhizal fungal dominance with increasing soil depth (Carteron *et al.*, 2020), thereby reducing opportunities for interguild competition. Finally, decreased soil moisture due to EcM fungi can impede decomposition processes (Koide & Wu, 2003), but our system is located in a northern temperate forest characterized by a humid continental climate with precipitations throughout the year, where water is not thought to be limiting. At least three other experimental studies have found a positive combined effect of roots and EcM fungi on decomposition (Zhu & Ehrenfeld, 1996; Subke *et al.*, 2011; Malik, 2019). In our case, it is worth noting that the strongest positive net effect was observed in the fragmented horizon where there are: (i) high root colonization by EcM and AM fungi, (ii) high abundance of saprotrophic and mycorrhizal fungi and (iii) high fine root density (Carteron *et al.*, 2020). Most studies that have studied the impact of mycorrhizas on decomposition have focus on the most recent litter (L) layer, whereas here we show that important processes occur in deeper (organic) horizons. Our results suggest that vertical stratification should be taken into account to better understand the effect of mycorrhizas on the decomposition process.

Arbuscular mycorrhizal fungi are known to produce compounds that can, for example, alter microbial community or promote soil aggregation thus modulating decomposition rate (e.g. Hodge

et al., 2001; Gui *et al.*, 2017; Xu *et al.*, 2018). Decomposition can even be reduced by AM fungi, potentially through antagonistic interactions with free-living saprotrophs (Leifheit *et al.*, 2015; Carrillo *et al.*, 2016). In our field experiment, we found no evidence of a Gadgil effect exerted by AM fungi that would counterbalance their positive impacts on decomposition. As expected, decomposition in the upper three organic horizons in AM forest was not reduced with the 1 µm-pore mesh bags (where mycorrhizal hyphae were thought to be excluded), but in fact tended to increase. Given that AM fungi lack a strong degradation machinery (Tedersoo & Bahram, 2019), our results support the view that priming of organic matter decomposition might be an important nutrient acquisition strategy for them through the production of exudates and necromass (Wurzburger & Brookshire, 2017; Frey, 2019). It is worth noting that with the 1 µm-pore mesh bags, decomposition in AM forests tended to be slower than in EcM forests, suggesting that their free-living saprotrophic communities have different capacities to degrade organic matter (see results after two years in Fig. 2). Microbial communities in AM forest might be less efficient at degrading organic matter due to their more easily-decomposed litter contrary to what has been observed for other AM systems in microcosm experiments (Taylor *et al.*, 2016). Evaluating the response of the saprotrophic community using molecular tools over long-term experiment would be an interesting way to better understand decomposition processes *in situ*, in order to complement studies that focus on laboratory manipulations of mycorrhizal abundance (Verbruggen *et al.*, 2017). It would also allow us to experimentally assess if the abundance of saprotrophs shifts in deeper horizons when AM and EcM fungi are excluded (e.g. Lindahl *et al.*, 2010; Sietiö *et al.*, 2019).

Leaf litter decomposition rates are known to be positively linked with initial N concentration and inversely with lignin (Prescott, 2005; Berg & McClaugherty, 2014). Overall net effect of mycorrhizas over decomposition is known to be controlled by substrate quality and local microbial community composition (Fernandez *et al.*, 2019; Smith & Wan, 2019). As expected, we found a strong effect of soil depth with deeper (i.e. "older") horizons decomposing more slowly. In general, the litter of EcM-associated trees tend to have a lower quality than AM trees such as lower C:N and lignin:N ratios (Lin *et al.*, 2017), which may drive soil C accumulation in the short-term. In our field sites, litter in EcM stands had lower quality compared to AM stands. The EcM stands were mostly composed of American beech. However, American beech litter is less recalcitrant than many conifers (Moore *et al.*, 1999), which may explain discrepancies with other studies from coniferous EcM forests in which Gadgil effects have been observed (Fernandez & Kennedy, 2016;

Smith & Wan, 2019). In temperate forests, AM plants tend to produce leaf litter that decomposes more rapidly *in situ* than that of EcM plants (Keller & Phillips, 2019). Similarly, litter originating from AM patches decomposed more quickly than EcM litter after one year but interestingly, this was not the case after two years in our experiment. This is consistent with previous studies showing that sugar maple leaf litter tend to decomposes more quickly during the first years after senescence (McHale *et al.*, 1998; Lovett *et al.*, 2016), but tends to be more similar to American beech after several years (within standard error range, see Lovett *et al.*, 2016). Community of decomposers in EcM forests may be efficient at decomposing recalcitrant organic matter (Fernandez *et al.*, 2019). Contrary to the results of Midgley *et al.* (2015) obtained from another study system, we observed HFA in EcM forests but not in AM forests. The efficiency of the microbial decomposers present in EcM soil for decomposing organic matter may be true regardless of litter type and quality. Furthermore, we found no evidence that fragmented (F) and humic (H) horizons in AM stands decomposed faster than the same horizons in EcM stands (but see Jacobs *et al.*, 2018). Taken together, these results suggest that the significant impact of initial litter chemistry on decomposition diminishes after the first year of decomposition and that microbial decomposer community may adapt to 'home' substrate quality.

Reducing decomposer diversity reduces litter decomposition rate (Handa *et al.*, 2014; Li *et al.*, 2020), but this effect is context-dependent and the effect of soil fauna is variable across focal species (Makkonen *et al.*, 2012). Smaller mesh size are known to reduce the potential diversity of soil fauna that are important for decomposition processes (Hättenschwiler *et al.*, 2005). In our study, patches were mainly composed of American beech or sugar maple, and previous studies indicate that maple litter is generally preferred over beech litter by the soil fauna (Hättenschwiler & Bretscher, 2001; Jacob *et al.*, 2010). However, the difference in decomposition between American beech and sugar maple seems to decrease over time (Lovett *et al.*, 2016) and to be dependent on stand type of incubation (Côté & Fyles, 1994). Unlike most studies, we used litterbags that were designed to follow decomposition of the upper three organic horizons while avoiding soil trenching and tree girdling which confound the effects of roots and mycorrhizal fungi (Fernandez & Kennedy, 2016). Trenching is the historical and most used method to test the Gadgil effect, but it is known to directly affect soil drainage, increase soil moisture by impeding root water uptake and strongly disturb the system (Gadgil & Gadgil, 1971; Fisher & Gosz, 1986; Fernandez & Kennedy, 2016). Tree girdling is the most extreme alternative as it kills trees, also preventing

further research on the same site. Litterbags of 1 and 44 µm-pore size mesh might have also modified oxygen and moisture contents which could have altered the results, but even smaller pore size seems to allow well for the movement of water and nutrients (Allison *et al.*, 2013). In our experiment, the initial disturbance may have increased labile C but the persistence of this effect after two years may be rather limited. Furthermore, the observed effects of our exclusion treatment on mass loss increased between the first and second years of incubation suggesting persistent biological effects. Decreasing mesh size might have decreased soil moisture but we observed no impact on litter soluble content losses suggesting a rather low effect caused by mesh size, at least on the most labile fractions of C. It is possible that the use of litterbags with small mesh size limited the exposure to biophysical perturbations, which might hamper mass loss (Prescott, 2005; Berg & McClaugherty, 2014), but this was common to all treatments. To better predict soil C processes and stocks, more research may be needed to understand how interaction between mycorrhizas, soil fauna, plant inputs and variables such as soil moisture, or bulk density impact decomposition (Lin *et al.*, 2017).

Our sampling design allowed us to spatially distinguish decomposition processes in the upper three horizons and assess the fate of young to older organic matter overcoming some limits of short-term experiments. The overall net effect of mycorrhizas on decomposition was positive regardless of mycorrhizal type, but varied throughout the soil profile. Mycorrhizal impact tended to be highest in the fragmented horizon, pointing to older organic horizons acting as hotspots of decomposition, and suggesting that future studies should focus on this horizon to link mycorrhizas with decomposition dynamics and soil C sequestration. Further analyses would allow to better understand if the greater decomposition could be due to higher microbial biomass, leading to higher enzymatic activities. As expected from previous studies (e.g., Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019), C stocks were greater in EcM stands compared to neighboring AM stands in this northern temperate forest even though decomposition was greater in EcM soils, and positively influenced by the broader fungal network. This indicates the potential importance of others factors such as litter quantity, soil fauna and moisture level in regulating C dynamics. The quality and composition of litter is important for short-term C release, but the microbial community, including root-associated fungi and mycorrhizal-associated organisms (Netherway *et al.*, 2020), potentially have a strong impact on a longer-term which is important for C sequestration (Cotrufo *et al.*, 2015). Our study shows that forests dominated by different mycorrhizas have distinct impacts in soil

organic matter dynamics. As such, tree mycorrhizal type should be considered in future studies to increase our capacity to predict C dynamics and ecosystem functioning more generally.

Acknowledgements

We are grateful to the two anonymous reviewers for critical the suggestions that significantly improved the manuscript. We would like to thank the staff from the Station de biologie des Laurentides (SBL) of Université de Montréal for facilitating the field work. Funding, including scholarships to AC, was provided by Discovery Grants to EL (RGPIN-2014-06106, RGPIN-2019-04537) by the Natural Sciences and Engineering Research Council of Canada (NSERC) as well as a "Nouveau Chercheur" grant (2016-NC-188823) by the Fonds de recherche du Québec sur la Nature et technologies (FRQNT). AC would like to sincerely thank the following institutions for providing generous scholarships: FRQNT (Dossier 272522), Institut de recherche en biologie végétale, Centre de la science de la biodiversité du Québec, Centre d'étude de la forêt and Université de Montréal through the "Bourse d'excellence Hydro-Québec".

Authors' contributions

EL and AC conceived the ideas and designed methodology; AC and FC collected and analyzed the data; AC and EL interpreted the results; AC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary information

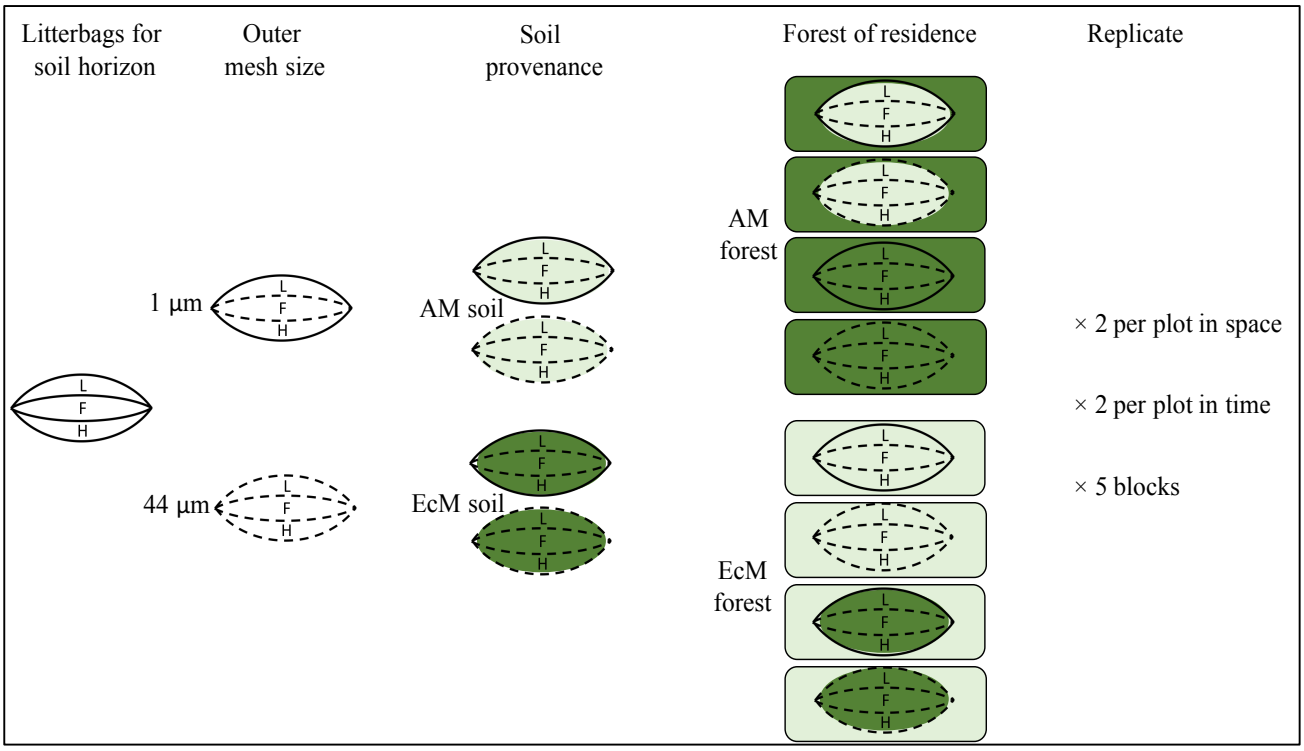

Figure S1. Factorial design of the reciprocal transplant experiment. There were 160 litterbags composed of three horizons (L, F, H, standing for litter, fragmented and humic horizon respectively) for a total of 480 incubated soil samples.

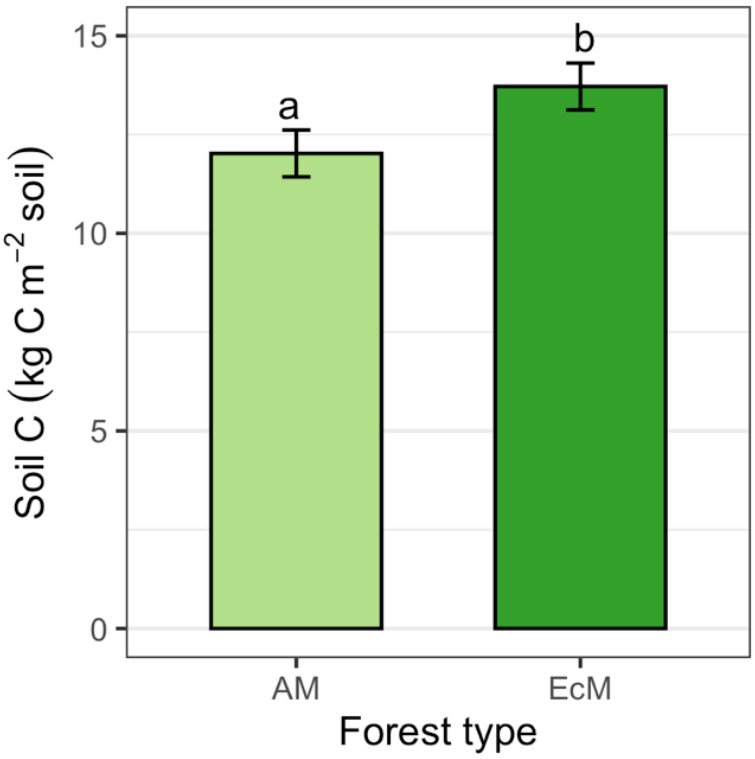

Figure S2. Stocks of organic carbon in the upper 20 cm of soil in arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) forest types. Stocks differed significantly (one-way analysis of variance, *P*-value < 0.001). Means ± 1 SE are shown (*n* = 5).

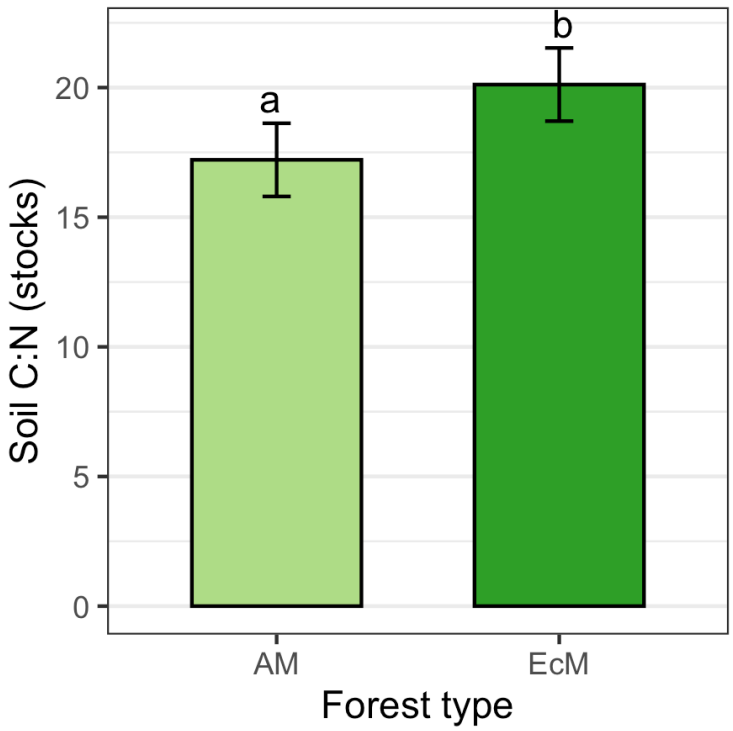

Figure S3. C:N ratio in the upper 20 cm differed significantly (one-way analysis of variance, *P*-value = 0.024) between AM and EcM forests. Means ± 1 SE are shown (n = 5).

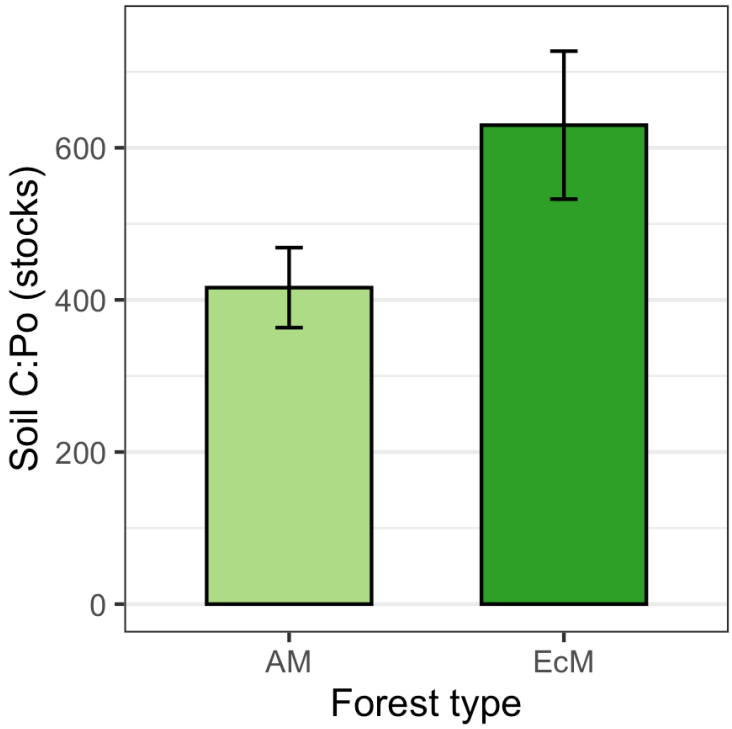

Figure S4. C:P_o ratio in the upper 20 cm differed but not significantly (one-way analysis of variance, *P*-value > 0.05) between AM and EcM forests. Means ± 1 SE are shown (*n* = 5).

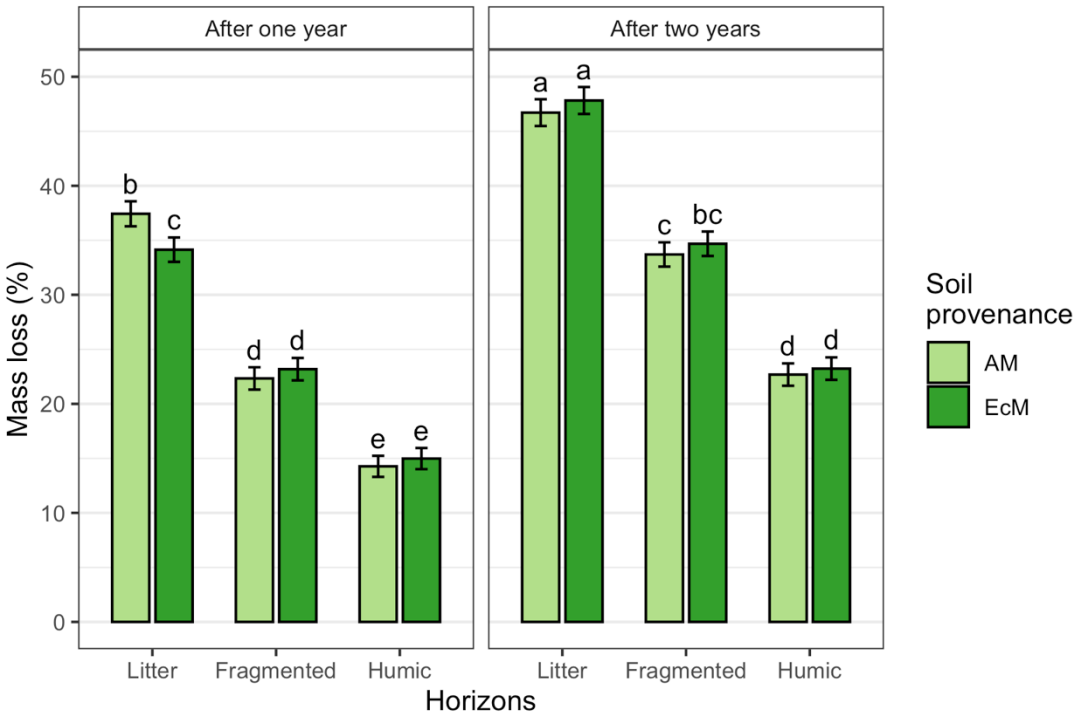

Figure S5. Mass loss after one and two years of the three upper horizons originating from arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests. Means ± 1 SE are shown (n = 20). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

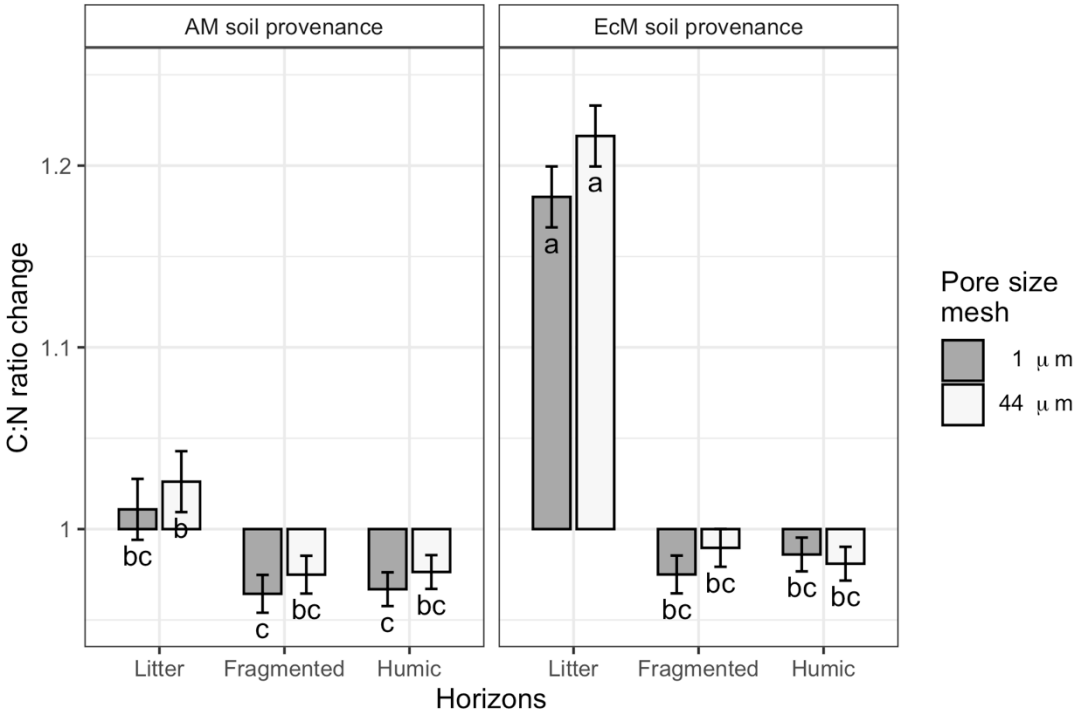

Figure S6. Changes in C:N ratio of the three upper horizons originating from the arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests in litterbags with pore size mesh of 1 µm (grey bars) and 44 µm (white bars). Means ± 1 SE are shown ($n = 20$). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

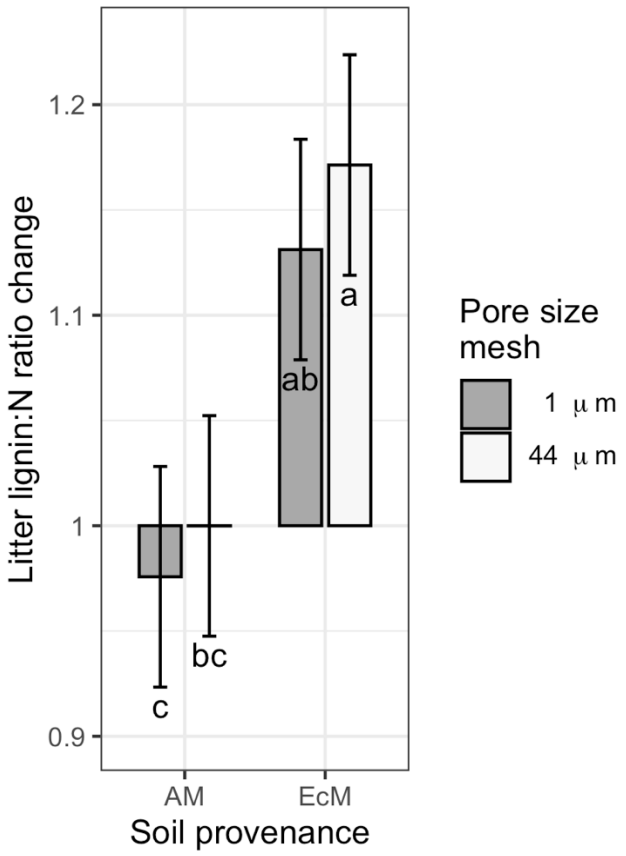

Figure S7. Changes in lignin:N ratio in litter (i.e. L horizon) incubated arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests in litterbags with pore size mesh of 1 μm (grey bars) and 44 μm (white bars).. Means ± 1 SE are shown ($n = 20$). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

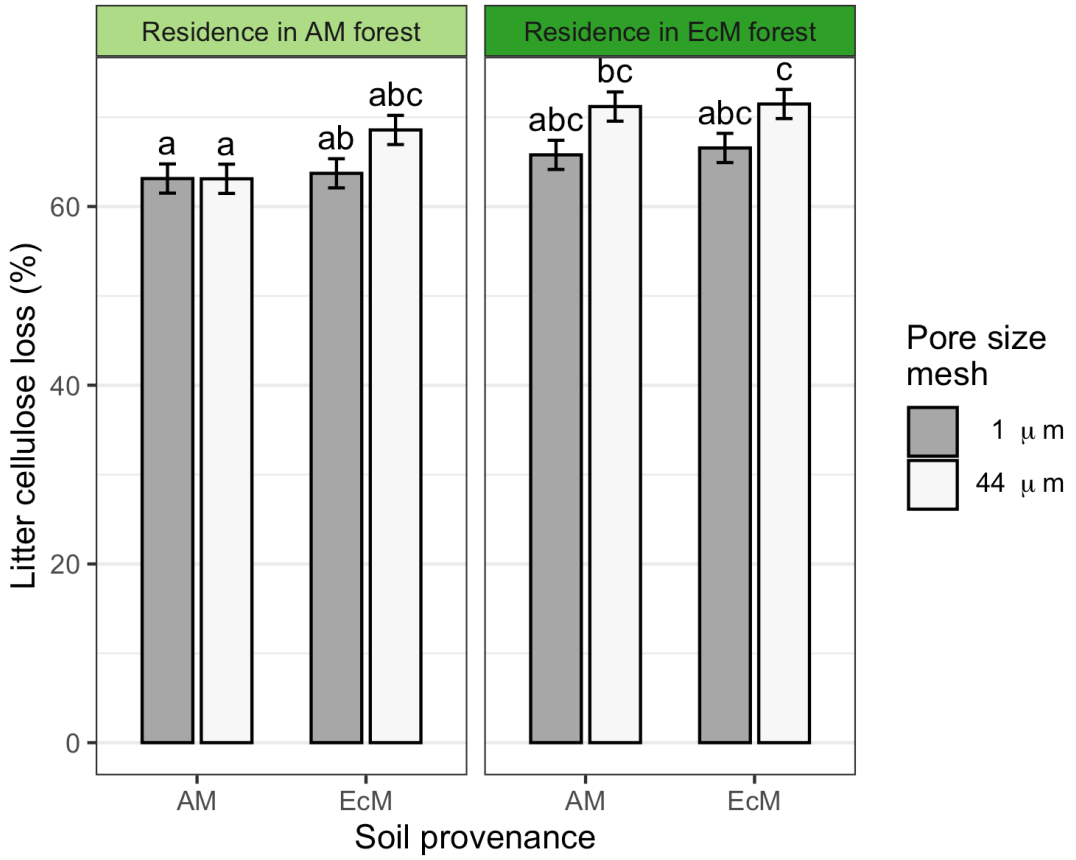

Figure S8. Loss of cellulose in litter (i.e. L horizon) incubated for two years in arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests in litterbags with pore size mesh of 1 µm (grey bars) and 44 µm (white bars). Means ± 1 SE are shown ($n = 20$). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

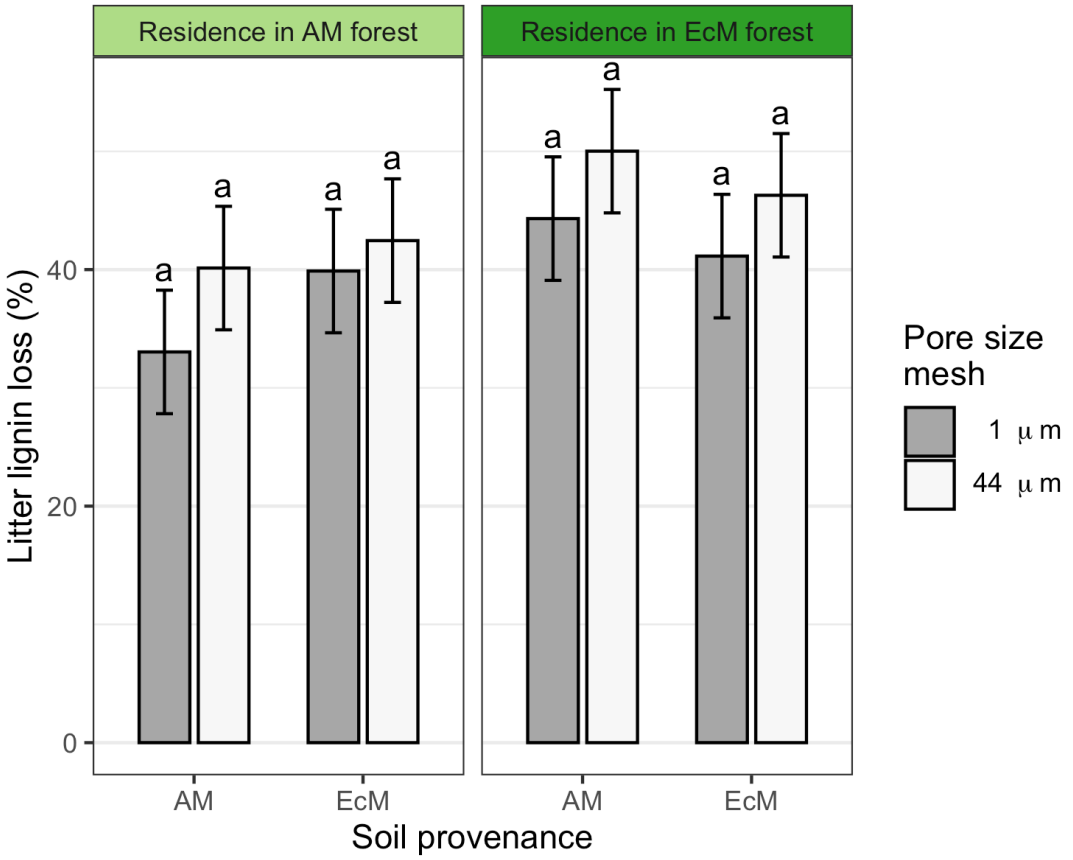

Figure S9. Loss of lignin in litter (i.e. L horizon) incubated for two years in arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests in litterbags with pore size mesh of 1 µm (grey bars) and 44 µm (white bars). Means ± 1 SE are shown (n = 20). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

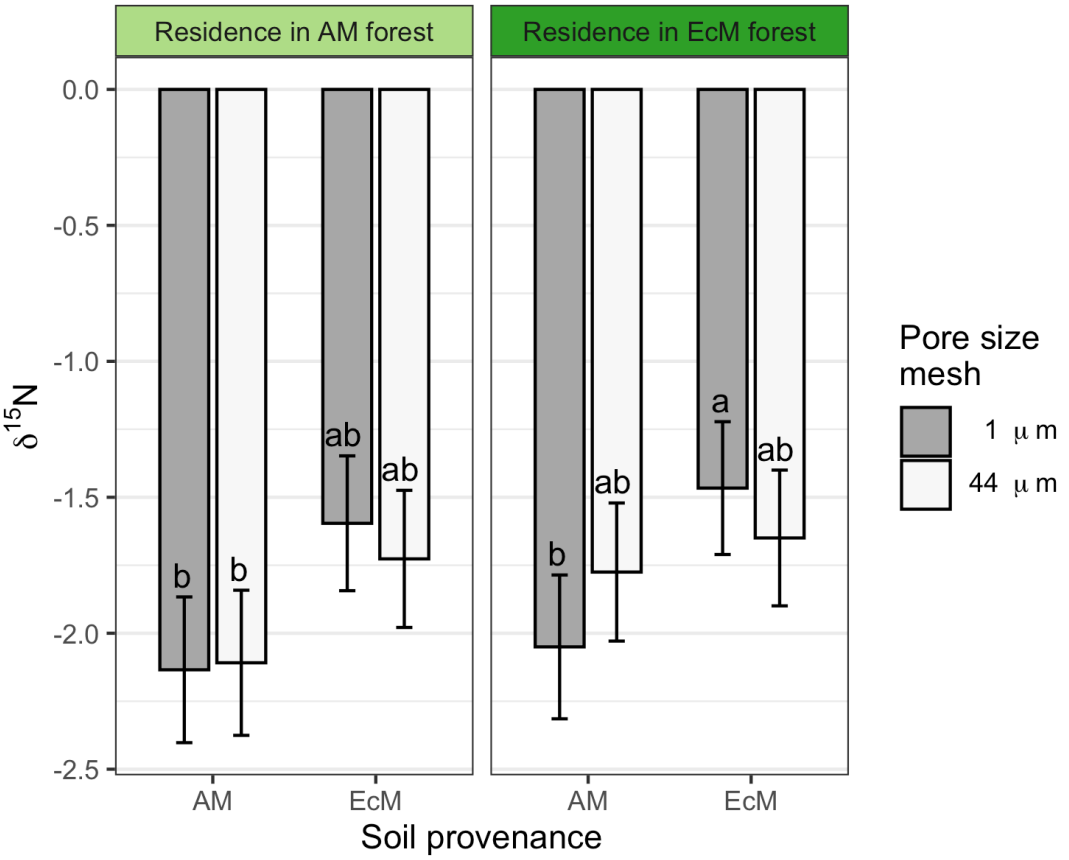

Figure S10. Change in ^{15}N in fragmented horizons after two years of incubation in arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) forests in litterbags with pore size mesh of 1 μm (grey bars) and 44 μm (white bars). Means ± 1 SE are shown ($n = 5$). Multiple comparison using Tukey's honestly significant difference post-hoc test, different letters indicates significant differences (P-value < 0.05).

Table S1. For each plot, species basal area (m^2 ha^{-1}) and their mycorrhizal strategy (AM: Arbuscular mycorrhizal, EcM: Ectomycorrhizal). Only individuals of 5 cm diameter and more at breast height were measured.

Species / Plot	*Acer saccharum* (AM)	*Fagus grandifolia* (EcM)	*Acer pensylvanicum* (AM)	*Acer rubrum* (AM)	*Betula papyrifera* (EcM)
AM plot 1	20.3	1.73	1.12	0	0
AM plot 2	28.3	2.6	0	0	0
AM plot 3	29.1	2.8	1.4	0	0
AM plot 4	31.5	3.24	0.18	4	0
AM plot 5	37.6	2.58	0	0	0
EcM plot 1	6.89	26.2	0	0	4.36
EcM plot 2	1.21	38.7	0.25	0.24	0
EcM plot 3	2.8	23.8	3.26	0	0
EcM plot 4	14.5	23.1	0.05	0	1.44
EcM plot 5	3.67	29.6	0.06	0	2.94

Table S2. Effects tests from the full model simultaneously explaining decomposition in arbuscular mycorrhizal and ectomycorrhizal forests.

Fixed effects	num DF	den DF	*F*-value	*P*-value
Intercept	1	206	669.30	**<0.0001**
Soil provenance	1	206	5.70	**0.0179**
Horizon	2	206	1537.07	**<0.0001**
Time	1	206	969.28	**<0.0001**
Mycorrhizal exclusion	1	206	24.23	**<0.0001**
Forest of residence	1	206	19.71	**<0.0001**
Soil provenance × Horizon	2	206	4.23	**0.0159**
Soil provenance × Time	1	206	1.31	0.2537
Horizon × Time	2	206	11.44	**<0.0001**
Mycorrhizal exclusion × Forest of residence	1	206	0.19	0.6615
Horizon × Mycorrhizal exclusion	2	206	4.48	**0.0125**
Horizon × Forest of residence	2	206	2.18	0.1156
Time × Mycorrhizal exclusion	1	206	6.57	**0.0111**
Time × Forest of residence	1	206	6.93	**0.0091**
Soil provenance × Horizon × Time	2	206	3.61	**0.0288**
Horizon × Mycorrhizal exclusion × Forest of residence	2	206	0.78	0.4613
Time × Mycorrhizal exclusion × Forest of residence	1	206	0.15	0.6976
Horizon × Time × Mycorrhizal exclusion	2	206	0.27	0.7620
Horizon × Time × Forest of residence	2	206	1.87	0.1562
Horizon × Time × Mycorrhizal exclusion × Forest of residence	2	206	0.01	0.9862

Table S3. Observed values of initial litter chemistry of the upper three horizons (litter - L, fragmented - F, humic - H) of arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) forest. Means and standard deviations are shown (n = 5).

	Horizon	AM-dominated forest	Standard deviation	EcM-dominated forest	Standard deviation
Total C (%)	L	46.61	0.57	47.69	0.43
	F	44.43	1.10	46.74	0.90
	H	41.07	2.64	46.01	1.54
Total N (%)	L	2.08	0.26	1.75	0.12
	F	2.17	0.10	2.10	0.15
	H	2.23	0.13	2.30	0.13
Hemicellulose (%)	L	10.85	1.32	11.30	0.85
	F	8.17	0.85	9.61	0.92
	H	5.70	0.90	6.68	0.98
Cellulose (%)	L	16.13	1.24	19.35	0.97
	F	11.73	1.38	14.90	1.70
	H	10.69	1.25	11.31	1.15
Lignin (%)	L	19.80	1.13	22.69	1.78
	F	23.10	2.88	26.45	3.35
	H	19.19	2.80	24.03	2.60

Transition tempérée-boréale au Mont Saint-Joseph, Notre-Dame-des-Neiges.

CHAPITRE 3 – Les propriétés abiotiques et biotiques du sol limitent l'établissement en forêt boréale d'une espèce d'arbre tempéré dominante

Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests

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Keywords: Plant-soil interactions, sugar maple, temperate-boreal ecotone, range expansion, mycorrhizas

Published in: *Journal of Ecology*

DOI: https://doi.org/10.1111/1365-2745.13326

Abstract

Climate warming is expected to cause the poleward and upward elevational expansion of temperate plant species, but non-climatic factors such as soils could constrain this range expansion. However, the extent to which edaphic constraints on range expansion have an abiotic (e.g. soil chemistry) or biotic (e.g. micro-organisms) origin remains undetermined. We conducted greenhouse experiments to test if the survival and growth of a major North American temperate tree species, *Acer saccharum* (sugar maple), is independently or jointly constrained by abiotic and biotic properties of field-collected soils from within and beyond the species' elevational range. Abiotic factors, particularly low base cation concentrations were major constraints to seedling establishment in boreal forest soils (beyond the range edge), but insufficient arbuscular mycorrhizal fungal inoculum (biotic factor) also strongly reduced seedling performance in these soils. Our results suggest that forecasting future changes in forest composition under climate warming requires consideration of soil properties as well as the mycorrhizal status of tree species.

Introduction

Climate warming has caused many terrestrial and aquatic organisms to expand their ranges poleward and upward in elevation (Parmesan, 2006; Pecl *et al.*, 2017). If plant distributions were primarily determined by climatic conditions, plant distributions should shift geographically in concert with climate, but many studies show that suitable climatic conditions for a given species shift much faster than species range limits (Zhu *et al.*, 2012; Corlett & Westcott, 2013; Savage & Vellend, 2015). Although such lags in species range expansion can be due to demographic factors such as propagule availability (Engler *et al.*, 2009), they may also indicate negative impacts of non-climatic factors (Van der Veken *et al.*, 2007; Putnam & Reich, 2017). Reduction in survival, growth and fecundity are often observed in plants that are transplanted beyond their range limits (Stanton-Geddes & Anderson, 2011; Hargreaves *et al.*, 2014), but the underlying causes are rarely known. Further investigation – experimental studies in particular – are needed to understand the underlying processes and external drivers of species range limits and potential range shifts (Sexton *et al.*, 2009; Chen *et al.*, 2011).

Plant establishment beyond current geographic range limits could be constrained due to biotic and/or abiotic factors, with many such factors involving belowground soil characteristics (Chapin *et al.*, 1994; Lafleur *et al.*, 2010; Tomiolo & Ward, 2018). For example, beyond range edges the positive effects of soil biota such as mutualists can be reduced or absent and the negative effects of generalist soil-borne pathogens can be increased. Similarly, unfavorable soil chemical properties (e.g. low pH) or physical structure (e.g. thicker litter layer) beyond a species' range could impede plant establishment. By contrast, there are many reported cases of plant species that actually show higher establishment success outside their current range. For instance, species can escape their native soil-borne pathogens when establishing outside their range, as described for invasive plants under the "enemy release hypothesis" (Keane & Crawley, 2002; Liu & Stiling, 2006). However, interactions among abiotic and biotic factors could lead to more complex outcomes such as the "happy edge", where success is highest at the edge of a species' range (Urli *et al.*, 2016). Abiotic and biotic factors have often been treated separately in studies of range limits, but they might interact in important ways – a topic largely unexplored to date (Gaston, 2009; Lau *et al.*, 2008; Sexton *et al.*, 2009; but see Johnson *et al.*, 2017).

Elevational gradients are valuable model systems to understand how abiotic and biotic factors independently or jointly influence range shifts in response to climate change (HilleRisLambers *et al.*, 2013), and they are comparable in many (but not all) respects to latitudinal gradients over longer distances (Diaz *et al.*, 2003; Sundqvist *et al.*, 2013). Strong gradients in vegetation composition can occur over short spatial scales at ecotones, with the temperate-boreal ecotone as a striking example (Evans & Brown, 2017). Temperate forests are usually dominated by broadleaf, deciduous trees. By contrast, boreal forests are dominated by coniferous trees on soils that tend be more acidic and nutrient-poor than those of temperate forests, with important impacts on plant growth (Collin *et al.*, 2017; Evans & Brown, 2017). Soil microbial communities – also important for plant performance – can also be highly variable along elevational gradients and among forest types (Yang *et al.*, 2014; Geml, 2017). For example, ectomycorrhizal associations are dominant in boreal forests, but coexist with arbuscular mycorrhizas in temperate forests (Read & Perez-Moreno, 2003; Phillips *et al.*, 2013). Therefore, even if climatic conditions in the boreal forest becomes suitable for temperate plants, their establishment could nonetheless be strongly constrained not only by physical substrate conditions but also the absence of mutualistic organisms such as arbuscular mycorrhiza fungi (Evans & Brown, 2017). Therefore, understanding the abiotic and biotic belowground processes constraining the establishment of temperate tree species into boreal forests is essential to predicting the future distribution of the temperate forest with increasing temperature.

Our study sought to determine the establishment success of a dominant temperate tree (*Acer saccharum*; hereafter sugar maple) in soils sampled along an elevational gradient from the temperate (core range) to the boreal (beyond) forest, and to understand the relative importance of abiotic and biotic belowground factors. To do so, we conducted two greenhouse experiments: one using unmanipulated soil originating from the three forest types (i.e., temperate, mixed and boreal), and a second involving manipulations of soil biota. Based on the hypothesis that abiotic and biotic soil properties constrain upward elevational range expansion, we predicted that: (i) sugar maple seedlings would show higher survival and performance in soils from within the species range, (ii) these soil effects would be due both to abiotic conditions and also biotic factors, both of which should be more favorable within the species range. Alternatively, release from specialized soil pathogens could result in higher seedling performance at or beyond the species' range edge. If seedling survival or performance varies according to inoculum source on replicate samples of the

same soil origin, we can infer an important role of biotic factors. On the other hand, differences among sterilized samples of different soil origins would be indicative of effects of abiotic factors. Soil pH, carbon, nitrogen, phosphorus, cations, base saturation and root colonization by arbuscular mycorrhizal fungi were measured as potential drivers of seedling survival and performance.

Material and methods

Study system

The study system is located in Parc national du Mont-Mégantic, a protected area of 55 km² in south-eastern Québec, Canada. The study area has been described in detail elsewhere (Brown & Vellend, 2014; Savage & Vellend, 2015). Mont Mégantic is part of the Monteregian Hills, mainly composed of leucogranite and syenite at the surface (Feininger & Goodacre, 2003). Soils are ferro-humic and humo-ferric shallow podzols with a sandy loam texture derived from rocky glacial tills with talus slope at higher elevation (Marcotte & Grantner, 1974). The climate in this region is characterized by warm, wet summers and cold winters with abundant snowfall (SEPAQ, 2010). Elevation in the park ranges from 430 m to 1105 m above sea level (asl). Average temperatures range from -10.2 °C in January to 17.3 °C in July with possible daily maxima above 30°C and an annual mean of 3.9 °C at low elevations (599 m asl). At high elevation (1089 m asl), average temperatures range from -12.4 °C in January to 14.9 °C in July for an annual mean of 1.2 °C (data available from 2013 to 2017 for weather stations IQUBECNO2 and IQUBECNO3 at www.wunderground.com/weatherstation/overview.asp). With decreasing temperature, the length of the growing season is reduced from ~100 days at low elevations to ~80 days at high elevations (SEPAQ, 2010).

Since 1950, the mean annual temperature in our study region of southern Québec has increased by up to 2 °C and by 2050 it is predicted to further increase between by 1.7–4.6 °C (Ouranos, 2015). If temperature limits the distribution of sugar maple, the species is expected to migrate upward in elevation and northward in latitude (Frumhoff *et al.*, 2007). Studies have shown that sugar maple can successfully establish in boreal forests, probably favored by the relatively broad tolerance of seedlings and seed germination to variable soil conditions (Kellman, 2004; Solarik *et al.*, 2016), yet the species is known to be sensitive to acidic soils (St. Clair *et al.*, 2008). At least one study has reported upward elevational migration of sugar maple (Beckage *et al.*, 2008). However, sugar

maple establishment in boreal forests is known to be limited by both aboveground and belowground factors, such as unsuitable soil and seed predation (Brown & Vellend, 2014; Collin *et al.*, 2017). The studied gradient exhibits a striking elevational transition from a sugar maple dominated temperate forest at low elevation to the boreal forest at high elevation, where sugar maple is absent except near the ecotone. This elevational gradient constitutes an ideal study system for our research exploring the relative importance of abiotic and biotic factors on sugar maple establishment into boreal forests because it allows us to minimize variation in important factors such as parent material, aspect and regional climate (local temperature declines with increasing elevation – the gradient of primary interest).

Study sites and soil sampling

Our soil sampling sites were on the eastern slope of Mont Saint-Joseph (45°27' N 71°06' W), which is underlain by uniform parent material (i.e. syenite), from 723 m to 914 m asl. Categorization of the plots was based on elevation as well as on the canopy dominance of sugar maple. Temperate forest plots were dominated by sugar maple, mixed plots had approximately 50% canopy cover of sugar maple, whereas sugar maple was absent from boreal forest plots. To obtain 10 plots of 20 m × 20 m distributed evenly within each forest type, sampling was performed along 10 elevational transects with one plot of each of the three forest types per transect (see Fig. S1): temperate forest (723–821 m asl), mixed forest (748–882 m asl) and boreal forest (875–914 m asl), according to previous studies (Urli *et al.*, 2016). The ecotone between these two forest types, the elevation of which fluctuates somewhat north to south, is a mixture of maple (*Acer* spp.), fir (*Abies balsamea*), and spruce (*Picea* spp.), with abundant yellow birch (*Betula alleghaniensis*).

Soil samples were collected on the eastern slope of Mont Saint-Joseph in June 2016. In each plot, four soil pits were dug in order to obtain representative soil samples at the plot level. For each pit, soil from the top 20 cm was collected separately for different horizons. Organic horizons were separated as L (litter; original structures easily distinguishable), F (fragmented; partial decomposition, structures difficult to recognize), and H (humus; decomposed organic matter, original structures indistinguishable), while the mineral horizons were Ae (characterized by leaching/eluviation of clay, Fe, Al or organic matter) and B (characterized by illuviation/enrichment in organic matter and accumulation of Fe or Al oxides) (Groupe de travail sur la classification des sols, 1998). Because soil profiles differed along the elevation gradient (Fig.

S2), the thickness of each horizon was recorded in each pit, so that it could be recreated in experimental pots. Samples were bulked for each horizon in each plot, and different horizons were kept separate.

Experimental design

To test if boreal soils (biotic and abiotic properties combined) constrained sugar maple establishment, we used fresh untreated soil sampled from the three forests in a first experiment. Starting sample size was 10 for each forest type, so 30 pots in total. In the second (concurrent) experiment, to disentangle the effects of biotic (i.e. soil inoculum) and abiotic (i.e. soil origin) factors on tree establishment, we applied four soil treatments to the soil from each sampling site: (i) sterilization without inoculum (referred to as sterile soil), (ii) sterilization followed by inoculation with boreal forest soil (boreal inoculum), (iii) sterilization followed by inoculation with mixed forest soil (mixed inoculum), (iv) sterilization followed by inoculation with temperate forest soil (temperate inoculum). Inoculation was done by adding 7 % (mass basis) of fresh soil.

We used gamma ray irradiation to sterilize soils because it has fewer effects on soil chemistry compared to other soil sterilization methods (McNamara *et al.*, 2003). The soils were irradiated to a minimum of 50 kGγ (Nordion Inc., Laval, Canada). An experimental unit consisted of a subsample of the soil from a given field plot, subjected to one of the four treatments. For the second experiment, starting sample size was 10 for each treatment combination, and so there were 120 pots: four treatments × three soil origins × 10 replicates (transects).

Prior to the experiment, sugar maple seeds were cold stratified to break dormancy. This was performed at the Berthier Seed Center (Sainte-Geneviève-de-Berthier, Québec). After emergence, seeds were planted in the experimental pots. Seedlings were grown for two growing seasons at ~20–30 °C (July 2016–June 2017) with a dormant winter pause of three months at ~3–5 °C (December 2016–February 2017). In all pots, horizons were kept separate (including inoculum) to maintain realistic podzolic soil profiles. The experiment was conducted under controlled conditions within research greenhouses of the Montréal Botanical Garden (Québec, Canada). Soil was placed into 1-L pots (20 cm high × 5 cm wide). The amount (i.e. thickness) of soil by horizon in the pots depended on actual site measurements (averaged by plot). One seedling was planted per pot after the radicle had emerged. During the first month after transplantation, dead seedlings were immediately replaced with live ones, but after one month we considered mortality to be a treatment

effect and not transplant shock. A shade cloth (allowing passage of 36 % of natural light) was positioned over the pots to reduce light in the greenhouse and simulate a partially shaded environment during the first year of growth. Pots were arranged in 10 blocks, with all the samples from the three plots in a given transect (1–10 in Fig. S1) in the same block. Soil inoculation after sterilization was done using inoculum from the same block (e.g. sterilized temperate soil inoculated with a boreal soil from the same transect).

Soil chemical analyses

For each soil horizon in each field plot, we measured several chemical properties. Soil was first air-dried and sieved (2 mm mesh size for organic horizons and 6 mm mesh size for mineral horizons) prior to analysis for organic carbon (C), total nitrogen (N), total phosphorus (P), labile inorganic P and pH. Total C and N contents were determined by automated combustion and gas chromatography with thermal conductivity detection using a Vario MICRO cube analyzer (Elementar, Langenselbold, Germany). Total P was determined by ignition at 550 °C followed by extraction in 1 M sulfuric acid. Soil pH was determined in both deionized water and 10 mM $CaCl_2$ using a glass electrode, and a soil-to-solution ratio of 1:8 for L and F horizons, 1:4 for H horizon and 1:2 for A, B horizons. After Bray-1 extraction, Bray P (labile P) in the extraction material was determined using automated molybdate colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO). Exchangeable cations were determined for all H, Ae and B horizons by extraction in 0.1 M $BaCl_2$ (2 hours, 1:30 soil to solution ratio) and detection by inductively-coupled plasma optical-emission spectrometry (ICP–OES) with an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA). Total exchangeable bases (TEB) was calculated as the sum of the charge equivalents of Ca, K, Mg and Na. Effective cation exchange capacity (ECEC) was calculated as the sum of the charge equivalents of Al, Ca, Fe, K, Mg, Mn and Na. Base saturation was calculated as (TEB / ECEC) × 100.

Seedling measurements

Surviving seedlings from the two experiments were harvested in June 2017 and processed individually within 24 h. For each seedling, leaves, petioles, stems and roots were separated, measured, and weighed before and after oven-drying at 60 °C for 72 h. Total biomass was estimated as the dry weight of all structures combined. Other size traits were measured but not used in the analysis due to strong correlations and thus redundancy (Table S1). A representative sample of the

roots of each seedling were cleared in 10% w/v KOH, then stained in an ink and vinegar solution at 90°C (Vierheilig *et al.*, 1998). Colonization of the root system by fungal structures was determined using a semi-quantitative scale following a protocol (available at dx.doi.org/10.17504/protocols.io.36rgrd6) modified from Zemunik *et al.* (2018). Using standard light microscopy, we recorded structures of arbuscular mycorrhizal fungi such as hyphae, arbuscules, vesicles, coils as well as fungal endophytes (presence of chytrids, hyphae diameter less than 2 μm with presence of microsclerotia).

Statistical analysis

To quantify the effect of soil origin (forest type) on seedling survival and biomass (*experiment 1*), we used a linear mixed-effect models to compare the impacts of the three types of forest soil (fixed factor) along 10 elevational transects (random factor). To test the relative importance of abiotic and biotic factors and their potential interaction (*experiment 2*) in a crossed experimental design, we used a hierarchical model; this model compared the impacts of the abiotic components of different soil origins (i.e. initially sterilized temperate, mixed or boreal soil) and the four biotic (inoculum source) treatments (i.e. sterile soil, inoculum of temperate, mixed or boreal soil) on seedling survival and biomass. Soil of experiment 2 were sampled along the 10 elevational transects (random factor), therefore soil origin and inoculum source (fixed factors) are nested within transects in the model. We calculated coefficients of variation among treatment means to compare the impact of biotic vs. abiotic factors.

For both experiments, survival and final biomass were first modelled individually, and then jointly using a Hurdle analysis providing a measure of performance that integrates survival and biomass (hereafter, performance, which is survival multiplied by biomass). We used the Bernoulli distribution for survival, and the gamma distribution for biomass (see model specification in the supplementary material). For the biomass estimation, only surviving seedlings were used (see Tables S2 and S3 for corresponding sample sizes). We implemented a Bayesian approach using JAGS (Plummer, 2003), since initial data analyses with general linear mixed effect models in R revealed significant issues regarding model convergence due to the large number of zeros in the data (>50%) and the hierarchical design. The model ran an update on three parallel chains of length 500,000 and a thinning rate of 10 following a run with three parallel chains of length 5,000 and a burn-in of 4,000 iterations with a thinning rate of 10, for a total of 150,000 iterations conserved.

We used uninformative priors for the shape parameter and semi-informative priors for all betas (model coefficients) for both parts of the model (see model specification in the supplementary material for further details). Convergence was assessed for each parameter estimate by visually inspecting the three Markov chains and by examining the $\hat{R}$ values which quantify consistency (Zuur & Ieno, 2016). Model validation was then assessed visually by plotting the residuals against the fitted values and with each covariate in the model. No significant heterogeneity issues, and no clear outliers in residual patterns, were found. Model fit was assessed using Pearson's residuals χ^2 by comparing the observed residuals over residuals from data simulated under the model. The lack-of-fit statistic $\chi^2_{obs}/\chi^2_{sim}$, which is expected to be equal to 1 if the model fits the data perfectly (Kery & Schaub, 2011), was equal to 0.82, indicating a good model fit. Adjusted-R^2 values were used as approximate assessments of the percentage of variance that is explained by the models. This was done by linearly fitting observed values to their predicted values. Soil characteristics were modelled using linear mixed-effect models and root colonization by bootstrapping. Analyses with root hyphal colonization as an explanatory variable of dry mass, and with soil characteristics as explanatory variables of performance, were done using generalized linear mixed-effect models. For the statistical analysis, we used R (R Core Team, 2018) with the following packages: *brms* (Bürkner, 2017), *dplyr* (Wickham *et al.*, 2017), *emmeans* (Lenth, 2019), *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2018), *lattice* (Sarkar, 2008), *nlme* (Pinheiro *et al.*, 2012), *R2jags* (Su & Yajima, 2015), *reshape2* (Wickham, 2007), *rjags* (Plummer, 2018).

Results

Seedling survival, biomass and performance along the elevational gradient (Experiment 1)

Seedling survival and biomass of survivors were more than twice as high in untreated soils from temperate and mixed forests compared to soils from boreal forests (Fig. 1a–b). However, we note that the 90 % credible intervals for predicted seedling survival and biomass overlap among forest types. Overall seedling performance was much lower in boreal soils, and the most favorable soil tended to be from the mixed forest (Fig 1c); indeed, there was a 77 % decrease in mean performance in boreal soils compared to mixed-forest soils, which differ from one another with >90 % confidence (see Table S5 for a summary of the results).

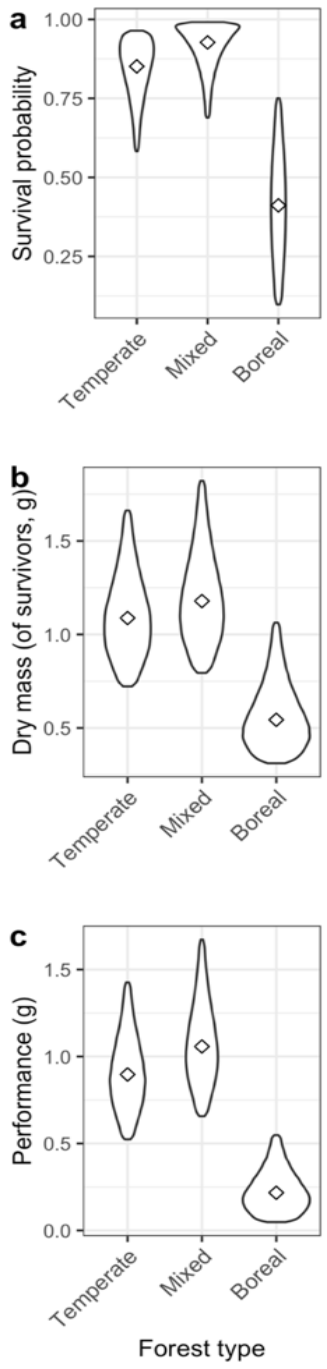

Figure. 1. Effects of soils originating from the different forest types (along the elevational gradient) on the (a) survival probability, (b) dry mass and (c) performance (i.e. dry mass including survival probability) of sugar maple seedlings. In these violin plots, the width of the polygon represents the density of the expected values. Upper and lower limits of the violin plots represent 90% credible intervals (the vertical length of each polygon). Diamonds show medians.

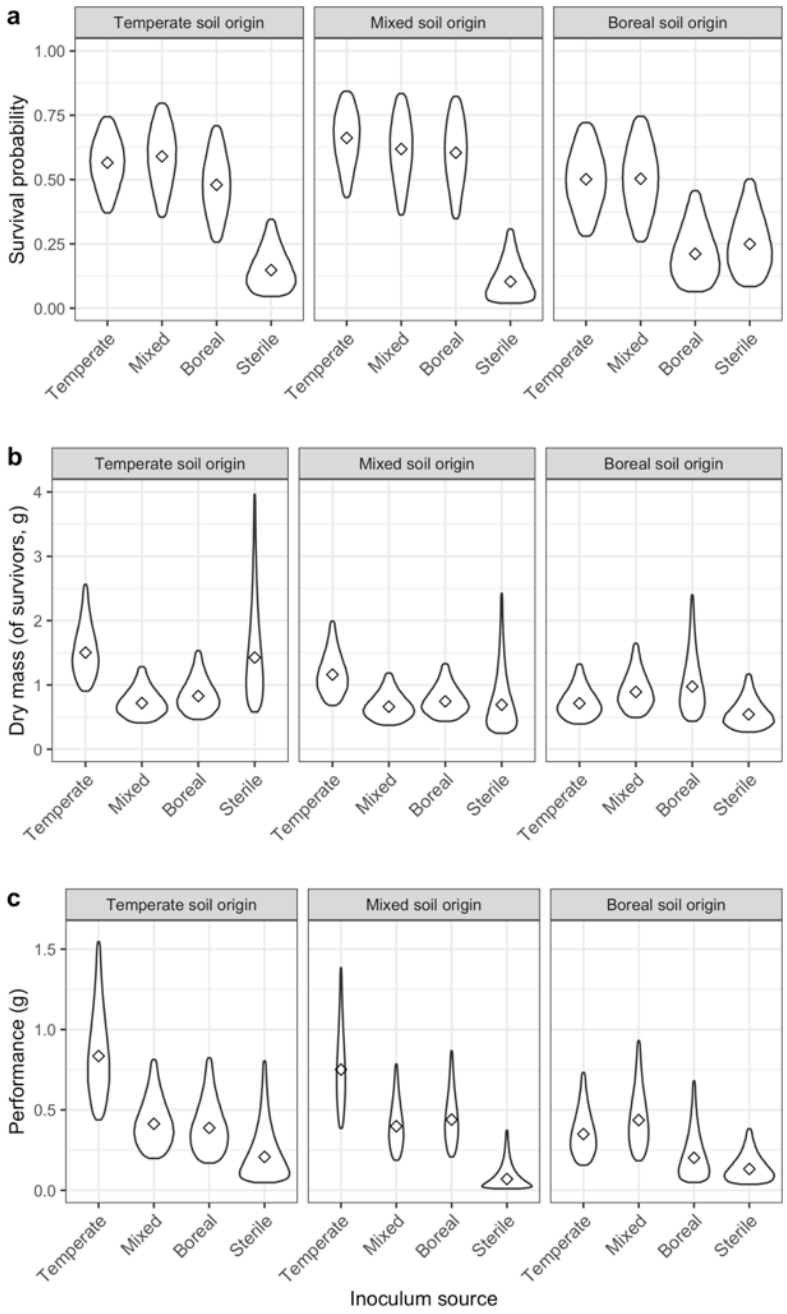

Figure 2. Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic factors) on sugar maple seedling (a) survival probability, (b) dry mass and (c) performance (i.e. dry mass including survival probability). Only one individual survived in sterilized temperate soil, so the expected dry mass showed large uncertainties which limits our predictions (i.e. the fit of the model). In these violin plots, the width of the polygon represents the density of the expected values. Upper and lower limits of the violin plots represent 90% credible interval. Diamonds show medians.

Overall performance impacted by abiotic and biotic factors (Experiment 2)

The integrated measure of performance (i.e. survival multiplied by biomass) showed differences of moderate magnitude among soil origins and inoculum sources (Fig. 2; see also Table S6 for a summary of the results). Performance was lower in the treatments with boreal soil origin (on average 37 % lower compared to temperate soil origin) and with boreal soil inoculum (44 % lower). Performance was greatest in soils of temperate origin and with the temperate inoculum source. Considering soil origin and inoculum source simultaneously (Fig. 2c), the performance of seedlings grown in temperate or mixed-forest soil was relatively low if the inoculum did not come from the temperate forest. For temperate and boreal inocula, the boreal soil origin had a detrimental effect on seedling performance. In the absence of inoculum (i.e. in sterile soils), seedling performance was always low.

The model that included the interaction term (soil origin × inoculum source) fit the data better (higher adjusted-R^2), suggesting that the effects of inoculum source on overall performance depended on soil origin and *vice-versa* (Fig. 2c). For soils of temperate origin, mean values for each inoculum source (i.e. from temperate, mixed and boreal forests, not including sterile soils) had a coefficient of variation (CV) of 45 %; the CV was 30 % in the mixed-forest soil and 29 % in the boreal soil. The magnitude of the soil origin effect on seedling performance (calculated as the CV among medians on sterilized soils) was 47 %.

Seedling survival and biomass impacted by abiotic and biotic factors (Experiment 2)

Survival was strongly impacted by the inoculum source (i.e. soil biota), but the magnitude of effect varied across soil origins. Survival was especially low in sterile soil (Fig. 2a). Overall, seedlings grown in sterile soil had, on average, 57 % lower survival probability compared to the treatment with boreal inoculum and 89 % lower compared to the treatment with temperate inoculum (see Table S6 for a summary of the results). Although the 90 % credible intervals overlapped for survival among different inoculum sources, average survival was lower in boreal and sterile inoculum (Fig. S3). When soil origin and inoculum source were considered simultaneously, the probability of survival was clearly lower within sterile soils regardless of soil origin.

The final biomass of surviving seedlings tended to be greater in soils originating in the temperate forest, being 36 % and 44 % greater than in mixed-forest and boreal soils, respectively (Fig S3). When the impact of soil origin and inoculum source were considered simultaneously, biomass showed a large difference between the temperate inoculum and the other inocula if the seedlings where grown in soils of temperate and mixed-forest origin (Fig 2b). The effect of the boreal soil origin on seedling biomass was negative regardless of the inoculum (mean biomass lower than 1 g). The effect of the temperate inoculum was approximately twice as high in temperate soil than in boreal soil.

Change in soil properties along the elevational gradient

Averaged across horizons, soil pH, effective cation exchange capacity (ECEC), and base saturation tended to decrease from temperate to boreal soils (Fig. 3). In contrast, the soil C:N ratio and labile P tended to increase along the elevational gradient (Fig. 3). As expected, soil in mixed forests tended to have intermediate values of soil characteristics except for total P, which was highest in mixed forests. All the soil physico-chemical parameters measured were strongly influenced by depth (see Fig. S4). The first two organic horizons (L, F) had high pH, C:N ratio and labile P. The Ae horizons tended to have lowest values of pH, ECEC, C:N ratio and total P in all forest type. Soil properties in the Ae horizon in temperate forest were variable, but this horizon was encountered in only two plots. Seedling performance was positively correlated with ECEC (Fig. S5), with an estimated effect size different from zero with 90 % confidence.

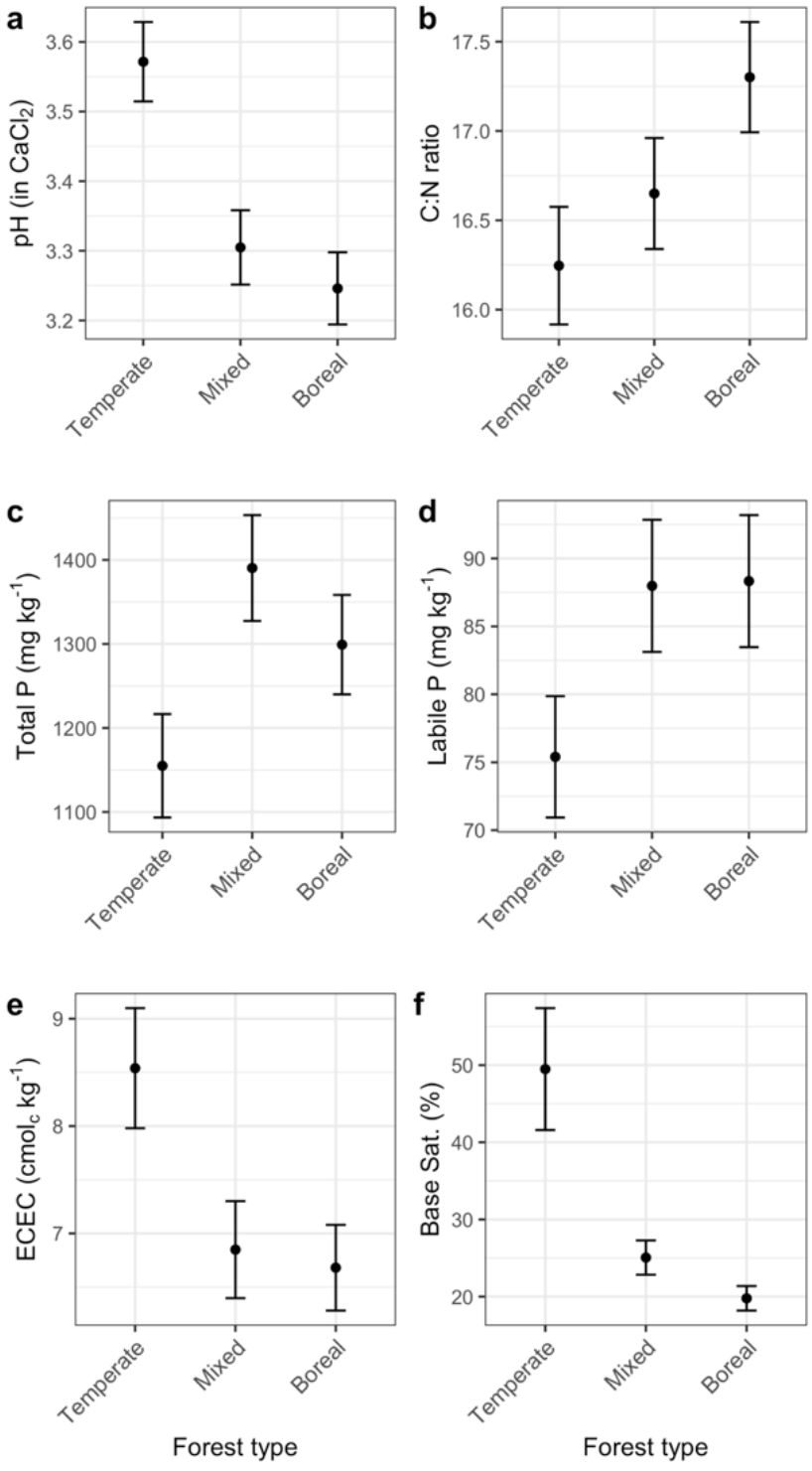

Figure 3. Soil characteristics for each forest type (temperate, mixed, and boreal): (a) pH (in $CaCl_2$), (b) C:N ratio, (c) total P, (d) labile P (e) effective cation exchange capacity (ECEC) and (f) base saturation. Values were averaged across horizons, and error bars represent the standard error of the mean of the estimated parameters.

Abiotic and biotic factors impact root colonization by fungi

Seedlings grown in fresh (unsterilized) temperate soil tended to have higher colonization by hyphae, arbuscules and endophytes compared to seedlings grown in the mixed-forest and boreal soils (experiment 1; Fig. S6). Mycorrhizal root colonization in fresh soils was higher than in soils initially sterilized with or without subsequent inoculum (experiment 2, Fig. S7). Inoculum source and soil origin had important impacts on root colonization by fungi (Fig. 4). Seedlings that were grown with the temperate inoculum had higher root colonization by arbuscular mycorrhizal fungal hyphae compared to seedlings with mixed-forest or boreal inoculum (Fig. 4). Seedlings grown in soils of temperate origin were generally more strongly colonized (Fig. 4). In sterile soil, hyphae were very rare and arbuscules never recorded (Fig. 4, Fig. S8). Similar trends were observed for coils (Fig. S8). As expected, colonization by endophytes was lower in sterilized soil and more evenly distributed among soil types and inoculum treatments (Fig. S8). The presence of vesicles did not show a clear pattern. Seedling dry mass was positively correlated with colonization by coils, arbuscules and hyphae, and negatively correlated with endophytes (Table S4). Furthermore, hyphal root colonization was positively correlated with higher biomass of seedlings that survived (Fig. S9).

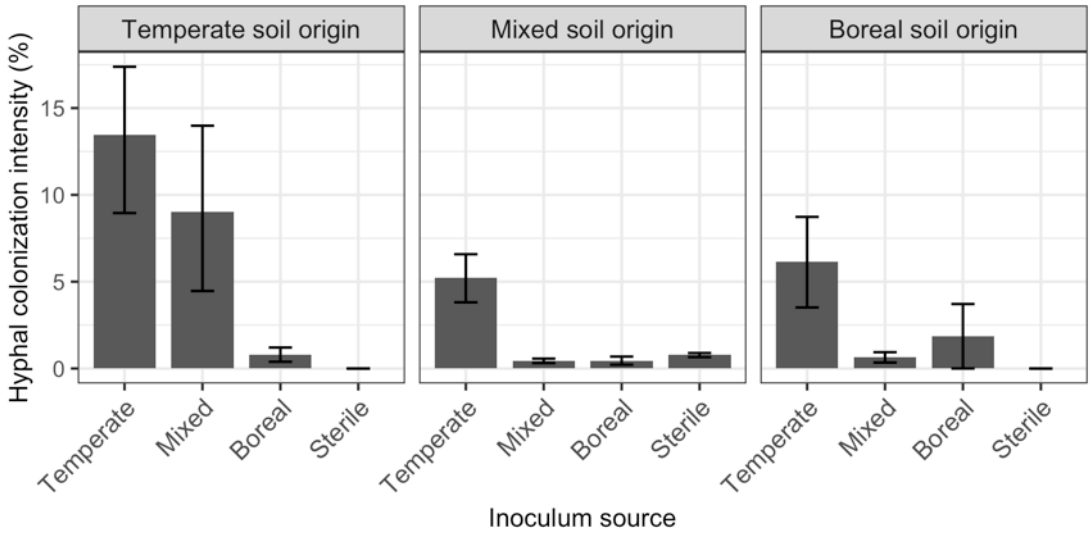

Figure 4. Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic factors) on observed root colonization intensity by hyphae in sugar maple seedlings. Error bars represent the standard error of the mean of the observed parameters.

Discussion

Our study provides novel insights into the importance of non-climatic factors in constraining plant establishment and range expansion by disentangling the relative importance of soil abiotic factors (physico-chemical characteristics) and biotic properties (soil biota). The combined effects of abiotic and biotic soil factors greatly diminished the potential survival and growth of sugar maple seedlings in the boreal forest. In sterilized soils (i.e. with soil biota eliminated), seedling survival and growth were always very low, suggesting a crucial role of beneficial soil biota, most likely arbuscular mycorrhizal fungi. In addition, given strong differences in seedling performance among soils of different origin – even when sterilized – our study also points to an important role of soil abiotic properties, most likely base cations, in constraining the establishment of sugar maple in the boreal forest. Together, our results show how soil abiotic and biotic factors can jointly constrain the establishment of a dominant temperate tree species into boreal forests. Such belowground factors should be considered when projecting future tree species distributions with climate change.

Under projected changes in climate, many temperate tree species have been predicted to expand their distributions beyond the current temperate-boreal ecotone (McKenney *et al.*, 2007). If not limited by dispersal and demographic factors, this shift is predicted to be of dozens of kilometers northward by the end of the current century. However, based on geographic distributions of seedlings vs. adult trees, few North American tree species show signs of ongoing northward shifts (i.e. seedlings occurring further north than adult trees), despite recent increases in mean annual temperature (Zhu *et al.*, 2012). Plant-soil interactions are known to influence plant performance and might be a major factor limiting temperate tree migration (Vissault, 2016; Pither *et al.*, 2018). Sugar maple specifically is expected to migrate beyond its current range, toward the boreal forest (Frumhoff *et al.*, 2007; Talluto *et al.*, 2017), but edaphic conditions have been hypothesized to constrain such range expansion (Cleavitt *et al.*, 2014). Our study shows that sugar maple expansion is likely to be constrained by lower seedling survival and growth on boreal soils (Fig. 1) and, importantly, that such edaphic constraints have joint abiotic (e.g. low base cations) and a biotic (e.g. low arbuscular mycorrhizal fungal inoculum potential) causes. Declines in seedling performance are often observed in plants that are transplanted beyond their range limits, and our study contributes further evidence in the literature that non-climatic factors can play a central role (Tomiolo & Ward, 2018).

Mycorrhizal associations may be an important predictor of plant species distributions (Pringle *et al.*, 2009; Klironomos *et al.*, 2011). This symbiosis can even allow plants to expand their niche (Gerz *et al.*, 2018). The lack of mycorrhizal symbionts has been a major factor determining the spread of some introduced plants, as for ectomycorrhizal *Pinus* spp. (Nuñez *et al.*, 2009; Dickie *et al.*, 2010). However, arbuscular mycorrhizal fungi (AMF) are very ancient plant symbionts (Field & Pressel, 2018) and many species have a cosmopolitan distribution (Morton & Bentivenga, 1994; Davison *et al.*, 2015; but see Bruns & Taylor, 2016), dispersing over short and long distances (Egan *et al.*, 2014; Correia *et al.*, 2019), and showing low host specificity (van der Heijden *et al.*, 2015). Therefore, it has been suggested that the distributions of plants that form arbuscular mycorrhizal associations might not be constrained by the presence of the fungal symbionts (Richardson *et al.*, 2000). For example, an observational study that compared adult and seedling distributions suggested that differences in northward range expansion of North American temperate tree species is not predictable based on the type of mycorrhizal association (Lankau *et al.*, 2015). However, northward of temperate forests, there are boreal forests that are mainly dominated by trees that form ectomycorrhizal associations (e.g. *Picea* spp.) (Read & Perez-Moreno, 2003), which may act as a barrier for arbuscular mycorrhizal plant species since arbuscular mycorrhizal fungi are obligate symbionts. Our results suggest that boreal soils are not favorable to the symbiosis between arbuscular mycorrhizal fungi and the seedlings of sugar maple. As such, our study highlights the importance of considering the mycorrhizal status of plants in both "donor" and "recipient" communities when trying to forecast range expansions.

The poorer performance of seedlings under sterilized and boreal conditions further suggests that arbuscular mycorrhizal fungi are most likely to be the reason for the observed biotic effect. In fact, we found considerably lower root colonization intensity by arbuscular mycorrhizal fungi in seedlings inoculated with boreal forest soils (Fig. 4), and a positive correlation between seedling biomass and the amount of mycorrhizal root colonization (Fig. S9). The few arbuscular mycorrhizal fungi that might be present in boreal soils because of understory plants or fungal spore dispersal (Öpik *et al.*, 2008) appear to be insufficient for roots of sugar maple seedlings to be well colonized. This is supported by the fact that unsterilized fresh soils (used in experiment 1) tended to favor seedling performance and root colonization compared to the corresponding inoculum treatments on sterilized soil (see Fig. S6 and S10). This is possibly due to the presence of a lower number of viable mycorrhizal propagules (e.g. fewer fragments of colonized roots) in the

inoculated sterilized soil. Soil biotic factors strongly influenced the performance of sugar maple seedlings, and particularly their survival, as suggested by previous studies (Cleavitt *et al.*, 2011, 2014; Brown & Vellend, 2014; Putnam & Reich, 2017). It has also been shown that fungal and bacterial belowground communities on sugar maple roots are different between areas of high abundance and the elevational range limit (Wallace *et al.*, 2018). In agreement with other studies, soil biota acted as important drivers of success of plant establishment (Pringle *et al.*, 2009; Ma *et al.*, 2018).

Performance of sugar maple seedlings was negatively impacted in terms of survival and subsequent growth by the abiotic component of boreal soil. Compared to soils from temperate forests, boreal soils tend to be more acidic and nutrient poor (e.g. lower availability of cations and nitrogen, Fig. 3), characteristics that are known to affect the nutrition of sugar maple at early stages of development (Collin *et al.*, 2017). This supports the hypothesis that upward and northward migration of sugar maple could be constrained by unsuitable soil physico-chemical properties. It is worth noting that soil chemistry was strongly influenced by depth. The Ae horizons characteristic of podzols tended to show the lowest concentrations of nutrients and pH, which could affect seedling growth, thus highlighting the importance of maintaining ecological realism by reconstructing soil profiles within the experimental units (Heinonsalo *et al.*, 2004). Litter layer depth also can play an important role, acting as a barrier to seedling establishment (Cleavitt *et al.*, 2011). Although sugar maple seedlings express broad tolerance for diverse abiotic soil factors (Arii & Lechowicz, 2002; Kellman, 2004), the presence of soil mutualists seems important as suggested by low performance in the sterile soil. Arbuscular mycorrhizal fungi are also sensitive to abiotic factors but their presence is crucial for the plant partner for nutrient acquisition, particularly phosphorus (Smith & Smith, 2011; Hodge & Storer, 2014), as well as for defense against pathogens (Smith & Read, 2008; Jung *et al.*, 2012). Soil chemistry can influence seedlings both directly via nutrient availability and indirectly via effects on the soil biota. For example, sugar maple root colonization by arbuscular mycorrhizal fungi is known to diminish when soil pH is decreased (Coughlan *et al.*, 2000; Juice *et al.*, 2006), which might explain the lower colonization and performance of seedlings grown in boreal soils (where pH was lower), thus negatively impacting their overall seedling performance, even when inoculated with temperate forest soil.

One must be cautious in using results from a greenhouse experiment to draw inferences about dynamics in the field, given additional, untested factors that can also influence plant performance. For example, intraspecific variation via local adaptation or maternal effects (e.g. on seed size) – not assessed in this study – may be important for sugar maple establishment (Walters & Reich, 2000; Solarik *et al.*, 2018). In addition, environmental parameters such as temperature can affect sugar maple germination, seedling survival and growth (Fisichelli *et al.*, 2015; e.g. Solarik *et al.*, 2016; Wright *et al.*, 2018). Responses of soil microorganisms to climate change are difficult to predict but will inevitably influence many abiotic and biotic factors (Jansson & Hofmockel, 2019), some of which that could feedback positively to plant performance, potentially facilitating range expansion. For example, it has been experimentally shown that higher soil temperature can stimulate microbial activity that increases mineralization of organically bound nutrients (Zak *et al.*, 1999; Wan *et al.*, 2005), which can facilitate nutrient acquisition by sugar maple, although this also limits the benefits provided by AM fungi (St. Clair *et al.*, 2008). Availability of light and water can strongly influence sugar maple performance (discussed in detail by St. Clair *et al.*, 2008). These environmental features could interact in complex ways with mutualistic or harmful organisms (e.g. Hawkes *et al.*, 2008; Sanders-DeMott *et al.*, 2018). In our study, temperature, light and water availability were experimentally controlled to avoid any potential cofounding effects with the factors of primary interest in this study – soil chemistry and microbiota. While it is possible that different levels of these environmental factors would have altered our experimental results, we have no a priori reason to suspect that the effects of soil factors specifically were qualitatively different than what one would expect in the field. Indeed, the relatively high temperatures experienced in the greenhouse might reflect expected future conditions with climate warming. A better understanding of the impacts of the interactions among temperature, light and water availability with biotic factors at the different stages of development of sugar maple would be needed to better forecast its future distribution.

Our study builds on several others at the same field site (Mont Mégantic) or in the same region (southern Québec) focused specifically on non-climatic belowground factors that might limit or favor sugar maple's establishment into the boreal forest (Brown & Vellend, 2014; Urli *et al.*, 2016; Collin *et al.*, 2018). Our study highlights the importance of one group of beneficial soil biota, namely arbuscular mycorrhizal fungi. However, the possible effect of soil-borne pathogens merits further investigation. In previous studies, sugar maple showed negative conspecific density

dependence (Johnson *et al.*, 2012) and increased seedling survival in the boreal forest at Mont Mégantic (in a field experiment) with or without protection from insect herbivores, leading Urli *et al.* (2016) to hypothesize potential release from soil pathogens in the boreal forest. In contrast, our experiment points to an overall net positive effect of soil biota in this system, and other studies have not found strong negative plant-soil feedbacks for sugar maple (McCarthy-Neumann & Ibáñez, 2012; Bennett *et al.*, 2017). The low performance of sugar maple seedlings on sterile soils from all sources suggests that the beneficial role of soil mutualists such as arbuscular mycorrhizal fungi outweighs potential negative impacts of soil-borne generalist pathogens, at least at our field site. Furthermore, compared to sterile soils, seedlings showed marked positive responses to soil biota (inocula) when growing on soils from within their current range (temperate and mixed forests), and weaker responses when grown in boreal soil (Fig. 2). That said, we must be cautious in extrapolating results from the greenhouse to the field. Our study focused mainly on soil micro-organisms as biotic factors, but sugar maple might also be susceptible to other enemies such as seed-consuming rodents for seed predation (Brown & Vellend, 2014) or insect herbivores (Urli *et al.*, 2016). Beyond its elevational range, sugar maple seedlings appear to be favored by release from insect herbivory (Urli *et al.*, 2016); however, our results suggest that the presence of mutualist organisms might remain a key factor for its establishment, as other studies have suggested for annual plants and shrubs (Stanton-Geddes & Anderson, 2011; Morriën & van der Putten, 2013; Sedlacek *et al.*, 2014).

Belowground mutualists can be important determinants of plant distributions, especially in a context of range expansion and invasion (Richardson *et al.*, 2000). Therefore, the incorporation of microbial ecology and especially mycorrhizal ecology into predictive ecosystem models might have great potential (Johnson et al., 2006; Treseder et al., 2012). Specifically, our results suggest that integrating belowground traits such mycorrhizal status may improve modelling future changes in forest composition and functioning (Brzostek *et al.*, 2017). Some classic ideas in biogeography suggest that species distributions are limited by biotic factors (e.g. competition) at their warm edges (e.g. at low latitude or elevation) and by abiotic factors (e.g. harsh climate) at their cold edges (e.g. Dobzhansky, 1950; Pianka, 1966 and references therein). Evidence in support of this idea includes studies having shown that climatic and soil physico-chemical factors are important determinants of plant distributions (Coudun *et al.*, 2006; Bertrand *et al.*, 2012; Beauregard & de Blois, 2014). On the other hand, our results indicate that even at cold range limits biotic factors such as soil

microbial mutualists can be important determinants of potential range shifts, and thus need to be incorporated into forecasts of future changes in terrestrial ecosystems.

Acknowledgements

We are grateful to two anonymous reviewers and an associate editor for critical suggestions that significantly improved the manuscript. We would like to thank Rose-Marie Gazaille, Azucena Hernández, Myriam Lalonde and Florian Piel for the field and the laboratory assistance. We thank the authorities of Parc national du Mont Mégantic for facilitating access to the field site. Funding, including scholarships to AC, was provided by a Discovery Grant to EL (RGPIN-2014-06106) by the Natural Sciences and Engineering Research Council of Canada (NSERC), and by a seed grant to EL and MV awarded by the Centre de la Science de la Biodiversité du Québec (CSBQ). AC received additional support from scholarships of the Institut de Recherche en Biologie Végétale, the Université de Montréal, and the Fonds de recherche du Québec - Nature et technologies.

Authors' contributions

EL, MV and AC conceived the ideas and designed methodology; AC, VP, FB and BT collected the data; XGM and AC analyzed the data; AC, EL and MV interpreted the results; AC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Code and data availability

Code for statistical analysis is available at https://doi.org/10.5281/zenodo.3533170. Data are available at: https://doi.org/10.5281/zenodo.3524285.

Supplementary information

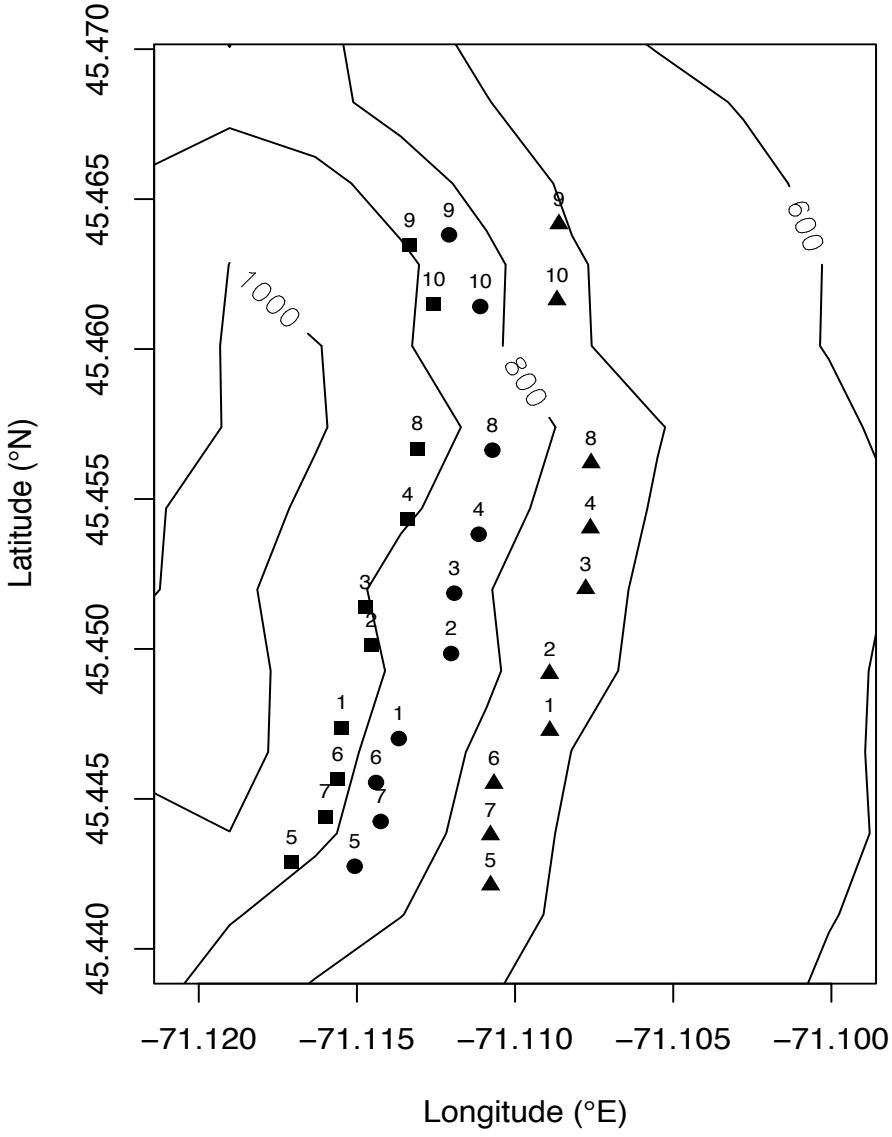

Figure S1. Distribution of the soil sampling plots along the elevational gradient (east to west) of the eastern slope of Mont Saint-Joseph (Qc, Canada) and the three forest types: temperate (square), mixed (circle), boreal (triangle). Transects 1 to 10 are in order of sampling time and correspond to blocks within the greenhouse. Elevations of the contour lines are in meters above sea level.

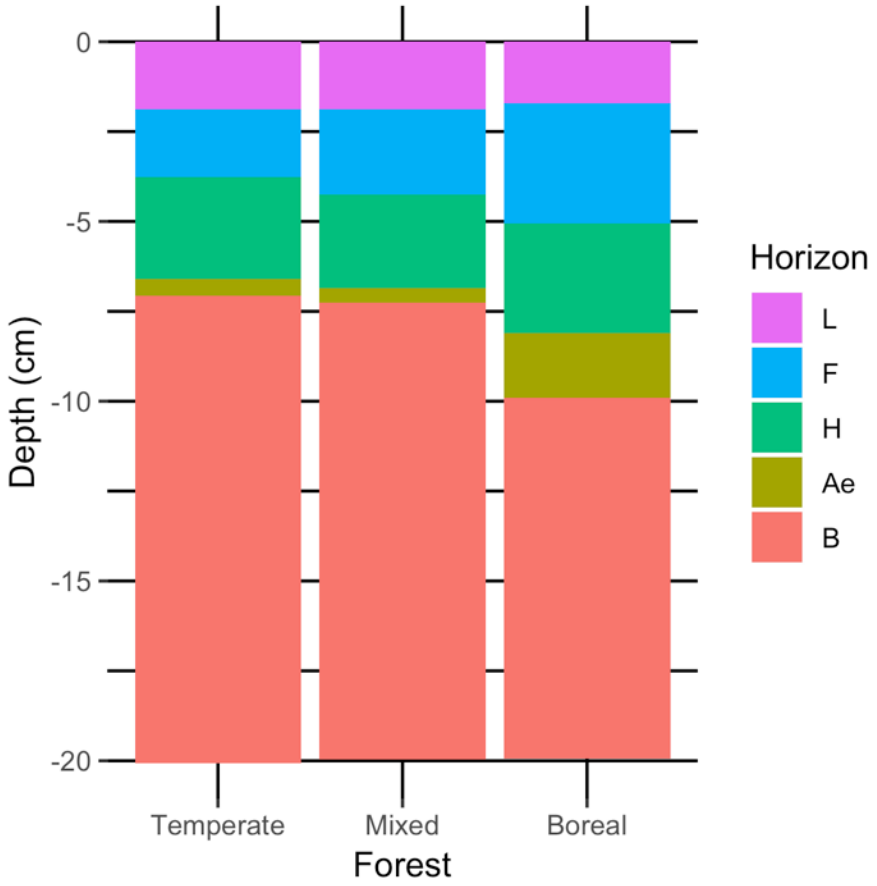

Figure S2. Soil profile by horizons of the three type of forests averaged across the 10 transects based on four pits of 20 cm depth.

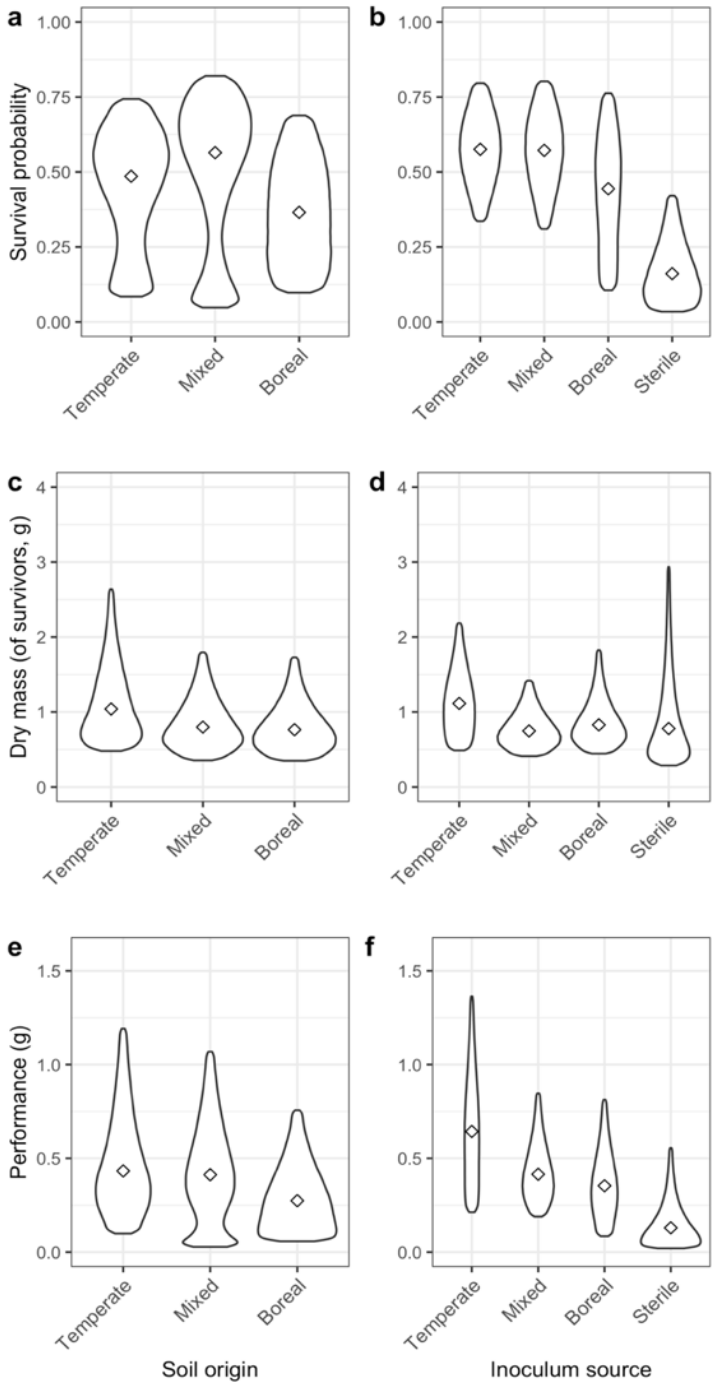

Figure S3. Average effects soil origin (abiotic and biotic factors) and inoculum source (only biotic factors) on sugar maple seedling survival (a, b), biomass (c, d) and performance (e, f). In these violin plots, the width of the polygon represents the density of the expected values. Upper and lower limits of the violin plots represent 90% credible interval. Diamonds show medians.

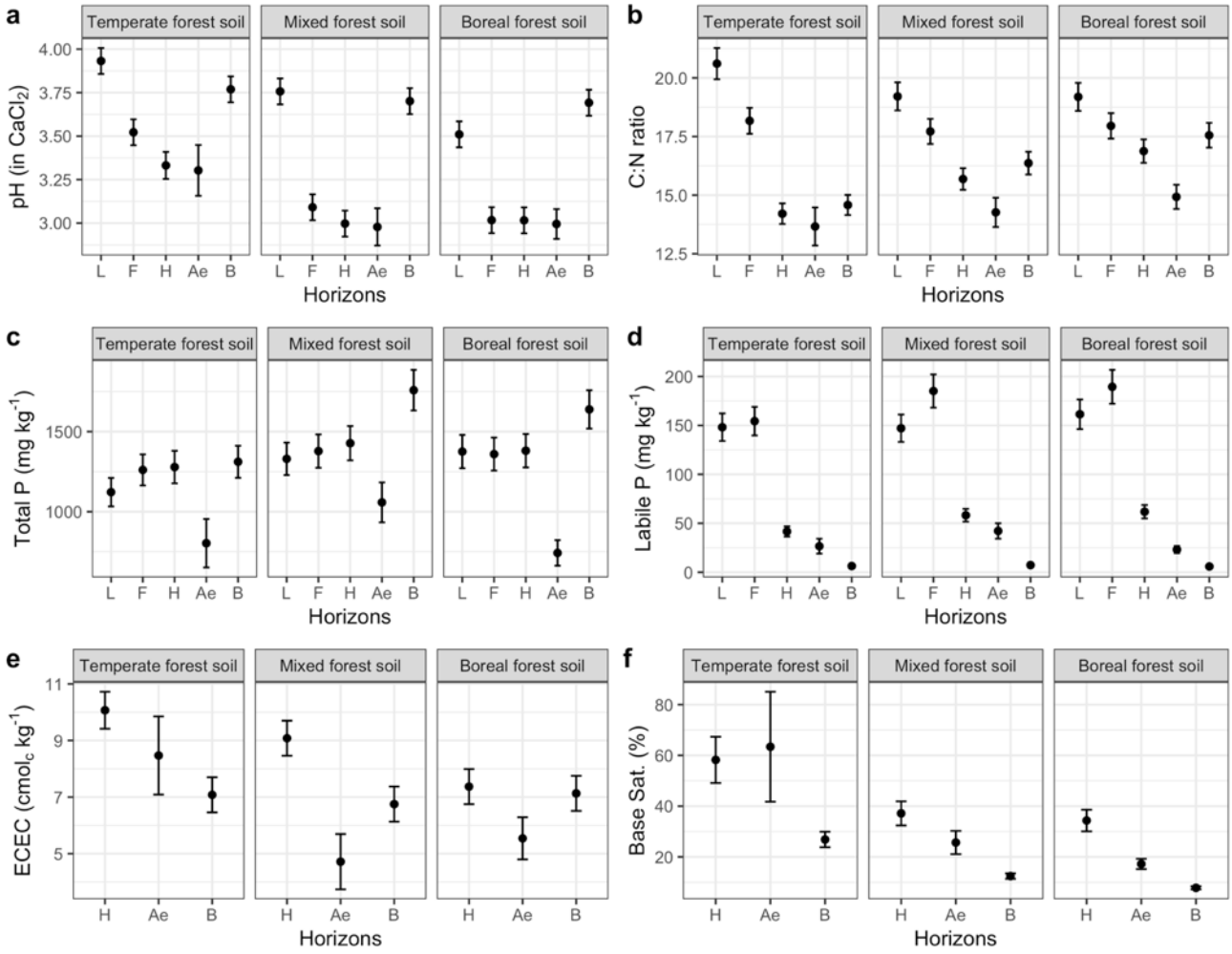

Figure S4. Soil characteristics for each forest type by horizons (a) pH (in $CaCl_2$), (b) C:N ratio, (c) total P, (d) labile P (e) effective cation exchange capacity (ECEC) and (f) base saturation. ECEC and base saturation were not calculated on highly organic sample (L and F horizons). Error bars represent the standard error of the mean of the estimated parameters.

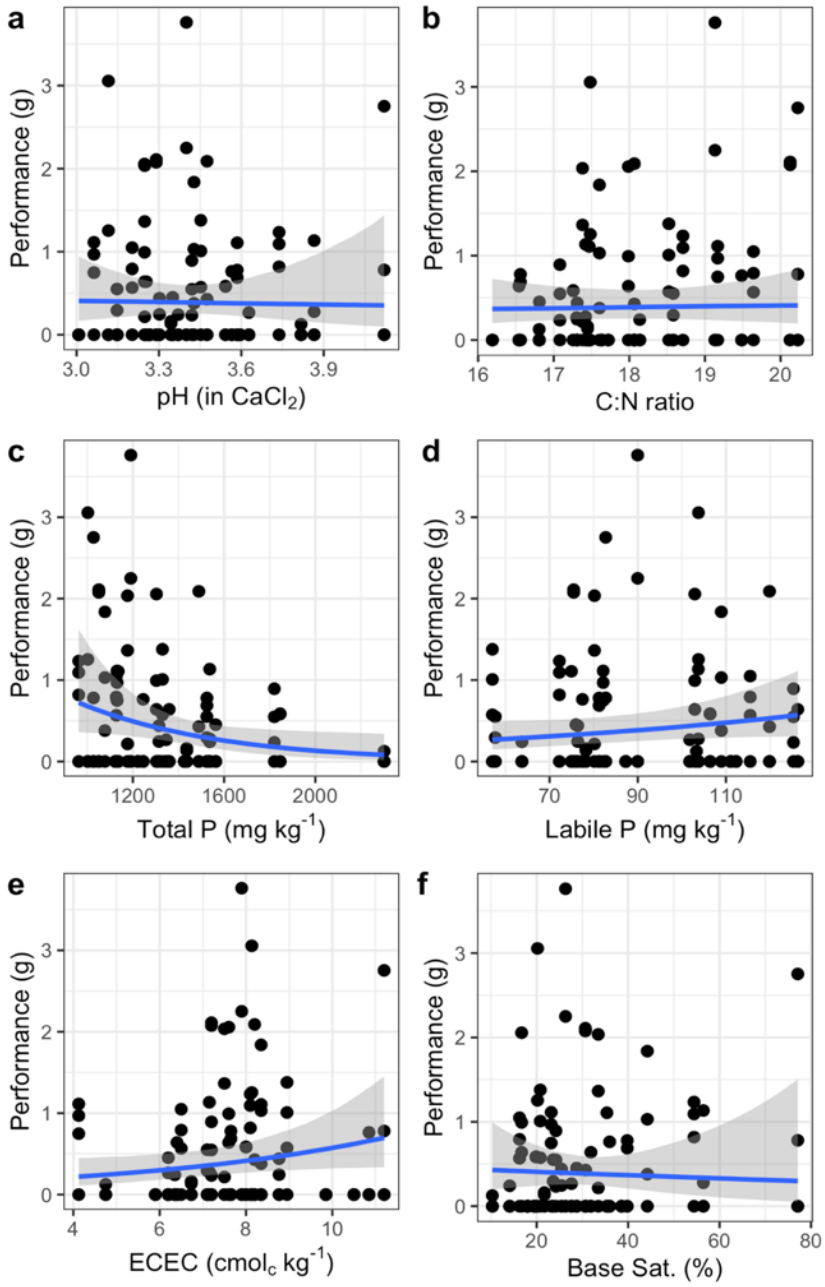

Figure S5. Plots of marginal effects of (a) pH (in $CaCl_2$), (b) carbon:nitrogen ratio, (c) total phosphorus, (d) labile (Bray) P (e) effective cation exchange capacity (ECEC) and (f) base saturation on sugar maple seedling performance. Values of soil variables were averaged across horizons. Blue lines represent the slopes with credible intervals at 90 % shown in shaded grey. ECEC had an estimate of effect that differed from zero with 90% confidence. Modelling was done using a Hurdle analysis with the soil variables as fixed factors and block as a random factor.

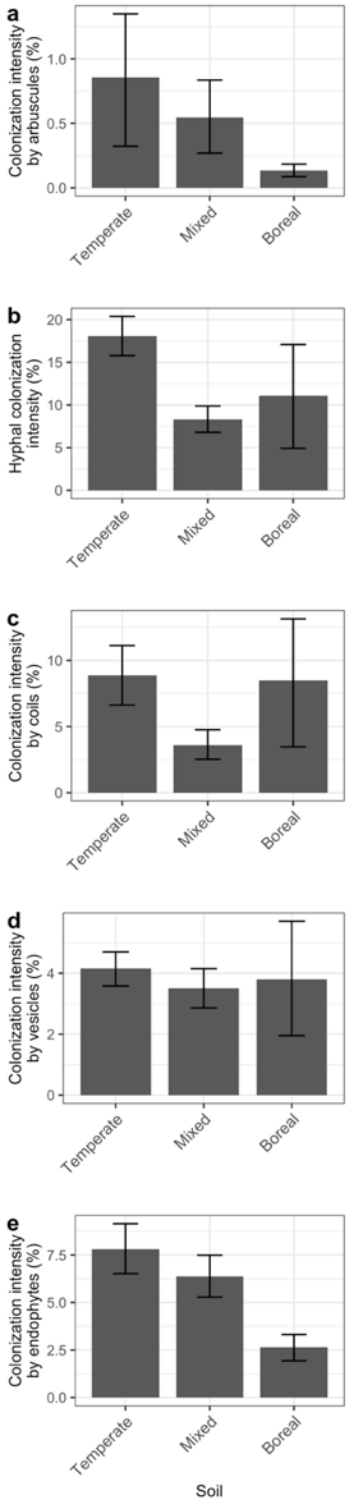

Figure S6. Root colonization (experiment 1) by different fungal structures: a) arbuscules, b) fungal hyphae, c) coils, d) vesicles and e) fungal endophytes. Error bars represent the standard error of the mean of the observed parameters.

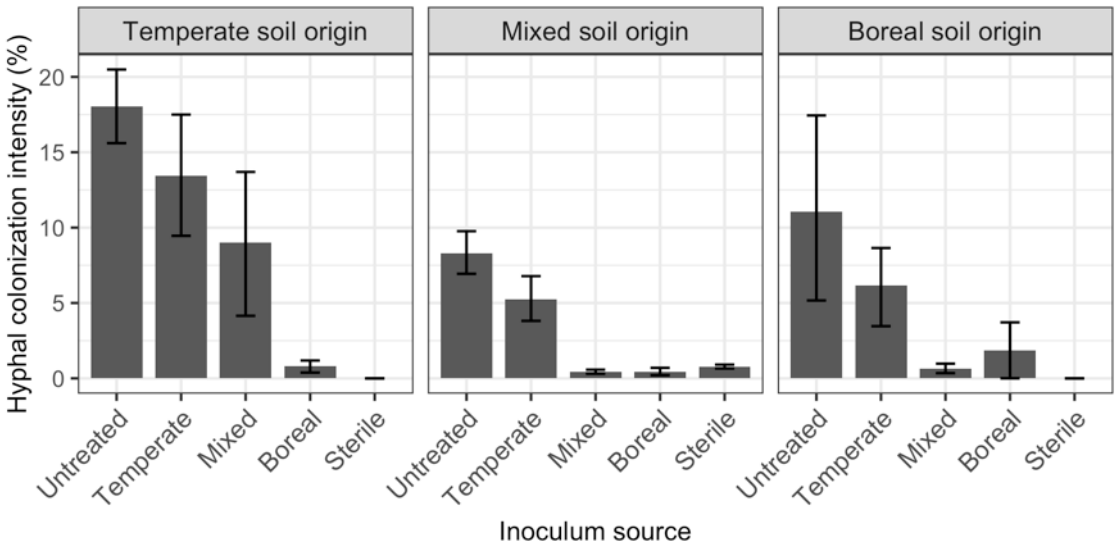

Figure S7. Effects of soil origin combined with inoculum source from experiment 1 and untreated soil from experiment 2 on hyphal root colonization of sugar maple seedlings. Error bars represent the standard error of the mean of the observed parameters.

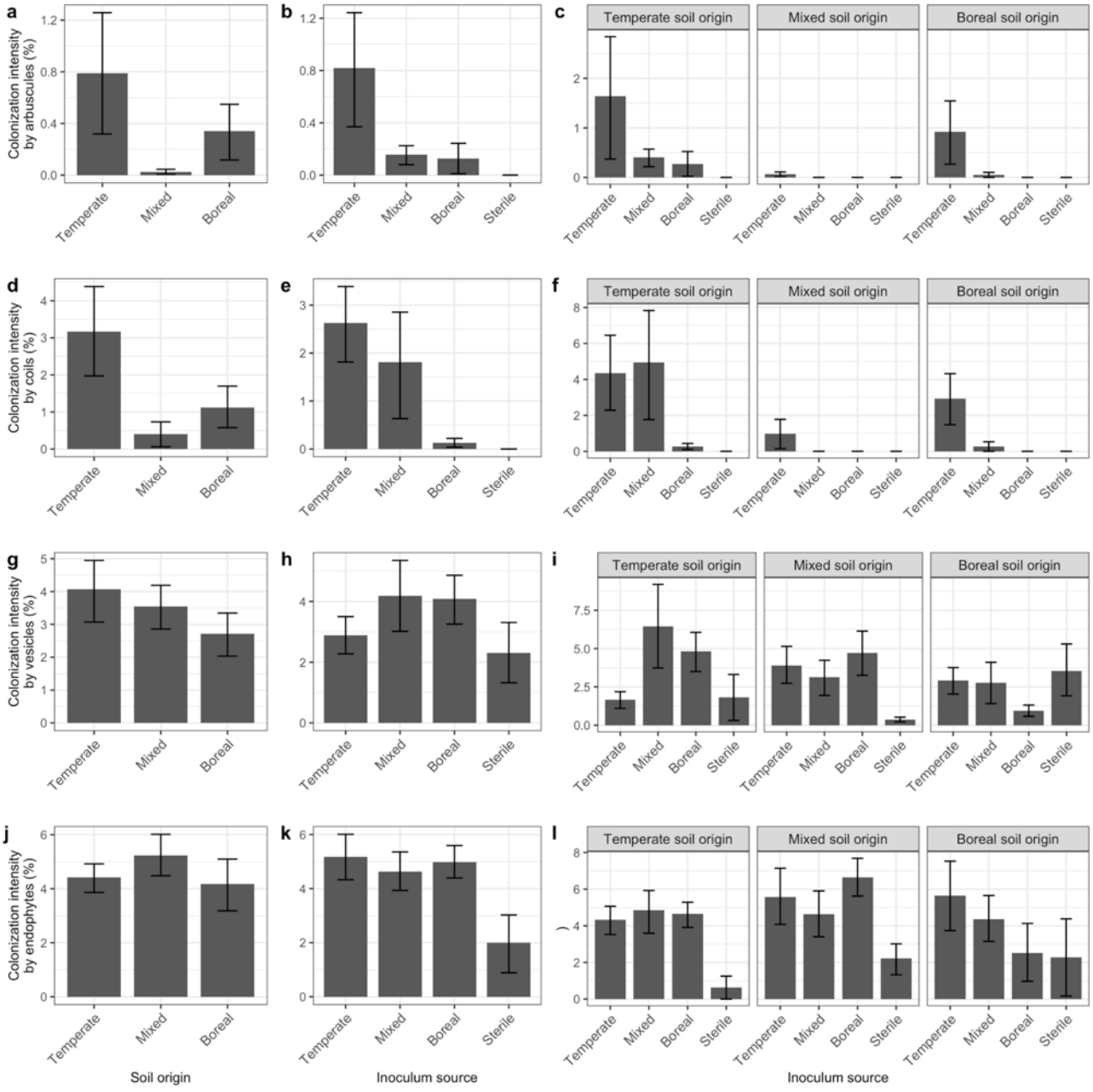

Figure S8. Root colonization (experiment 2) by different fungal structures: arbuscules (a, b, c) and coils (d, e, f), fungal vesicles (g, h, i) and fungal endophytes (j, k, l). Error bars represent the standard error of the mean of the observed parameters.

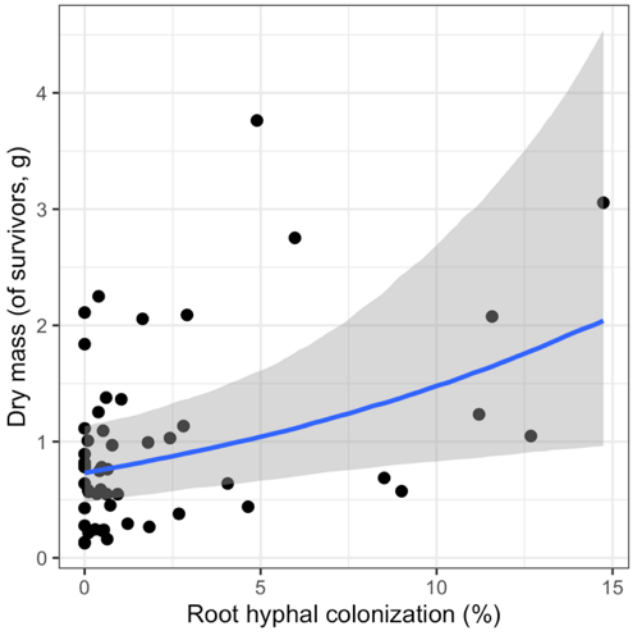

Figure S9. Plot of the marginal effect of root hyphal colonization on sugar maple seedling dry mass. Analysis was done using a generalised linear mixed-effects model with root hyphal colonization as a fixed factor and block as a random factor. The blue line represents the slope with credible interval at 90 % shown in shaded grey. The estimate of the slope differs from zero with 90% confidence. Note that two seedlings with much higher root hyphal colonization (>39%) than the others (<15%) were removed from the analysis; although the positive effect of colonization on dry mass still holds when these two extreme values are included.

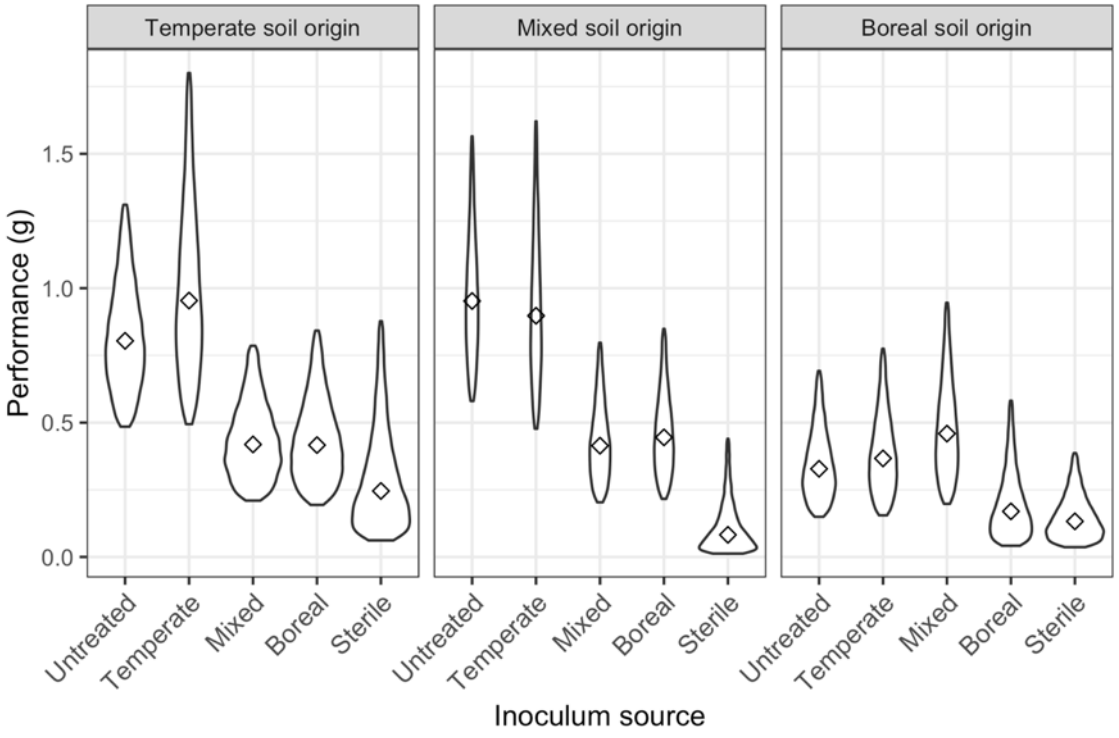

Figure S10. Comparison of the performance of sugar maple seedlings in untreated soil *vs* treated soil (temperate, mixed or boreal inoculum and sterile) of the same soil origin (temperate, mixed or boreal). Based on the same Hurdle analysis than experiment 1 but combining data of untreated and treated soil (experiments 1 and 2). Means are shown with 90% credible intervals.

Table S1. Spearman's rank correlation between dry mass and other measured seedling traits for the experiment 1 (sample size is 21) and experiment 2 (sample size is 54).

	Leaf area	Stem length	Root length
Dry mass	0.87***	0.57***	0.94***
Experiment 1			
Dry mass	0.88***	0.61***	0.94***
Experiment 2			

*** *P*-values < 0.001.

Table S2. Observed number of seedlings that survived in experiment 1 and subsequent sample size for the modelling of dry mass.

	Forest type		
	Temperate	Mixed	Boreal
Survivors	9	9	4

Table S3. Observed number of seedlings that survived in experiment 2 and subsequent sample size for the modelling of dry mass.

	Soil origin											
	Temperate				Mixed				Boreal			
Survivors	18				21				15			
Inoculum source	Temperate	Mixed	Boreal	Sterile	Temperate	Mixed	Boreal	Sterile	Temperate	Mixed	Boreal	Sterile
Survivors	6	6	5	1	7	6	6	1	5	5	2	3

Table S4. Spearman's rank correlation between dry mass and traits of fungal colonization for experiment 1 (sample size is 21) and experiment 2 (sample size is 54).

	Arbuscules	Hyphae	Vesicles	Coils	Endophytes
Dry mass *Experiment 1*	0.22	0.26	0.13	0.34	0.11
Dry mass *Experiment 2*	0.46***	0.32*	0.13	0.49***	-0.29*

* *P*-values < 0.05; ** *P*-values < 0.01; *** *P*-values < 0.001.

Table S5. Results of the Hurdle analysis for experiment 1. Effect of forest type on survival probability, dry mass and performance of sugar maple seedlings. Mean with standard error and credible interval (CI) at 90%.

	Forest type	Mean	Standard error	Lower CI	Higher CI
Survival probability	Temperate	0.82	0.12	0.58	0.96
	Mixed	0.89	0.10	0.69	0.99
	Boreal	0.42	0.20	0.10	0.75
Dry mass (g)	Temperate	1.13	0.30	0.72	1.66
	Mixed	1.23	0.34	0.79	1.82
	Boreal	0.60	0.27	0.31	1.06
Performance (g)	Temperate	0.93	0.29	0.52	1.43
	Mixed	1.10	0.33	0.66	1.67
	Boreal	0.25	0.17	0.05	0.55

Table S6. Results from the Hurdle analysis for experiment 2. Effect of soil origin and inoculum source on survival probability, dry mass and performance of sugar maple seedlings. Mean with standard error and credible interval (CI) at 90%.

	Soil origin	Inoculum source	Mean	Standard error	Lower CI	Higher CI
Survival probability	Temperate	Temperate	0.56	0.11	0.37	0.74
		Mixed	0.58	0.13	0.35	0.80
		Boreal	0.48	0.14	0.26	0.71
		Sterile	0.17	0.09	0.05	0.35
	Mixed	Temperate	0.65	0.13	0.43	0.84
		Mixed	0.61	0.14	0.36	0.83
		Boreal	0.60	0.14	0.35	0.82
		Sterile	0.13	0.09	0.02	0.31
	Boreal	Temperate	0.50	0.13	0.28	0.72
		Mixed	0.50	0.15	0.26	0.75
		Boreal	0.23	0.12	0.06	0.46
		Sterile	0.27	0.13	0.08	0.50
Dry mass (g)	Temperate	Temperate	1.59	0.54	0.90	2.56
		Mixed	0.77	0.29	0.41	1.28
		Boreal	0.89	0.35	0.46	1.53
		Sterile	1.75	1.27	0.58	3.96
	Mixed	Temperate	1.23	0.42	0.68	1.99
		Mixed	0.71	0.26	0.37	1.18
		Boreal	0.80	0.30	0.44	1.33
		Sterile	0.94	0.98	0.25	2.42
	Boreal	Temperate	0.77	0.30	0.39	1.32
		Mixed	0.96	0.38	0.49	1.65
		Boreal	1.14	0.69	0.44	2.40
		Sterile	0.61	0.31	0.27	1.17

Performance (g)	Temperate	Temperate	0.89	0.36	0.44	1.55
		Mixed	0.45	0.20	0.20	0.81
		Boreal	0.43	0.21	0.17	0.82
		Sterile	0.29	0.29	0.05	0.80
	Mixed	Temperate	0.80	0.32	0.39	1.38
		Mixed	0.43	0.19	0.19	0.78
		Boreal	0.48	0.22	0.21	0.87
		Sterile	0.12	0.17	0.01	0.37
	Boreal	Temperate	0.39	0.19	0.16	0.73
		Mixed	0.48	0.24	0.18	0.93
		Boreal	0.26	0.23	0.05	0.68
		Sterile	0.16	0.12	0.04	0.38

Modelling specification

1. Gamma distribution part of the model

Bayesian theorem:

$$P(\mu, r|Y) \propto P(Y|u, r) \times P(u) \times P(r)$$

where $Y \sim Gamma(u, r)$

Gamma distribution likelihood function:

$$f(y|\mu, r) = \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{\frac{y \times r}{\mu}}$$

$$L(y|\mu, r) = \prod_{i=1}^{n} f(y|\mu, r) = \prod_{i=1}^{n} \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{\frac{y \times r}{\mu}}$$

where $log(\mu_i) = \theta c_i \times Xc_i + a_{c_i}$ and

$$\theta c_i \times Xc_i = \beta_{c1} + \beta_{c2-4}\text{Soil origin} + \beta_{c5-9}\text{Inoculum source} + \beta_{c10-24}(\text{Soil origin} * \text{Inoculum source})$$

The index c refers to the continuous (gamma) distribution part of the model and a_{c_i} refers to the random intercept block for the continuous part of the model. Xc_i refers to a matrix of dummy variable for the different inoculum source, soil origin and their interaction. Theta (θc_i) is a matrix containing the betas.

For experiment 1, there is only one forest as predictor which gives:

$$\theta c_i \times Xc_i = \beta_{c1} + \beta_{c2-4}\text{Forest type}$$

Priors:

Random effect (intercept)

$a_{c_i} \sim N(0, \tau_c)$

$$f(a_{c_i} \mid 0, \tau_c) = P(a_{c_i} \mid 0, \tau_c) = \frac{1}{\sqrt{(1/\tau_c)}\sqrt{2\pi}} \times e^{\frac{-(a_{c_i}-0)^2}{1/\tau_c}}$$

Where $\tau_c = 1/\sigma_c \times \sigma_c$

and $\sigma_c \sim U(0,100)$

Fixed effect thetas

$\theta c_i \sim N(\mu_{\theta ci}, \sigma^2)$

$$f(\theta c_i \mid \mu_{\theta ci}, \sigma^2) = P(\theta c_i \mid \mu_{\theta ci}, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} \times e^{\frac{-(\theta c_i - \mu_{\theta ci})^2}{\sigma^2}}$$

where $\mu_{\theta ci}$ was fixed to 0 and variance was fixed to 3.

Shape parameter

$r \sim U(a, b)$

where a was fixed to 0 and b was fixed to 5

$$f(r \mid a, b) = P(r \mid a, b) = \frac{1}{b-a}$$

Posterior distribution:

$$P(\mu, r \mid Y) = \prod_{i=1}^{n} \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{\frac{y_i \times r}{\mu}} \times \prod_i^n \frac{1}{\sigma\sqrt{2\pi}} \times e^{\frac{-(\theta c_i - \mu)^2}{\sigma^2}} \times \frac{1}{b-a} \times \prod_i^n \frac{1}{\sqrt{(1/\tau_c)}\sqrt{2\pi}} \times e^{\frac{-(a_i-0)^2}{1/\tau_c}}$$

2. Bernoulli distribution part of the model

Bayesian theorem:

$P(\pi|Y) \propto P(Y|\pi) \times P(\pi)$

where $Y \sim Bern(\pi)$

Bernoulli distribution likelihood function:

$f(y|\pi) = \pi^{y} \times (1-\pi)^{1-y}$

$$L(y|\pi) = \prod_{i=1}^{n} f(y|\pi) = \prod_{i=1}^{n} \pi^{y} \times (1-\pi)^{1-y}$$

where $logit(\pi_i) = \theta b_i \times Xb_i \times a_{b_i}$ and

$$\theta b_i \times Xb_i = \beta_{b1} + \beta_{b2-4}\text{Soil origin} + \beta_{b5-9}\text{Inoculum source} + \beta_{b10-24}(\text{Soil origin} * \text{Inoculum source})$$

The index b refers to the binary part of the model and a_{b_i} refers to the random intercept block for the binary part of the model. Xb_i refers to a matrix of dummy variable for the different inoculum source, soil origin and their interaction. Theta (θb_i) is a matrix containing the betas.

For experiment 1, there is only one forest as predictor which gives:

$$\theta c_i \times Xc_i = \beta_{c1} + \beta_{c2-4}\text{Forest type}$$

Priors:

Random effect (intercept)

$a_{b_i} \sim N(0, \tau_b)$

$$f\left(a_{b_i} \mid 0, \tau_b\ \right) = \ P\left(a_{b_i} \mid 0, \tau_b\ \right) = \ \frac{1}{\sqrt{(1/\tau_b\ )}\sqrt{2\pi}} \times e^{\frac{-(a_{b_i}-0)^2}{1/\tau_b}}$$

where $\tau_b\ = 1/\sigma_b \times \sigma_b$

and $\sigma_b \sim U(0{,}100)$

Fixed effect thetas

$\theta b_i \sim N(\mu_{\theta bi}, \sigma^2)$

$$f(\theta b_i \mid \mu_{\theta bi}, \sigma^2\ ) = \ P(\theta b_i \mid \mu_{\theta bi}, \sigma^2) = \ \frac{1}{\sigma\sqrt{2\pi}} \times e^{\frac{-(\theta b_i-\mu_{\theta bi})^2}{\sigma^2}}$$

where $\mu_{\theta bi}$ was fixed to 0 and variance was fixed to 3

Posterior distribution

$$P(\pi|Y) = \ \prod_{i=1}^{n} \pi^{y_i} \times (1-\pi)^{1-y_i} \times \prod_{i}^{n} \frac{1}{\sigma\sqrt{2\pi}} \times e^{\frac{-(\theta b_i-\mu_{\theta bi})^2}{\sigma^2}} \times \prod_{i}^{n} \frac{1}{\sqrt{(1/\tau_b\ )}\sqrt{2\pi}} \times e^{\frac{-(a_{b_i}-0)^2}{1/\tau_b}}$$

3. Hurdle model

$$P(Y = y \mid \theta_c\ , \theta_b\ ) = \begin{cases} (1-\pi_i), & y_i = 0 \\ \pi_i \times f_{gamma}(Y|\mu, r), & y_i > 0 \end{cases}$$

where π =1 is considering a success

Model validation was implemented in one step (see the model code). The advantage of doing so is that the expected values and the Pearson's residuals could have been calculated within the model code (specified in the model code).

Explanation: Let f($Y_i \mid \theta$) be any distribution and $L(Y \mid \theta) = \prod_i^n f(Y_i \mid \theta)$ is likelihood function. Using the mathematical rule $e^{log(x)} = x$, we have: $\prod_i^n f(Y_i \mid \theta) = \prod_i^n e^{log(f(Yi \mid \theta))} = \prod_i^n e^{l_i}$, where $l_i = log(f(Yi \mid \theta))$. Using the fact that $0! = 1$ and something to the power of zero is define as 1, we can rewrite the likelihood function as the likelihood function of a Poisson distribution with observed values 0 and mean values $-l_i$. Since the mean of a Poisson distribution must be non-negative a positive constant C is added to the mean, such as $C - l_i > 0$, and does not affect the likelihood estimation.

$$L(Y \mid \theta) = \prod_i^n e^{l_i} = \prod_i^n \frac{(-l_i)^0 \times e^{-(-l_i)}}{0!} = \prod_i^n f_{poisson}(0 \mid -l_i) = \prod_i^n f_{poisson}(0 \mid -l_i + C)$$

All parameters within l_i could fit any distribution and their posterior distribution could be obtained within the JAGS function. Using the step function within the model code to figure out whether the biomass value for an observation y_i is equal to 0 or not, allow to determine which part of the log likelihood is to be calculated.

Forêt haute en couleurs, Mont Saint-Hilaire.

CHAPITRE 4 – La dominance mycorhizienne réduit la diversité des espèces d'arbres dans les communautés forestières

Mycorrhizal dominance reduces species diversity in forest-tree communities

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In preparation for publication.

One-sentence summary: Forests dominated by arbuscular mycorrhizas or ectomycorrhizas have low tree species diversity, while those comprising a mixture of these two strategies support a higher number of species.

Abstract

Plants that associate with different type of mycorrhizal fungi experience different plant-soil feedbacks, which tend to be positive for ectomycorrhizal compared to arbuscular mycorrhizal plants in early life stages. Along with patterns of plant diversity and mycorrhizal type across biomes, this has led to the hypothesis that increased dominance by ectomycorrhizas (relative to arbuscular mycorrhizas) reduces plant diversity, but this remain to be tested at the community level over large gradients. Here, we show that increased ectomycorrhizal proportion does not necessarily reduce forest tree diversity. Both ectomycorrhizal-dominated and arbuscular mycorrhizal-dominated forests show low diversity, while forests with a mixture of mycorrhizal strategies show the highest levels of tree diversity. Our findings suggest that mycorrhizal dominance, rather than mycorrhizal type, drives tree diversity.

Main text

Mycorrhizas – the most widespread terrestrial symbiosis on Earth – have long been known for their nutritional benefits to plants, and there is increasing interest in their potential role as drivers of local plant biodiversity (Tedersoo *et al.*, 2020). Species-rich tropical rainforests tend to be dominated by arbuscular mycorrhizal (AM) trees while species-poor boreal forests tend to be dominated by ectomycorrhizal (EcM) trees (Connell & Lowman, 1989; Brundrett, 1991; Allen *et al.*, 1995). This observation has led to the hypothesis that the AM strategy promotes plant diversity and while the EcM strategy promotes dominance by one or few species (Laliberté *et al.*, 2015; Tedersoo *et al.*, 2020). Small-scale studies of seedling recruitment support this hypothesis: EcM seedlings perform better when growing in soils near (or conditioned by) conspecific individuals (i.e. showing positive plant-soil feedbacks), whereas the opposite has been found for AM plants (Bennett *et al.*, 2017; Teste *et al.*, 2017). EcM networks sustained by mature trees are thought to provide greater protection to conspecific seedlings from soil-borne pathogens than AM networks, while also improving nutrient acquisition (van der Heijden *et al.*, 2015; Laliberté *et al.*, 2015). However, it is unknown whether these short-term effects on recruitment dynamics translate into persistent effects on canopy tree species composition and diversity. Indeed, neither the historical biome-level observations nor the individual-level studies of seedling recruitment directly test the hypothesis that EcM-dominated forests sustain lower tree species diversity than AM-dominated forests; broad-scale analyses of tree communities are needed to resolve this.

Here, we test the effect of mycorrhizal dominance (EcM vs. AM strategy) on tree species diversity across broad environmental gradients at the continental scale using the extensive grid-based inventory of naturally forested plots surveyed by the U.S. Department of Agriculture Forest Service (Forest Inventory and Analysis program). Selected plots (each composed of four subplots of 168 m^2) spanned the contiguous U.S. (Burrill *et al.*, 2018), with the number of tree species per plot ranging from 1 to 21 (Fig. 1a). As a predictor of tree diversity at the plot scale, we calculated the proportion of total basal area comprised of trees with the EcM strategy (Fig. 1b). Patterns of EcM and AM proportions are opposite (Fig. 1b, Fig. S1), and most plots are dominated by EcM and/or AM strategies (Fig. S2).

Environmental filtering from the regional flora is a dominant driver of local plant diversity (Laliberté *et al.*, 2014) and mycorrhizal distribution is known to be broadly linked with environmental factors that also influence plant diversity (Read, 1991). Therefore, we included effects of local abiotic factors (climatic, topographic and physiographic) in our models predicting plant diversity to test whether there was an independent effect of mycorrhizal dominance. We hypothesized that tree diversity would decrease monotonically as dominance by EcM tree increased.

As expected, tree species diversity was lowest in EcM-dominated forests (Fig. 1c). However, tree diversity was maximal when EcM tree basal area was ~50%, beyond which tree species diversity unexpectedly declined. As such, tree species diversity was lowest in forests dominated by either the EcM or AM strategies, and highest when there was an equal mixture of both strategies. Tree diversity was also influenced by local environmental conditions tended to influence tree diversity, especially temperature, topography and water availability (Fig. S3), but the negative effects of mycorrhizal dominance on tree diversity persisted (Fig. 1c).

Local species diversity depends on the regional species pool (Ricklefs, 1987), and we could expect that forests 100% dominated by either mycorrhizal type have a smaller potential number of species than forests with both types. As such, we applied a null model to first assess the expected relationship between tree diversity and proportion EcM based on random sampling from the species pool, and then to calculate the deviation between observed and expected values for each plot ("alpha-deviation"). The null model re-assigned a species identity to each individual tree in a given plot based on a random draw from the abundance-weighted subset of species in the regional pool of the same mycorrhizal type (either EcM or non-EcM). The null model thus preserves the value of proportion EcM of each plot. Regional pools were defined within each of 25 ecoregions (Cleland *et al.*, 2007), which represent areas with relatively similar ecological and environmental conditions (Fig. S4). The results show an overall negative alpha-diversity deviation, on average, likely resulting from environmental, demographic and stochastic processes that exclude some species locally. However, the hump-shaped relationship with the EcM proportion persisted (Fig. 1d, Fig. S5), indicating that the effect of mycorrhizal dominance is robust to potentially confounding effects of the species pool.

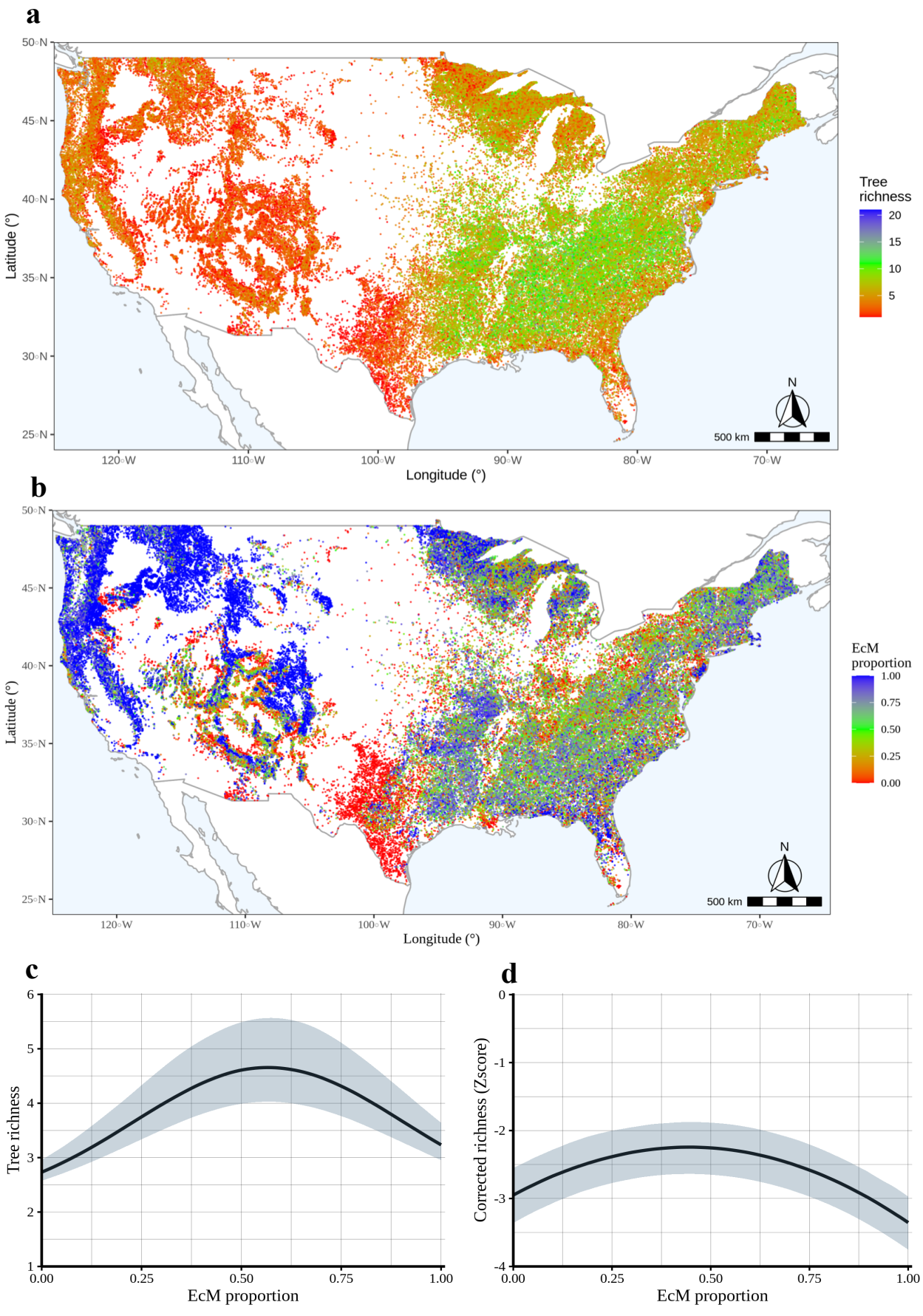
a
50°N
45°N
40°N
35°N
30°N
25°N
Latitude (°)
120°W
110°W
100°W
90°W
80°W
70°W
Longitude (°)
Tree richness
20
15
10
5
N
500 km
b
50°N
45°N
40°N
35°N
30°N
25°N
Latitude (°)
120°W
110°W
100°W
90°W
80°W
70°W
Longitude (°)
EcM proportion
1.00
0.75
0.50
0.25
0.00
N
500 km
c
Tree richness
6
5
4
3
2
1
0.00
0.25
0.50
0.75
1.00
EcM proportion
d
Corrected richness (Zscore)
0
-1
-2
-3
-4
0.00
0.25
0.50
0.75
1.00
EcM proportion

Figure 1. Tree richness and ectomycorrhizal (EcM) proportion at the community scale. (a) Map of EcM proportion (as the proportion of basal area of trees with DBH > 12.7 cm known to associate with EcM fungi); (b) Map of tree richness (number of tree species); Relationships between EcM proportion and (c) predicted and (d) corrected tree richness. Both (c) and (d) take into account potentially confounding environmental factors (elevation, orientation, physiography, precipitation, slope and temperature), and the lines indicate the regression curve between both variables and shaded areas represent 95% confidence interval of the regression.

Several mechanisms involving mycorrhizal type may combine locally to influence plant diversity (Tedersoo *et al.*, 2020). Our results suggest that EcM and AM dominance reduce local tree diversity across the U.S., for which there may be several explanations. The positive plant-soil feedbacks commonly experienced by EcM species (i.e. Laliberté *et al.*, 2015), might also occur in AM species at later life stages, leading to persistent dominance in adult forest-tree communities (Fig. S6). It is widely accepted that EcM plants may benefits more from EcM fungi in terms of nutrition and protection (van der Heijden *et al.*, 2015) but, given the likely higher maintenance costs for EcM fungi compared to AM fungi, the net benefits of the two mycorrhizal types might be similar (Tedersoo & Bahram, 2019). This could locally promote diversity where the mycorrhizal types co-occur.

Several lines of evidence suggest that higher tree diversity might be associated with the presence of multiple mycorrhizal types that co-occur at the local scale. It has been proposed that fine-scale spatial heterogeneity of soil nutrients may promote the coexistence of plants associating with different groups of fungi (Read, 1991). Such niche differentiation among plant mycorrhizal types potentially increases competition within mycorrhizal types, while enhancing coexistence of plants belonging to different mycorrhizal types (Smith & Read, 2008). Furthermore, fine-scale niche partitioning can promote coexistence of different mycorrhizal types (Taylor *et al.*, 2014) and ecosystems with a mixture of mycorrhizal strategies may in turn create environments that are more diverse and spatially heterogeneous (Mariotte *et al.*, 2018). Similarly, better root protection by EcM fungi is expected to strengthen plant-soil feedbacks leading to more positive conspecific density dependence (Bagchi *et al.*, 2014; Laliberté *et al.*, 2015; Bennett *et al.*, 2017), but it may also reduce overall soil pathogen loads at the plot scale (Bahram *et al.*, 2020), potentially favoring

plant diversity. Therefore, mycorrhizal mixture may promote overall plant diversity but this remains to be experimentally tested.

A number of studies have reported positive effects of a diverse inoculum of AM fungi on plant diversity and ecosystems functions (van der Heijden *et al.*, 1998; Maherali & Klironomos, 2007). Plant species richness as well as evenness increase in response to AM fungi inoculation (Lin *et al.*, 2015), and plant-soil feedbacks involving seedlings tend to be more negative in AM tree species (Bennett *et al.*, 2017). These results lead to the expectation of a positive effect of AM strategy on tree diversity. However, studies at the community level are typically conducted in grasslands (e.g. Hartnett & Wilson, 2002), which may not apply to long-lived trees in forests. As a result, the few studies of trees are typically at the level of individual seedlings (e.g. Mangan *et al.*, 2010; Bennett *et al.*, 2017; Teste *et al.*, 2017), and these short-term effects on seedling recruitment might not necessarily translate to canopy-level patterns involving mature trees. It is also worth noting that even though most tropical rainforests are both AM-dominated and host high tree species diversity, there is also a number of hyper-dominant tropical tree species forming AM associations (Peh *et al.*, 2011). Therefore, not all tropical forest communities are species-rich, even in neo-tropical forests where AM trees dominate (ter Steege *et al.*, 2013). Furthermore, recent evidence had cast doubt on the conventional hypothesis of lower plant diversity in EcM compared to AM systems assessing temperate and boreal sites (Bahram *et al.*, 2020). Thanks to an approach at the continental scale, our results show that mycorrhizal dominance – regardless of mycorrhizal type – shapes tree species diversity in forests with diversity maximized when different mycorrhizal strategies co-exist.

Patterns of mycorrhizal dominance and tree diversity have been historically considered among distant biomes, leading to the hypothesis that the EcM symbiosis reduces plant diversity, while the AM symbiosis promotes plant diversity (Read, 1991; Tedersoo *et al.*, 2020). The impact of mycorrhizal fungi on plant nutrition and plant soil-feedbacks, often studied at the individual level scale, have provided indirect support these hypotheses (Tedersoo *et al.*, 2020). However, forest-trees probably interact locally where mycorrhizal dominance favor positive plant-soil feedbacks, thus reducing diversity, and potentially leading to alternative stable states. On the contrary, mycorrhizal diversity could promote tree species diversity at the community level through equalizing and stabilizing mechanisms.

Materials and Methods (Supplementary)

Data collection

For this study, we used publicly available data from the U.S. Department of Agriculture Forest Service, known as the Forest Inventory and Analysis (FIA) program. Data were accessed from https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html on 28 February 2020. The primary objective of the FIA is to determine the extent, condition, volume, growth, and use of trees on U.S. forest land in order to frame realistic forest policies and programs (Burrill *et al.*, 2018). This database has been used to address many ecological questions across large scales and gradients (Zhu *et al.*, 2012; Phillips *et al.*, 2013; Jo *et al.*, 2019). Plots are distributed relatively evenly in forested areas across all of the lower 48 contiguous states. Plots location uncertainty is < 1.6 km (Burrill *et al.*, 2018). Each standard plot consists of four 7.3-m radius circular subplots (168 m^2) within which all stems > 12.7 cm diameter at breast height (DBH) are identified to species and measured. There is one center subplot surrounded by the three peripheral subplots, each at a distance of 36.6 m from the center subplot.

Prior to our analyses, the data set was filtered using several criteria following the FIA user guide for Phase 2 (Burrill *et al.*, 2018). We only kept: (i) census data from the most recent year available for each plot, (ii) standard production and standardized plots (i.e. "Sample kind code" of 1, 2 or 3) that were sampled the same way (i.e. "Plot design code" of 1, 220, 240, 311, 314, 328, 502, 505) (iii) data taken using the National Field procedures, (iv) forested, natural and undisturbed stands with no observable recent silvicultural treatment. If data were missing for any measured values or variables the plots were excluded. Otherwise, plots were retained if more than four individual trees were present. In total, we analyzed data for 84,448 plots containing 2,518,123 trees.

For each selected plot, topographic data (elevation, slope, aspect) and physiographic class (estimate of moisture available to trees) were accessed directly from the FIA database. Climatic data (i.e. average annual temperature, annual precipitation) were accessed from the PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate group (800-m spatial resolution; available at http://prism.oregonstate.edu/).

From the stem diameter measurements, total basal area was calculated for each species in each plot. Mycorrhizal strategy for each tree species was determined using Jo *et al.* (2019). Species were

listed as either ectomycorrhizal (EcM), arbuscular mycorrhiza (AM), non-mycorrhizal (NM) or both AM and EcM (AM+EcM).

Tree species richness was calculated as the number of observed tree species with DBH > 12.7 cm. Species richness (Fig. 1a) followed large scale tree diversity gradients previously mapped for the U.S. (Jenkins *et al.*, 2015). Abundance was incorporated into diversity indices using the exponential of Shannon's entropy index ($q = 1$) and the inverse of Simpson's concentration index ($q = 2$), calculated as proposed in Chao *et al.* (2014) based on Hill numbers (Hill, 1973).

Following the "National hierarchical framework of ecological units" (Cleland *et al.*, 2007) we defined 25 ecoregions and assigned one for each plot depending on its location (Fig. S4). Ecological units are defined as areas of similar surficial geology, lithology, geomorphic processes, soil groups and subregional climate.

Null model

We used a null model that re-assigned the species identity of the individuals in each plot based on random draws from the regional pool of tree species within ecoregions (Fig. S4), while keeping the total number of individuals per plot and the proportion EcM constant. Each species' abundance (i.e. its probability of being chosen by the null model) was calculated as the number of tree stems in the ecoregion, divided by the total number of stems across species. We ran 100 randomizations from which we calculated the diversity "deviation" (or "corrected" diversity) as the observed diversity minus the mean of the null distribution of diversity values, divided by the standard deviation of this distribution (i.e., Z-scores). Diversity measures were the same as for the observed data. Negative values of corrected diversity represent lower diversity than expected given random draws from the regional species pool. The null model was implemented in R (ver. 3.6.2; R Core Team, 2018).

Modeling

To quantify the effect of EcM proportion and the environmental variables on tree species diversity and corrected diversity, we used generalized linear mixed-effect models implemented in a Bayesian framework. Ecoregion was included as a random factor. For richness values ($q = 0$), we used the Poisson distribution and for $q = 1$ and $q = 2$ we used the Gamma distribution. Because diversity values start at one, distributions were truncated with lower bound < 1. For the corrected diversity,

we used the Gaussian distribution. Before modeling, environmental variables were scaled by. subtracting the mean and dividing by the standard deviation.

Analyses on diversity were conducted for $q = 1$ and $q = 2$, which showed similar patterns as $q = 0$ (Fig. S7). Robustness to the minimum number of trees per plot of the relationship between tree richness and EcM proportion was tested by running models with a threshold for a minimum number of individuals per plot of nine and 14 individuals (Figure S8). They showed similar pattern with a slight increase in maximum tree richness with an increasing threshold.

The models ran on four parallel chains of length 5,000 with a burn-in of 1,000 iterations with a thinning rate of 10. Uninformative priors were used as provided in the *brms* package (Bürkner, 2017). Convergence was assessed for each parameter estimate by visually inspecting the Markov chains and considered sufficient when the $\hat{R}$ was equal to one.

Data manipulation and statistical analyses were done using the R software (R Core Team, 2018) and the following main packages : *brms* (Bürkner, 2017), *data.table* (Dowle & Srinivasan, 2017) *dplyr* (Wickham *et al.*, 2017), *ggplot2* (Wickham, 2016), *ggpubr* (Kassambara, 2018), *ggspatial*, *reshape* (Wickham, 2007), *sf*, *vegan* (Oksanen *et al.*, 2017).

Acknowledgements

Funding, including scholarships to AC, was provided by Discovery Grants to EL (RGPIN-2014-06106, RGPIN-2019-04537) by the Natural Sciences and Engineering Research Council of Canada (NSERC) as well as a "Nouveau Chercheur" grant (2016-NC-188823) by the Fonds de recherche du Québec sur la Nature et technologies (FRQNT). AC would like to sincerely thank the following institutions for providing generous scholarships: FRQNT (Dossier 272522) and Université de Montréal through the "Bourse d'excellence Hydro-Québec".

Authors' contributions

EL, AC and MV conceived the ideas and designed the methodology. AC, EL and MV analyzed the data and interpreted the results. AC led the writing of the manuscript. All authors contributed critically to the manuscript.

Supplementary information

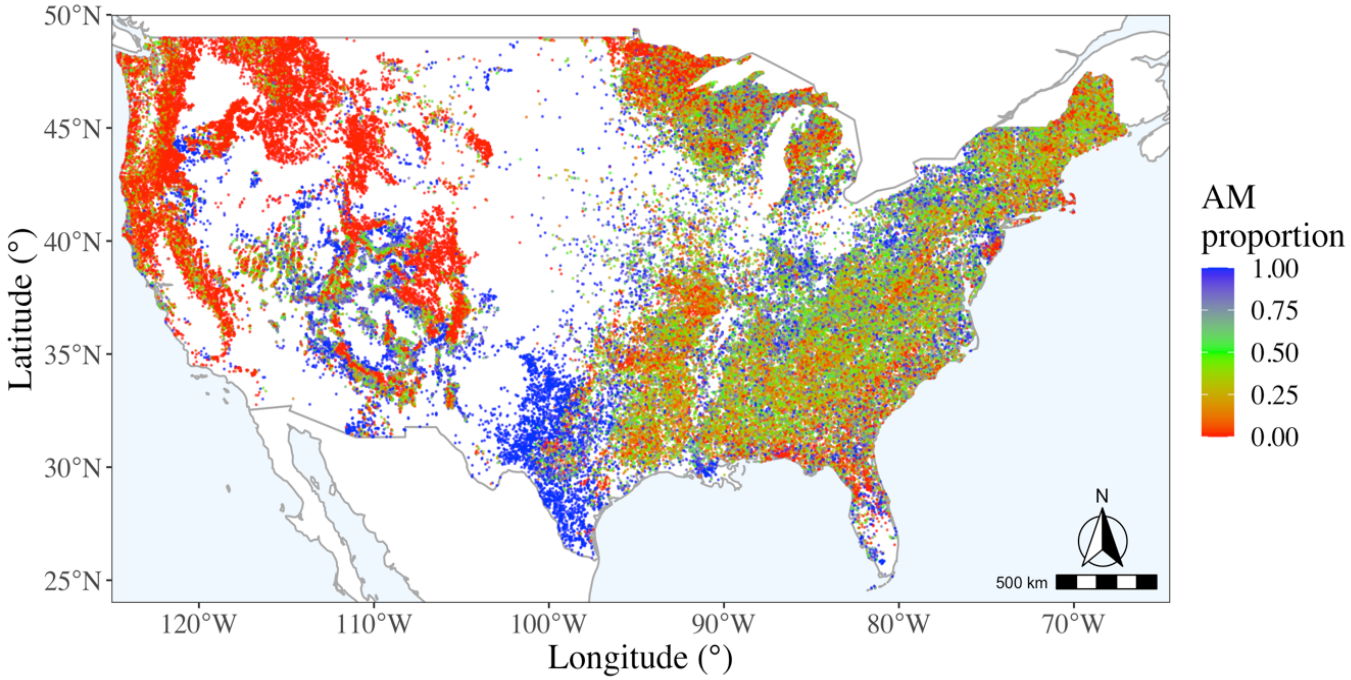

Figure S1. Map of arbuscular mycorrhizal (AM) proportion (as the proportion of basal area of tree with DBH > 12.7 cm known to associates with AM fungi).

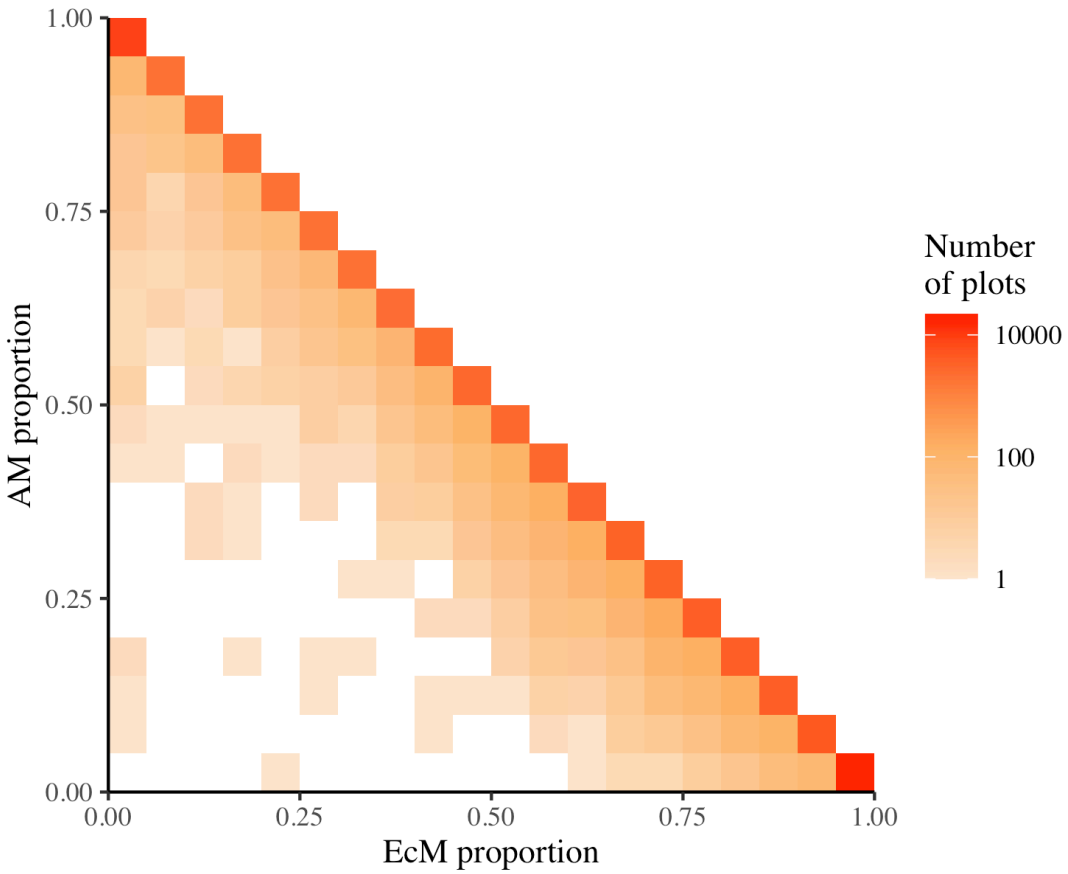

Figure S2. Relationship between ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) proportions in each plot. 95 % of the plots have a cumulative sum of AM and EcM proportions >.99 (i.e. most plots are located on the diagonal).

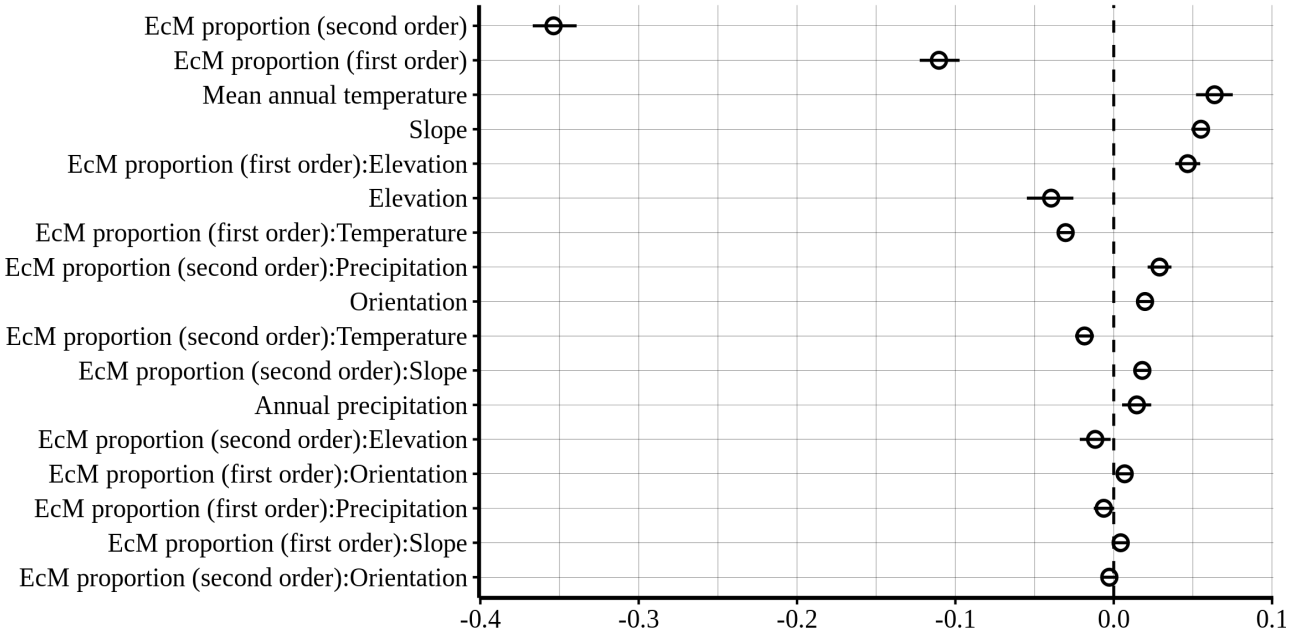

Figure S3. Posterior coefficient estimates (median and 95% credible interval) for the ectomycorrhizal (EcM) proportion and local environmental factors (elevation, orientation, precipitation, slope, temperature), and their interactions on alpha diversity of tree species.

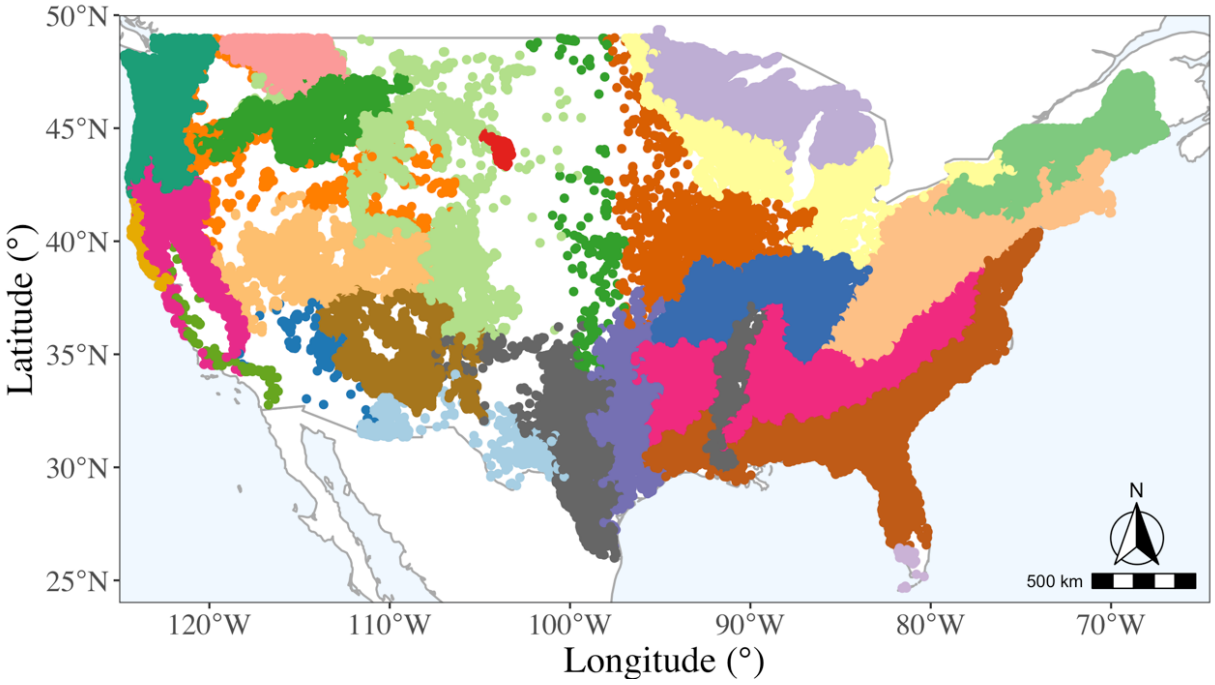

Figure S4. Map showing the plot location in the 25 ecoregions used in the models as random factor and in the null models as regional pools. Based on the "National hierarchical framework of ecological units" (Cleland *et al.*, 2007).

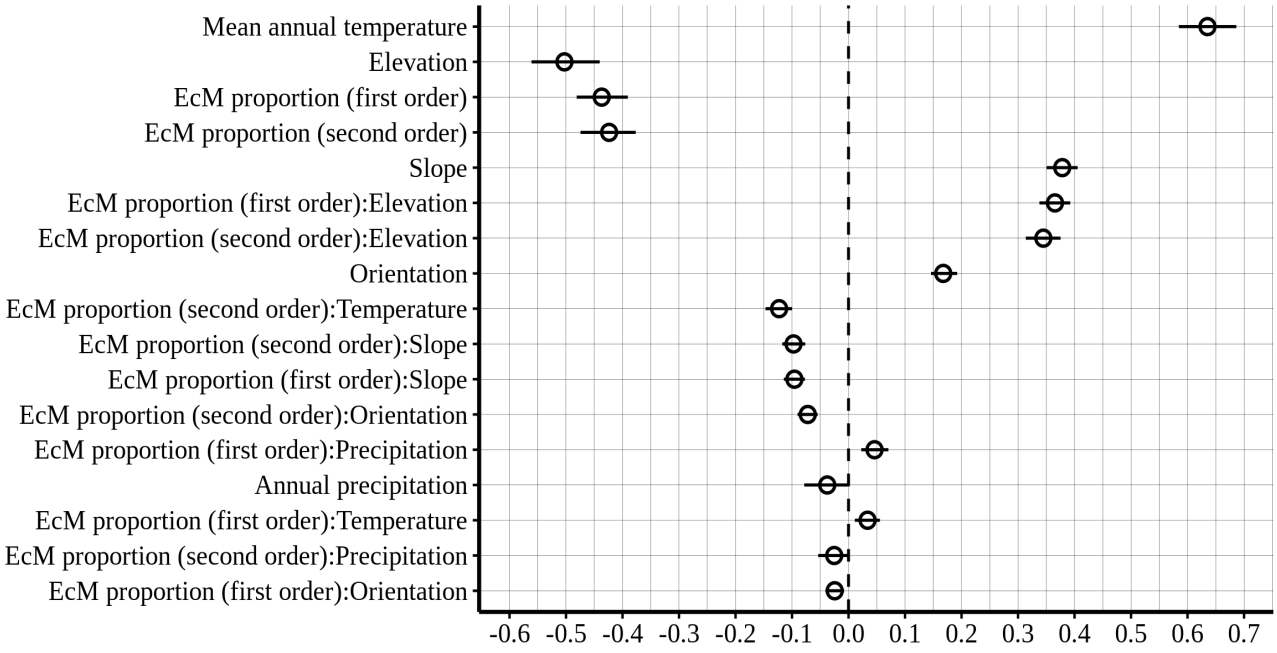

Figure S5. Posterior coefficient estimates (median and 95% credible interval) for the ectomycorrhizal (EcM) proportion and local environmental factors (elevation, orientation, physiography, precipitation, slope, temperature), and their interactions on alpha diversity deviation of tree species.

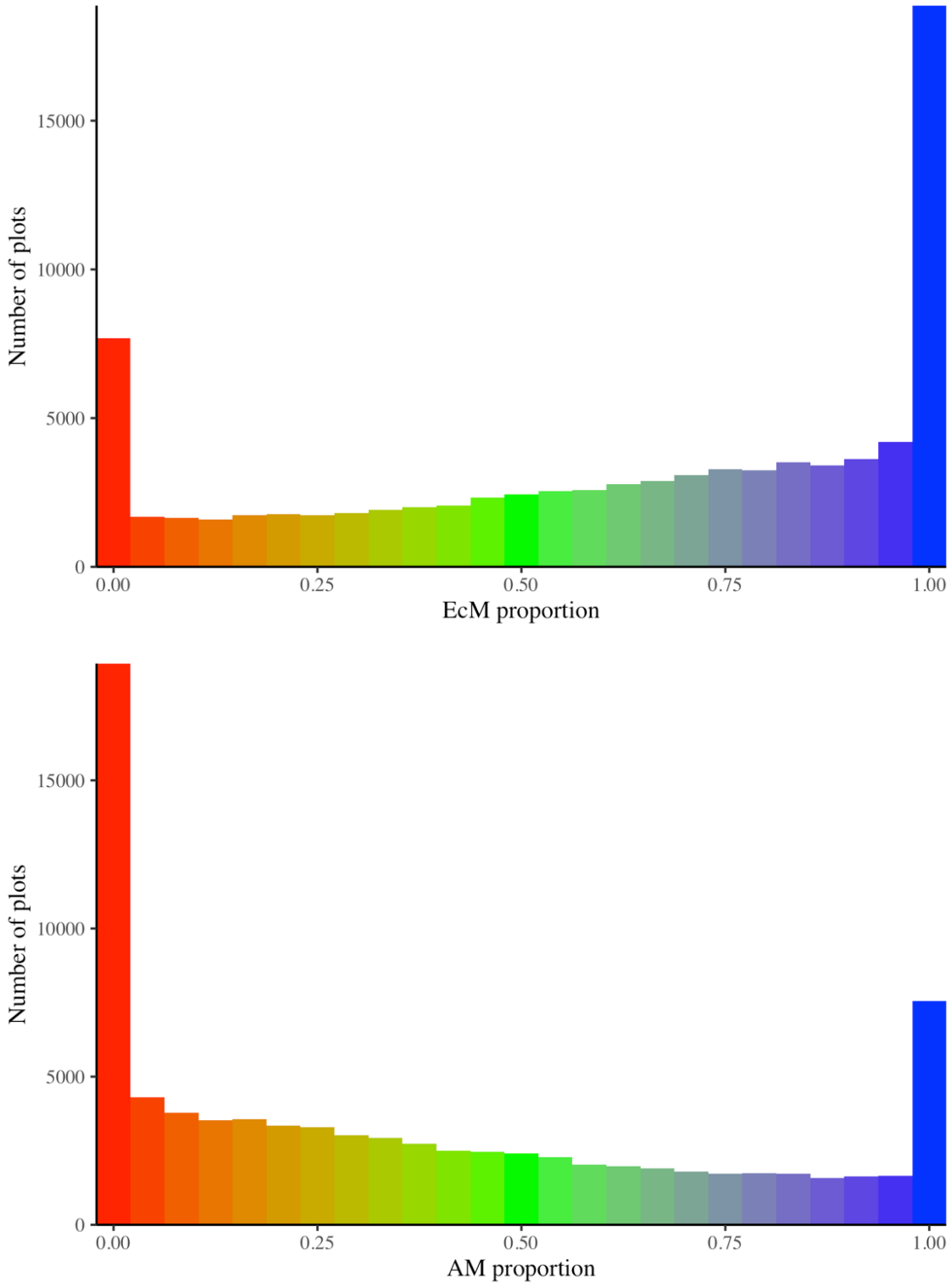

Figure S6. Relationships between the number of plots and ectomycorrhizal (EcM) proportion (top), and arbuscular mycorrhizal (AM) proportions (bottom).

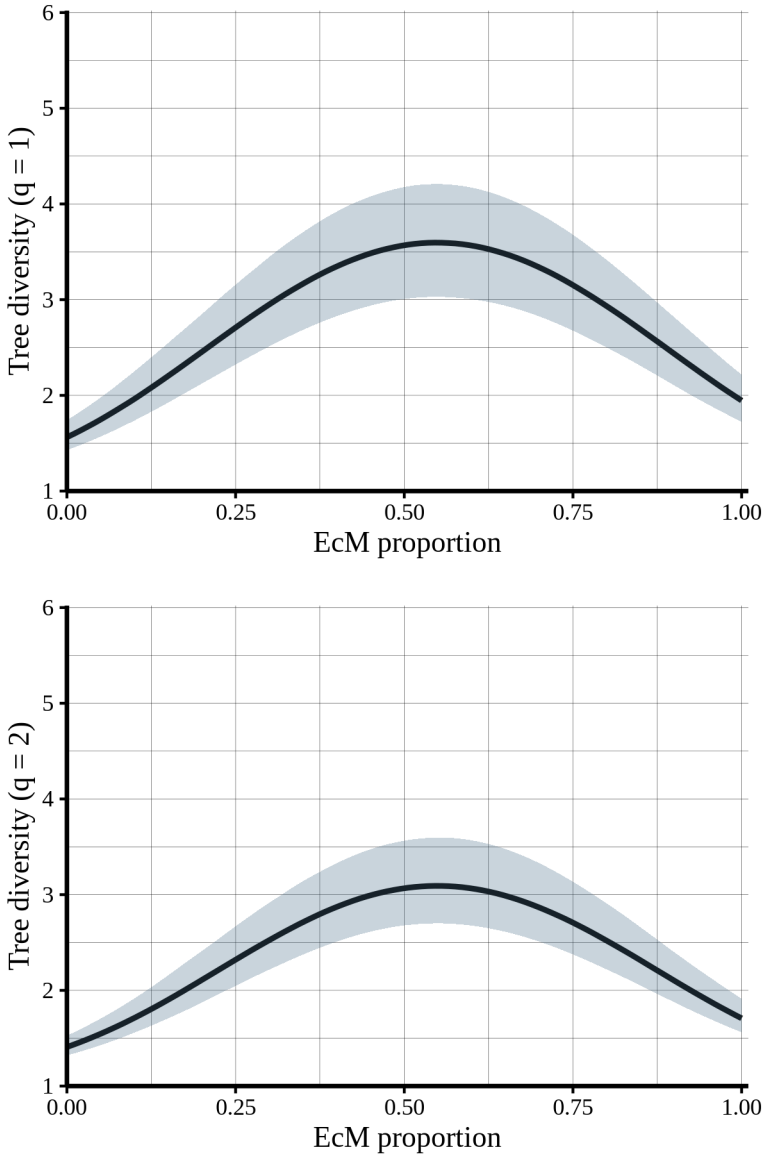

Figure S7. Relationships between ectomycorrhizal (EcM) proportion and model-predicted values of diversity for q = 1 (top) and q = 2 (bottom). Lines indicates regression curve between both variables. Shaded areas represent 95% confidence interval of the regression.

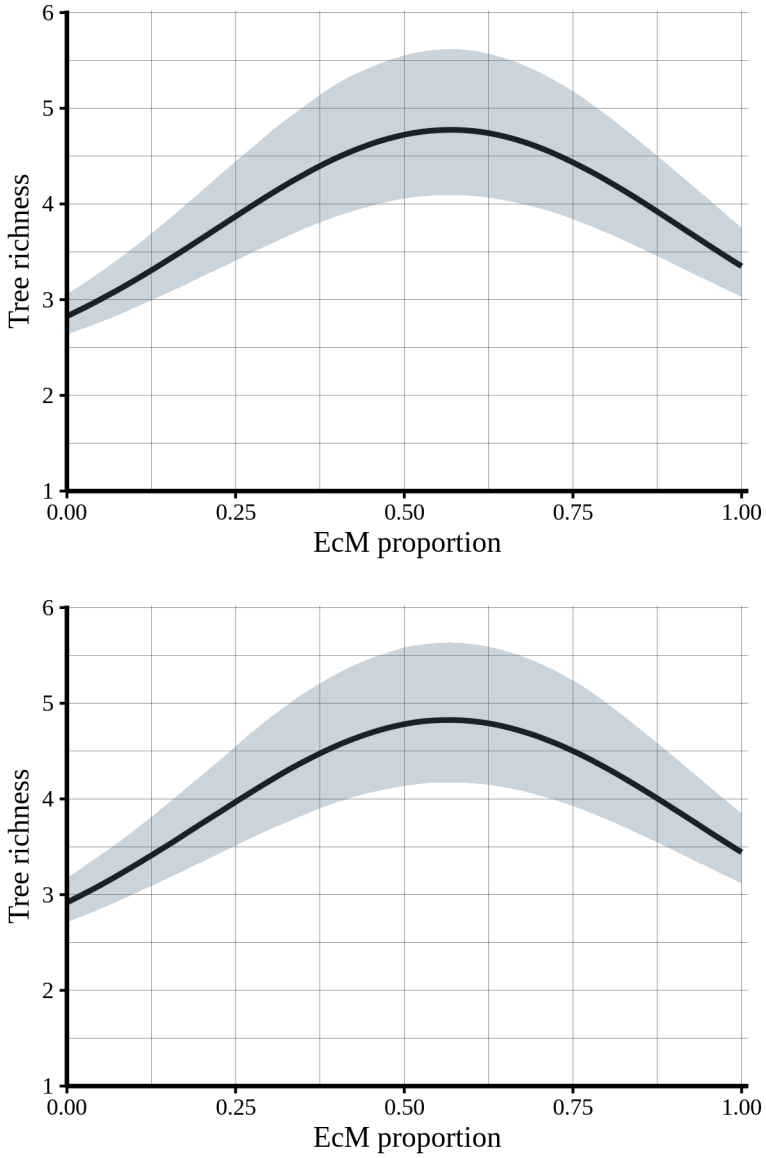

Figure S8. Relationship between EcM proportion and tree richness using thresholds for minimum number of individuals per plot of nine (top) and 14 (bottom) individuals. Lines indicates regression curve between both variables. Shaded areas represent 95% confidence interval of the regression.

Coucher de soleil sur la forêt amazonienne, Guyane.

CONCLUSION

1. Synthèse

Dans le but de mieux comprendre le fonctionnement des écosystèmes forestiers, cette thèse s'est focalisée sur l'étude de l'impact (local) de la dominance mycorhizienne sur les facteurs édaphiques abiotiques et biotiques, et sur les processus écologiques qui en découlent. En améliorant la compréhension de la distribution des microorganismes responsables de processus écologiques et en mesurant leurs impacts directs et indirects, il est désormais possible de mieux prédire la dynamique des communautés végétales et les cycles biogéochimiques. Plus spécifiquement, il s'agissait de quantifier les impacts de la dominance mycorhizienne et de la chimie du sol sur la distribution verticale parmi les différentes guildes de champignons (Chapitre 1), puis de mesurer leurs impacts sur la décomposition de la matière organique (Chapitre 2). Ensuite, il s'agissait de comprendre de quelle manière les facteurs abiotiques et biotiques du sol de forêts dominées par différents types de mycorhizes peuvent à leur tour influencer la dynamique végétale des écosystèmes forestiers à court terme de par l'établissement d'arbres (Chapitre 3) et, à plus long terme, en modulant la diversité en espèces d'arbres (Chapitre 4).

Les résultats présentés dans le Chapitre 1 ont permis de déterminer les changements verticaux dans la composition des communautés fongiques à travers les différents horizons du sol et le long d'un gradient de dominance mycorhizienne. Contre toute attente, le changement de la composition fongique (de saprotrophique à mycorhizienne) en lien avec l'augmentation de la profondeur était en général similaire le long du gradient mycorhizien (Smith & Read, 2008). En effet, l'hypothèse historique basée, notamment sur des observations d'écosystèmes distincts, supposait que la compétition entre les différentes guildes fongiques pouvait résulter en une ségrégation verticale davantage marquée avec les champignons saprotrophes à la surface, puis les champignons à EcM, et enfin les champignons à AM en profondeur dans les horizons plus minéraux. Ces résultats montrent aussi que les champignons saprotrophes tendent à être moins abondants dans les horizons organiques des forêts à EcM que dans ceux des forêts à AM ou en codominance AM-EcM, apportant un nouvel éclairage pour expliquer l'effet des mycorhizes sur le stockage du carbone dans les horizons supérieurs du sol (Phillips *et al.*, 2013; Soudzilovskaia *et al.*, 2015b). Les changements de composition de la communauté fongique étaient en grande partie dus à des différences dans la chimie du sol, plus marquées en observant les horizons d'une même forêt qu'en analysant un même type d'horizon dans des forêts différentes. Les résultats du Chapitre 1 soulignent ainsi l'importance de prendre en compte la structure verticale du sol et les changements chimiques associés lors de la

caractérisation des communautés fongiques qu'il contient (Dickie *et al.*, 2018; Yost & Hartemink, 2020). Ils suggèrent également que les champignons à AM ne sont pas limités aux horizons où les nutriments inorganiques prédominent (Bunn *et al.*, 2019). Les AM et les EcM pourraient donc avoir des niches verticales édaphiques plus similaires que ce qui a été conclu par le passé (Read, 1991; Neville *et al.*, 2002; Smith & Read, 2008). Ce chapitre offre désormais une nouvelle perspective quant aux interactions potentielles entre guildes fongiques, de sorte que les processus écologiques qui en résultent pourraient être influencés d'une manière différente de celle proposée jusqu'à présent, ce qui a par ailleurs été examiné dans les chapitres 2, 3 et 4.

Au sein du système étudié dans le Chapitre 1, la quantification des stocks de carbone des 20 premiers centimètres de sol a confirmé des quantités plus importantes dans les forêts dominées par les EcM que dans celles dominées par les AM, et ce, en accord avec des observations réalisées à l'échelle mondiale (Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019). Afin d'évaluer directement l'impact de la dominance mycorhizienne sur le cycle du carbone, une expérience *in situ* de décomposition a été réalisée. Cependant, aucune preuve de ralentissement de la décomposition de la matière organique par le réseau fongique en forêts à EcM n'a été révélée. À l'inverse, la décomposition dans ces forêts-là semble avoir été accélérée par la présence du réseau fongique local. Les résultats du Chapitre 2 s'opposent donc à une majorité d'études sur le sujet (Fernandez & Kennedy, 2016). De plus, la décomposition a été en moyenne plus rapide dans les forêts dominées par les EcM que dans celles dominées par les AM. La décomposition plus lente de la litière provenant des forêts à EcM et des horizons plus en profondeur met en lumière un effet majeur de la composition chimique et de l'origine de la matière organique sur le processus de recyclage du carbone et des nutriments, et potentiellement sur les interactions entre guildes fongiques (Fernandez *et al.*, 2019; Smith & Wan, 2019). L'horizon fragmenté, qui se situe juste en-dessous de la litière, se révèle être un point chaud de l'action du réseau fongique, or la majorité des études mesurant l'impact des champignons sur la décomposition de la matière organique ont tendance à se concentrer uniquement sur la litière (Fernandez & Kennedy, 2016; Frey, 2019). Ainsi, les résultats du Chapitre 2 indiquent que le ralentissement supposé de la décomposition de la matière organique par les EcM n'est pas généralisable. En effet, le contexte environnemental local tel que le climat et les traits fonctionnels des arbres dominants semblent être déterminants pour l'impact de la dominance mycorhizienne sur la dynamique du carbone et des nutriments (Fernandez & Kennedy, 2016; Netherway *et al.*, 2020). Les résultats du Chapitre 2 relèvent aussi que, plutôt

que de la ralentir, le réseau fongique peut avoir tendance à accélérer la décomposition, plaidant en faveur de l'importance de l'effet d'amorçage (*priming effect*) sur les microbes saprotrophes via la production d'exsudats et de nécromasse mycorhizienne (Kuzyakov, 2010; Frey, 2019). Ces résultats remettent désormais en cause un effet soi-disant uniforme et généralisé des différents types mycorhiziens sur les cycles du carbone et des nutriments (Tedersoo & Bahram, 2019). Cela amène à questionner les hypothèses proposées jusque-là concernant les effets de la dominance mycorhizienne sur les communautés végétales de par la modification des propriétés et processus édaphiques (Tedersoo *et al.*, 2020); hypothèses testées par la suite dans les chapitres 3 et 4.

En se basant à nouveau sur des parcelles forestières dominées par des EcM (forêt boréale dans ce cas d'étude), des AM (érablière) ou en codominance AM-EcM (écotone tempéré-boréal), les résultats présentés dans le Chapitre 3 ont permis de comprendre que les effets combinés des facteurs abiotiques et biotiques du sol ont considérablement réduit le potentiel de survie et de croissance des semis de l'érable à sucre (espèce d'arbre à AM) dans la forêt boréale, qui est riche en EcM. De plus, la faible performance des semis d'érable à sucre dans les sols stériles suggère un rôle bénéfique important des microorganismes présents dans le sol. Cette idée est appuyée par le fait que les semis ayant eu les meilleures performances contenaient une plus grande abondance de structures fongiques d'origine arbusculaire dans leurs racines, ce qui indique le rôle essentiel des champignons à AM. De plus, les forts écarts de performance des semis en fonction de la dominance mycorhizienne originale des sols soulignent l'importance des facteurs physico-chimiques dans la limitation de l'établissement de l'érable à sucre en forêt boréale, comme proposé par d'autres études (Graignic *et al.*, 2014; Collin *et al.*, 2017; Solarik *et al.*, 2020). Un des défis du cadre d'étude traitant des interactions plantes-sol est de mieux comprendre les mécanismes sous-jacents pour permettre une meilleure adaptation face aux changements climatiques (Sanders-DeMott *et al.*, 2016). Ainsi, ce chapitre fournit des preuves sur l'importance de la dominance mycorhizienne dans la détermination de l'aire de répartition des arbres de par la modification des conditions biotiques du sol (Lafleur *et al.*, 2010). Ces facteurs souterrains, non-climatiques, devraient être pris en considération pour mieux prédire la réponse des communautés végétales face aux changements climatiques (Brown & Vellend, 2014; Brzostek *et al.*, 2017). De plus, la combinaison des caractéristiques abiotiques et biotiques au niveau du sol de l'écotone tempéré-boréal, où la dominance mycorhizienne est partagée entre AM et EcM, n'a pas semblé limiter l'établissement des semis d'érable à sucre, qui y ont relativement bien performé. Cela soutient l'importance du sol

dans l'avantage compétitif (*happy edge*) de l'érable à sucre au niveau de l'écotone tempéré-boréal (Urli *et al.*, 2016); écotone qui se rétracte d'ailleurs au profit de la forêt tempérée sous l'effet des perturbations récentes (Brice *et al.*, 2020). Le Chapitre 3 permet donc de soulever un impact potentiellement important de la dominance mycorhizienne partagée entre AM et EcM dans le processus de maintien de la diversité à l'échelle de la communauté forestière; impact testé plus spécifiquement dans le Chapitre 4.

Dans un monde en plein changement, où la biodiversité s'érode de jour en jour, il est crucial de pouvoir identifier les mécanismes qui déterminent la composition des espèces dans les communautés végétales (Read, 1998). Les patrons de dominance mycorhizienne et de diversité végétale au niveau des biomes ont conduit à l'hypothèse générale selon laquelle l'augmentation de la dominance des EcM par rapport aux AM réduit la diversité végétale (Brundrett, 1991; Allen *et al.*, 1995). De plus, il est généralement admis que les rétroactions plantes-sol tendent à être plus positives pour les arbres à EcM que pour les arbres à AM dans leurs premiers stades de vie, grâce notamment à un réseau ectomycorhizien plus efficace contre les pathogènes et pour l'acquisition des éléments nutritifs (Laliberté *et al.*, 2015; Bennett *et al.*, 2017), et qu'elles sont maintenues par des processus édaphiques plus favorables aux EcM (Tedersoo *et al.*, 2020). Ainsi, les résultats du Chapitre 4 ont permis de mettre en évidence que, à l'échelle locale de la parcelle forestière, les forêts dominées par les EcM ne sont pas moins diversifiées en espèces d'arbres que les forêts à AM. Après avoir pris en compte les autres facteurs locaux potentiellement importants et le bassin régional d'espèces, la dominance mycorhizienne reste tout de même un facteur déterminant de la diversité locale des forêts étudiées sur de larges gradients environnementaux, au niveau continental. En outre, les forêts ayant une dominance partagée entre AM et EcM semblent abriter une plus grande diversité d'arbres, confirmant ainsi que la dominance mycorhizienne est un moteur du processus de maintien de la diversité végétale au niveau local (Tedersoo *et al.*, 2020). Suite à ces résultats, il résulte que des observations à plus long terme sont nécessaires pour déterminer si les effets à court terme sur le recrutement d'espèces se traduisent ou non par des effets persistants sur la composition des communautés forestières d'arbres. La question d'échelle revêt toute son importance lorsqu'on observe de près le lien existant entre mécanismes locaux de rétroactions plantes-sol à petite échelle spatiale et patrons de diversité (Levin, 1992), et elle pourrait s'avérer cruciale pour déterminer adéquatement quelle sera la réponse des écosystèmes forestiers face aux changements environnementaux qui sont de plus en plus sévères.

Il est désormais reconnu par la communauté scientifique que l'écologie des plantes au niveau physiologique, des populations et des communautés, ainsi que les cycles biogéochimiques terrestres, ne peuvent plus être considérés en dehors du contexte de la symbiose mycorhizienne (Chagnon *et al.*, 2016; Martin *et al.*, 2018). L'ensemble des résultats présentés dans cette thèse démontrent, de surcroît, le rôle primordial qu'exerce la dominance mycorhizienne à l'échelle locale sur certains facteurs clés du sol, modulant ainsi des processus écologiques fondamentaux pour le fonctionnement des écosystèmes terrestres et le climat (Fig. 1).

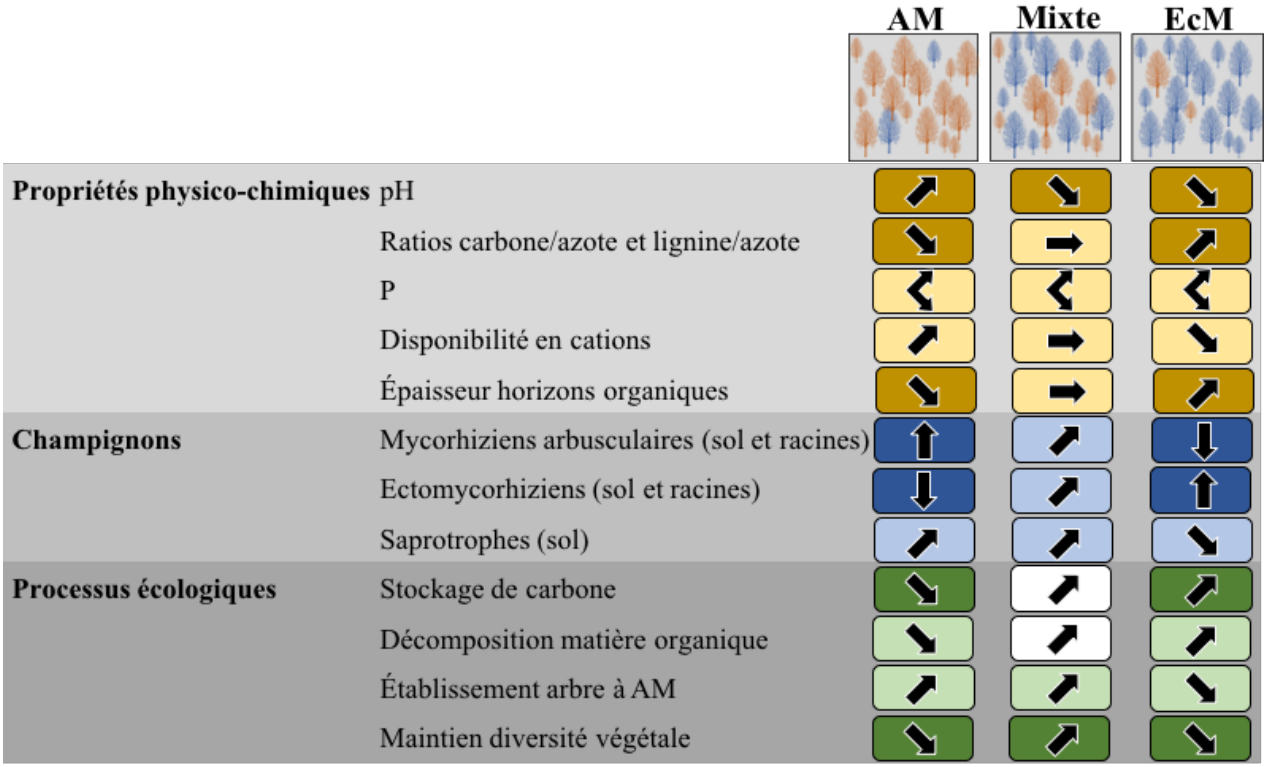

Figure 1. Résumé des principaux constats marquants de cette thèse qui illustrent l'impact de la dominance mycorhizienne sur les propriétés physico-chimiques du sol, les guildes fongiques, et les processus écologiques en forêt. Les flèches indiquent la direction et l'intensité de l'effet d'un type de dominance par rapport aux autres. Les flèches pointant vers le haut indiquent un effet relatif plutôt positif, et les flèches pointant vers le bas indiquent un effet négatif. Les flèches encadrées par une teinte plus sombre indiquent quant à elles une plus grande certitude dans le résultat, et un encadré blanc signale une hypothèse non testée. AM : mycorhizes arbusculaires; EcM : ectomycorhizes; Mixte : dominance partagée entre AM et EcM. Figure inspirée de Bardgett *et al.* (2014).

2. Modèles d'études, approches et défis

Cette thèse s'est appuyée sur un système modèle : la forêt d'érable à sucre (érablière), située au nord de la répartition de la forêt tempérée. Présente au sein d'un climat continental, il y fait particulièrement froid et humide, avec des précipitations tout au long de l'année dont environ un tiers sous forme neigeuse. Or, les érables à sucre sont colonisés par des Glomeromycètes pour former des AM, plus communs dans les climats chauds (Soudzilovskaia *et al.*, 2015a). Les érablières sont largement dominées par les AM, bien que l'on puisse également y trouver des champignons à EcM et à ErM (Chapitre 1). Non loin de ces érablières, prospèrent des peuplements forestiers d'une toute autre nature : des hêtraies, composées principalement de hêtre à grandes feuilles s'associant avec des champignons à EcM (Duchesne *et al.*, 2005). Il est donc possible de trouver des forêts dominées par des EcM à côté de forêts qui, elles, sont dominées par des AM (Chapitre 1). Cette « expérience naturelle » permet de tester nombre d'hypothèses au regard de l'effet de la dominance mycorhizienne sur les processus écologiques des forêts tempérées nordiques. Par ailleurs, la dynamique de remplacement entre le hêtre et l'érable intrigue les écologistes depuis des décennies (Woods, 1979; Runkle, 1990; Arii & Lechowicz, 2002; Beaudet *et al.*, 2007; Nolet *et al.*, 2008, 2015; Gravel *et al.*, 2009) et a des conséquences pour la société étant donné que l'érable à sucre revêt d'une grande importance économique et historique, notamment pour son bois et la production du sirop (Maclver *et al.*, 2006; Tyminski, 2011), alors que le hêtre à grandes feuilles est qualifié d'indésirable par les forestiers et propriétaires terriens car son bois n'a que peu de valeur commerciale (Nelson & Wagner, 2014). À la limite nordique du domaine de l'érablière se situe la forêt boréale où les EcM règnent grâce à la grande abondance de conifères (Fortin *et al.*, 2016). Il est donc possible de retrouver, ici aussi, des forêts dominées par des AM relativement proches de forêts dominées par des EcM. Ce phénomène est accentué le long de pentes de monts situés à la limite tempérée-boréale (Chapitre 3). L'augmentation récente des températures devrait favoriser l'établissement d'arbres habituellement présents en forêt tempérée dans la forêt boréale, distante d'à peine quelques centaines de mètres, mais cela ne prend pas en considération une multitude de facteurs non-climatiques qui sont également importants (Lafleur *et al.*, 2010; Corlett & Westcott, 2013; Savage & Vellend, 2015). Ainsi, la dominance mycorhizienne semble être un facteur clé pour la migration des espèces d'arbres à AM tels que l'érable à sucre en forêt boréale (Chapitre 3). Il serait précieux de vérifier si c'est aussi le cas pour des feuillus à EcM de la forêt tempérée. Nonobstant, une plus grande connaissance des impacts de la dominance

mycorhizienne sur l'établissement des arbres en dehors de leur aire de répartition sera capitale pour mieux prévoir leurs futures distributions.

Peu d'études se sont penchées sur l'aspect temporel de la biodiversité et des fonctionnements écosystémiques au niveau souterrain, sujets pour lesquels il serait nécessaire de mettre en place des projets à long terme (Guerra *et al.*, 2020). L'approche visant à utiliser l'espace à la place du temps demeure donc indispensable pour l'étude de phénomènes prenant place à de larges échelles de temps, tels que la migration chez les espèces d'arbres (Schulze *et al.*, 2019). Dans certains cas, l'utilisation de gradients d'élévation permet en plus de contrôler certains effets confondants tels que la nature de la roche-mère (Walker *et al.*, 2010; Sundqvist *et al.*, 2013). Ces approches peuvent être combinées à un schéma expérimental répliqué en blocs, permettant ainsi d'utiliser des outils statistiques adaptés pour quantifier les différences de paramètres d'intérêts dans un contexte d'hétérogénéité spatiale (Dutilleul, 1993). Afin d'augmenter la représentativité spatiale et éviter ainsi les biais d'observations, les inventaires basés sur des grilles d'échantillonnage représentent une approche essentielle (Schulze *et al.*, 2019). La combinaison de ces approches dans les chapitres 1 à 4 de cette thèse a permis une focalisation sur les effets de la dominance mycorhizienne et de les quantifier (Fig. 2). Néanmoins, des études réparties dans différents écosystèmes sont nécessaires pour généraliser les conclusions d'études de cas individuelles. Ainsi, la généralisation des résultats obtenus dans cette thèse nécessiterait un effort de réplication au sein d'écosystèmes et de climats différents, en priorisant des systèmes où des plantes à AM et à EcM coexistent. C'est le cas notamment dans certaines forêts tropicales d'altitude (p. ex. à l'ouest du Panama; Corrales *et al.*, 2016), au sein des écosystèmes méditerranéens (p. ex. au sud-ouest de l'Australie; Zemunik *et al.*, 2015), et dans certaines plantations forestières (p. ex. sur l'Île Victoria en Argentine; Simberloff *et al.*, 2002). En parallèle, des expériences contrôlant pour l'environnement (p. ex. IDENT; Verheyen *et al.*, 2016) représenteraient des systèmes à exploiter pour distinguer les effets et les interactions entre diversité végétale, dominance mycorhizienne et disponibilité en eau.

Les résultats présentés dans cette thèse renforcent l'idée qu'il est important d'intégrer la stratégie mycorhizienne comme un trait fonctionnel souterrain afin de mieux comprendre les processus écologiques (Laliberté, 2017; Freschet *et al.*, 2020). De plus, les études à large échelle gagneraient en précision en intégrant la stratégie mycorhizienne comme un trait fonctionnel continu, et en utilisant par exemple des mesures de colonisation racinaire par les champignons mycorhiziens

(chapitres 1 et 3). Les différences interspécifiques de colonisation pourraient être estimées à l'aide de bases de données regroupant des observations racinaires sur l'ensemble de la planète et qui sont désormais disponibles (Soudzilovskaia *et al.*, 2020). Cela permettrait de définir la stratégie mycorhizienne de façon plus précise au niveau de l'espèce dans des approches à large échelle (p. ex. Chapitre 4). En outre, les variations fonctionnelles au sein de guildes microbiennes supposées homogènes peuvent être assez conséquentes, il est donc important d'en tenir compte comme pour le cas des champignons mycorhiziens (Kivlin, 2020). Cette diversité intra-guilde pourrait être mieux appréhendée si l'on classait les champignons en fonction de leur stratégie d'histoire de vie ou, encore plus précisément, en mesurant leurs traits fonctionnels en laboratoire et en milieu naturel (Chagnon *et al.*, 2013; Fernandez *et al.*, 2019). De plus, le dosage de l'activité enzymatique au sein de l'environnement peut apporter une indication fonctionnelle directe des communautés microbiennes et de leurs activités (Baldrian, 2014; Talbot *et al.*, 2015; Courty *et al.*, 2016). Même si les différences de caractéristiques entre AM et EcM peuvent causer une divergence dans les processus écologiques, le degré auquel ces variations significatives se produisent, que ce soit entre plusieurs groupes ou au sein d'un même groupe, pourrait affecter à son tour le degré auquel les différents patrons se manifestent (Smith & Peay, 2020). La simplification en types mycorhiziens a permis de nombreuses avancées en écologie, mais un affinement est donc maintenant nécessaire pour aller au-delà.

La mise en commun de bases de données permet la généralisation des résultats à de larges échelles. Ainsi, il a été mis en évidence qu'au niveau mondial, le climat semble exercer un certain contrôle sur la distribution des différents types mycorhiziens (Steidinger *et al.*, 2019). Or, nombre d'études menées à l'échelle mondiale, qui comparent la distribution et certaines autres caractéristiques d'écosystèmes dominées par des espèces végétales à AM et à EcM, ne sont pas indépendantes des variations climatiques (p. ex. Allen *et al.*, 1995; Averill *et al.*, 2014). En effet, les plantes à EcM tendent à dominer les forêts froides, alors que les plantes à AM sont plus abondantes à de basses latitudes, y compris dans les forêts tropicales où le climat est plus chaud. L'étude de parcelles forestières voisines dominées par des stratégies mycorhiziennes différentes représente donc une approche nécessaire pour mieux comprendre les différences clés des mycorhizes dans leurs impacts sur le fonctionnement des écosystèmes et sur la dynamique végétale (Phillips *et al.*, 2013; Bahram *et al.*, 2015; Tedersoo *et al.*, 2020). Cette approche permet d'isoler un maximum d'effets confondants tels que le climat ou la nature de la roche-mère. De par cette approche, certains

résultats présentés dans cette thèse contredisent certaines connaissances en écologie mycorhizienne, pourtant jusqu'ici considérées comme classiques (voir chapitres 1, 2 et 4). Cela souligne donc l'importance de l'utilisation de systèmes d'étude où se retrouvent des sites dominés par différentes types mycorhiziens (Tedersoo *et al.*, 2020), et du fait de combiner les différentes approches disponibles pour étudier les écosystèmes terrestres, telles que l'observation attentive, l'expérimentation et la modélisation (Schulze *et al.*, 2019). Ainsi, les résultats de cette thèse soulèvent une question importante quant à l'échelle à laquelle l'impact de la dominance mycorhizienne est mesuré et mis en lien avec l'hétérogénéité environnementale.

3. La (co)dominance mycorhizienne : la question d'échelle et de l'hétérogénéité environnementale

Le choix de l'échelle est crucial à l'heure d'étudier les mécanismes responsables d'un phénomène écologique d'intérêt (Levin, 1992) et les données acquises doivent correspondre à l'échelle des processus étudiés (Ricklefs, 2004). Cependant, est-il possible de définir une échelle correcte pour l'étude de l'impact de la dominance mycorhizienne sur des processus tels que le stockage du carbone ou le maintien de la diversité végétale ?

L'étude de l'impact de la symbiose mycorhizienne se concentre habituellement sur l'individu dans le but de déterminer, par exemple, le sens et l'intensité des rétroactions plantes-sol (Ehrenfeld *et al.*, 2005). Aussi, ces études sont souvent réalisées sur les premiers stades de vie des plantes (p. ex. Chapitre 3) ou sur des espèces de petite taille comme les herbacées (p. ex. Wagg *et al.*, 2015), et ce, pour des raisons pratiques (Tedersoo *et al.*, 2020). Les résultats tirés de ces études sont parfois interprétés à la lumière des observations faites à plus grande échelle au niveau de la communauté végétale ou du biome. Ainsi, plusieurs hypothèses en ont découlé concernant les processus d'interactions biotiques, de stockage de carbone et de maintien de la diversité végétale. Or, les résultats de cette thèse démontrent qu'au niveau de la communauté forestière, ces hypothèses ne sont pas forcément confirmées. En écologie, la communauté est avant tout délimitée dans l'espace (Morin, 2011), et à cela peut s'ajouter le potentiel d'interaction entre les différents membres de celle-ci. En ce sens, cette thèse s'est concentrée à l'échelle de la parcelle forestière (~400 à 800 m^2), supposant une interaction potentielle entre les différents arbres au sein d'une même communauté. Cette échelle semble pertinente pour l'étude de la dominance mycorhizienne, car elle permet de mesurer des processus ayant un effet à l'échelle macroscopique en forêt, tout en intégrant parmi les

différentes parcelles une certaine hétérogénéité environnementale, qui peut fortement influencer le contexte écologique (Fig. 2). Toutefois, ce choix arbitraire d'échelle au niveau de la parcelle forestière limite la prise en compte d'une hétérogénéité plus fine. Or, il a par exemple été démontré que l'hétérogénéité au niveau local, voire même micro-environnemental, peut avoir une grande importance sur des processus écologiques tels que la décomposition de la litière (Bradford *et al.*, 2016; Bélanger *et al.*, 2019) ou les interactions biotiques (Toju *et al.*, 2016; Šťursová *et al.*, 2016).

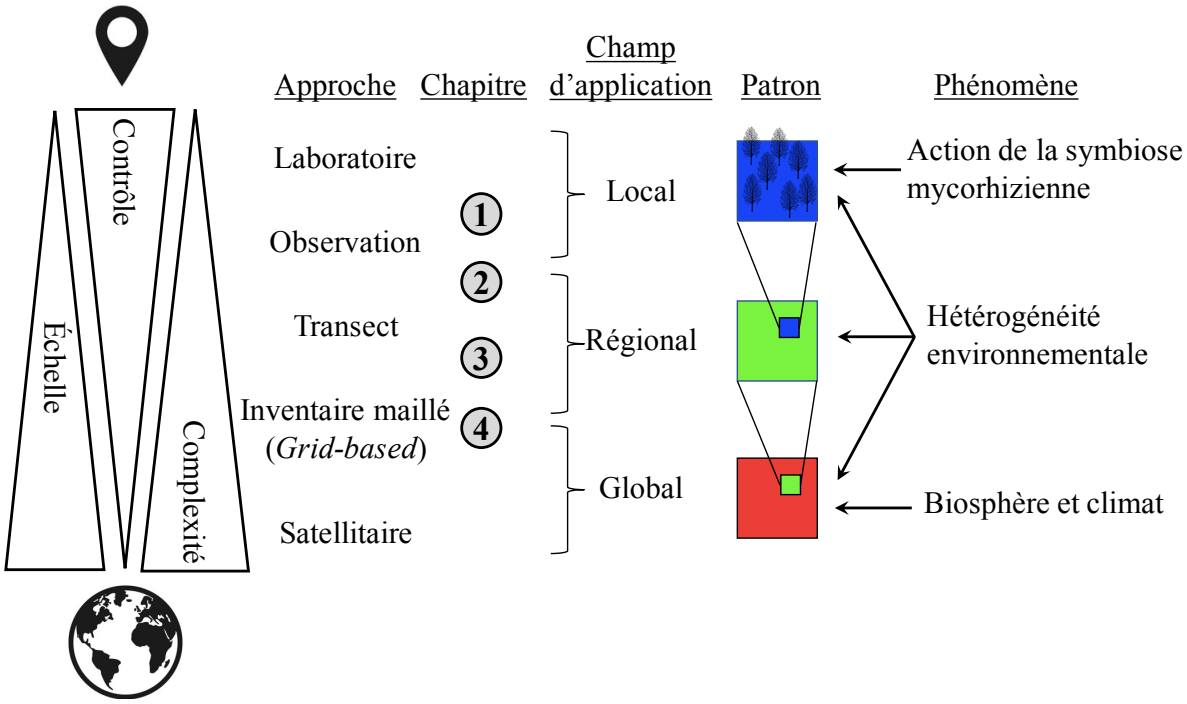

Figure 2. Une large diversité d'approches est disponible pour étudier l'impact de la dominance mycorhizienne à différentes échelles spatiales, dans un contexte d'hétérogénéité environnementale. Cette thèse présente l'action de la dominance mycorhizienne comme déterminante à l'échelle locale (parcelle forestière), or différents patrons peuvent être observables à des échelles plus larges. Par exemple, un biome pourrait être considéré comme AM (en rouge), mais plusieurs types mycorhiziens seraient présents à l'échelle régionale (systèmes mixtes, en vert), dû à la présence localement de certains peuplements EcM (en bleu). En outre, l'hétérogénéité environnementale peut être considérée à toutes ces échelles, impactant la compréhension des processus étudiés. Différentes approches permettent d'appréhender les processus à diverses échelles, puisque que plus l'échelle est large, plus les mécanismes sont complexes à intégrer et l'influence de covariables difficile à distinguer du phénomène d'intérêt. Les chiffres permettent de visualiser où se situent les chapitres de cette thèse en fonction des approches utilisées et à quelles échelles ils sont applicables.

De manière générale, l'hétérogénéité des facteurs biogéochimiques, au niveau spatial, est très élevée dans le sol (Hinsinger *et al.*, 2005; Baldrian, 2014), et influence grandement les communautés microbiennes, fongiques et mycorhiziennes (Chapitre 1; Wolfe *et al.*, 2007; Šturšová *et al.*, 2016). L'hétérogénéité à fine échelle des nutriments du sol permet quant à elle la coexistence d'espèces microbiennes (Ettema & Wardle, 2002; Baldrian, 2014), et pourrait ainsi favoriser la coexistence de plantes s'associant à différents groupes de champignons mycorhiziens (Read, 1991). De plus, le partitionnement des niches à petite échelle peut favoriser la coexistence de différents types mycorhiziens (Taylor *et al.*, 2014). Des études semblent révéler un certain antagonisme entre AM et EcM (Lodge, 1989; Lodge & Wentworth, 1990; Chen *et al.*, 2000), mais cela demeure encore mal compris et des évidences pointent vers le rôle primordial des conditions environnementales locales (Lambers *et al.*, 2008; Karliński *et al.*, 2010; Albornoz *et al.*, 2016). L'étude de plantes bimycorhiziennes (*dual-mycorrhizal*), qui développent des associations avec les champignons à AM et à EcM, présente un potentiel unique pour ce qui est de tester les interactions entre les champignons de ces deux types mycorhiziens. D'autre part, ces espèces bimycorhiziennes permettent de tester des hypothèses sur le rôle des facteurs abiotiques et biotiques dans la colonisation par les champignons à AM et à EcM, et ce sans l'effet confondant de l'espèce-hôte (Teste *et al.*, 2020). De plus, la différenciation de la niche entre les divers types de champignons mycorhiziens pourrait potentiellement accroître la concurrence au sein de ces derniers, tout en améliorant la coexistence de plantes appartenant à différents types mycorhiziens (Smith & Read, 2008). En retour, les écosystèmes présentant un mélange de stratégies mycorhiziennes pourraient créer un environnement plus diversifié et spatialement hétérogène (Mariotte *et al.*, 2018). Par conséquent, la coexistence de plusieurs types mycorhiziens pourrait potentiellement favoriser la diversité globale des arbres (Chapitre 4), mais cela reste à tester expérimentalement. Une meilleure compréhension des effets de l'hétérogénéité environnementale sur la biodiversité microbienne, dans le but d'en prédire la distribution et l'impact sur les processus écologiques, nécessitera désormais un effort dans la standardisation des échantillonnages et des avancées dans les approches modélisatrices utilisées (Lembrechts *et al.*, 2020).

Pour mieux quantifier de façon générale l'impact de la dominance mycorhizienne sur le fonctionnement de la biosphère et du climat, il sera essentiel de relier entre elles les études réalisées à différentes échelles (Fig. 2). Et afin de faire le pont entre les divers mécanismes et leurs patrons, l'utilisation de la télédétection semble être une approche prometteuse, car elle permet d'intégrer de

multiples échelles d'observation (Pettorelli *et al.*, 2018; Gamon *et al.*, 2020). Il est d'ores et déjà possible d'estimer à distance la proportion mycorhizienne à l'échelle locale (Fisher *et al.*, 2016), et il en est de même pour l'estimation du fonctionnement et de la diversité fonctionnelle des écosystèmes (Schweiger *et al.*, 2018). Non sans difficulté, la mesure des processus édaphiques semble elle aussi réalisable (Madritch *et al.*, 2020), ce qui permettrait ultimement de lier les compartiments aériens et souterrains d'un écosystème dans son ensemble et dans un contexte d'une hétérogénéité environnementale marquée.

La dominance mycorhizienne peut désormais être déterminée à plusieurs échelles (p. ex. système racinaire, parcelle, peuplement, biome). Pour mesurer son impact en forêt, l'échelle de la parcelle forestière (< 1 km^2) semble être un bon compromis car les effets des mycorhizes y persistent suffisamment pour pouvoir modifier le fonctionnement écosystémique. Cette échelle a permis de mettre en lumière l'importance des forêts qui ne sont pas dominées par un seul type mycorhizien (chapitres 1, 3 et 4). À l'échelle de la communauté d'arbres forestiers, les AM et EcM sont parfois en codominance (« forêts mixtes »). Ces forêts tendent à être ignorées dans les analyses, notamment car elles sont considérées comme peu abondantes (Brundrett, 1991), or ce n'est pas le cas (Chapitre 4). Les résultats de cette thèse soulignent par ailleurs l'intérêt de tester l'impact des mycorhizes en prenant en compte le gradient complet de proportion mycorhizienne (que ce soit AM ou EcM). Cependant, pour comprendre l'impact de la présence de plusieurs stratégies mycorhiziennes et de leurs interactions potentielles en forêt, il serait opportun de prendre en compte la composition du sous-bois. C'est par exemple le cas des sous-bois des forêts nordiques étudiées où se retrouvent de nombreuses espèces d'éricacées qui sont connues pour s'associer à des champignons à ErM (Smith & Read, 2008). Ce groupe de champignons dispose de caractéristiques saptrotrophiques encore plus développées que les autres champignons mycorhiziens et les éricacées possèdent une litière très récalcitrante (Tedersoo & Bahram, 2019). Les ErM ont donc le potentiel d'avoir un impact important et unique dans le cycle du carbone et des nutriments (Michelsen *et al.*, 1996; Clemmensen *et al.*, 2015), même si leur biomasse est généralement moins grande dans les écosystèmes forestiers que celle associée avec les EcM ou les AM. De plus, les ErM sont plus rarement étudiées, bien que leur importance, notamment au sein des écosystèmes nordiques, soit potentiellement considérable (Smith & Read, 2008; Tedersoo *et al.*, 2020; Vohník, 2020).

Il a été observé que la diversité des plantes est liée à la présence de multiples stratégies d'acquisition des nutriments (Zemunik *et al.*, 2015). Ainsi, il n'est pas étonnant que les forêts mixtes en stratégie mycorhizienne puissent être plus riches que les forêts dominées par un seul type mycorhizien. Cela pourrait potentiellement s'expliquer par une dynamique non-équilibrée qui favoriserait donc la diversité (Chesson, 2018). En effet, la grande abondance de forêts dominées à plus de 90% par des AM ou des EcM (Chapitre 4) serait possiblement la conséquence d'états stables alternatifs de la dynamique forestières, comme cela a été suggéré au sujet des forêts de l'Est des États-Unis (Averill, 2020). De plus, il semblerait qu'il y ait un avantage pour les systèmes mixtes dans la promotion de certains processus écologiques tels que la productivité végétale (Mariotte *et al.*, 2018; Martin-Guay *et al.*, 2018; Kambach *et al.*, 2019), avec un potentiel de sur-rendement (*overyielding*) des forêts plus riches en espèces en comparaison des monocultures (Ammer, 2019). En outre, les forêts mixtes sont des systèmes cruciaux pour la migration des plantes, offrant une zone de transition où les conditions abiotiques et la présence de microbes bénéfiques sont potentiellement adéquates pour un plus grand nombre d'espèces (Chapitre 3). L'étude des forêts mixtes représente ainsi une avenue capitale pour la compréhension des processus liés à l'hétérogénéité environnementale et pour la compréhension de la complémentarité écologique. L'aménagement forestier pourrait y gagner à prendre davantage en compte la mixité en terme de stratégies mycorhiziennes, voire même à l'intégrer à des approches agroforestières et d'ingénierie écologique (Chagnon & Brisson, 2017; Policelli *et al.*, 2020; Santana *et al.*, 2020), afin de soutenir davantage de services écosystémiques. Enfin, les propriétés biogéochimiques uniques des forêts mixtes pourraient promouvoir la résistance et la résilience des écosystèmes forestiers dans un futur désormais mêlé d'une grande incertitude quant aux moyennes et aux extrêmes de précipitations et de températures.

4. Épilogue

Les différents chapitres de cette thèse démontrent que la stratégie mycorhizienne des arbres au sein des forêts est un facteur local déterminant des processus écologiques (Fig. 1). En tant que tel, le type mycorhizien des arbres devrait être pris en compte dans les études futures afin d'accroître notre capacité à prévoir la dynamique du carbone et le fonctionnement des écosystèmes, mais aussi pour une meilleure gestion des forêts. Par exemple, il a été proposé que la plantation d'arbres à large échelle permettrait de séquestrer une grande partie du carbone émis annuellement dans l'atmosphère par les activités humaines (Bastin *et al.*, 2019) or, l'identité des espèces à planter doit

être prise en compte de par leurs caractéristiques propres et notamment leur stratégie d'acquisition des nutriments. En effet, en influençant les processus locaux dans le sol, le type mycorhizien d'espèces d'arbres ayant colonisé naturellement ou ayant été plantés est un facteur clés dans le stockage de carbone dans le sol à court, moyen et long terme (Clemmensen *et al.*, 2013; Craig *et al.*, 2018; Friggens *et al.*, 2020). Au sein de la forêt tempérée du Nord-Est de l'Amérique, le remplacement de l'érable à sucre par le hêtre à grandes feuilles a potentiellement des conséquences profondes sur les communautés microbiennes souterraines et notamment les communautés fongiques. Par rapport aux érablières, le sol dans les hêtraies étudiées au Chapitre 1 soutient une communauté fongique différente, considérablement plus riche en champignons à EcM et, cette communauté dégrade la matière organique plus rapidement (Chapitre 2). À court terme (quelques années), le remplacement des érablières par des hêtraies pourrait donc avoir un effet négatif sur les stocks souterrains de carbone organique. Cependant, la quantité de carbone accumulée dans les horizons organiques est plus élevée dans les hêtraies, dévoilant un effet positif sur les stocks de carbone à moyen terme (quelques dizaines d'années), comme dans de nombreuses autres forêts dominées par les EcM à travers la planète (Soudzilovskaia *et al.*, 2019). Pour élucider cet apparente contradiction entre stocks de carbone et décomposition de la matière organique, davantage de connaissances sur l'impact de la production de litière, la faune du sol et l'humidité seront nécessaires. En outre, les écosystèmes dominés par les EcM tendent à être plus susceptibles aux changements environnementaux (Jo *et al.*, 2019; Pugnaire *et al.*, 2019). Ainsi, l'impact de la dominance mycorhizienne sur la séquestration de carbone en forêt à moyen-long terme reste très incertain. La métagénomique représente un outil diagnostique indispensable afin de suivre et prédire l'impact des changements environnementaux, tel que le réchauffement climatique, sur les communautés microbiennes souterraines impliquées dans la régulation du stockage du carbone.

Outre la déstabilisation des écosystèmes forestiers, les changements climatiques permettraient, en théorie, une augmentation de la distribution de la forêt tempérée vers les pôles grâce au réchauffement moyen de la température (Corlett & Westcott, 2013). Cependant, l'établissement de l'érable à sucre plus au Nord en forêt boréale semble compromis. L'érable à sucre domine largement les peuplements forestiers à la limite nordique de la forêt tempérée, mais en forêt boréale la combinaison de facteurs abiotiques et biotique du sol y est néfaste à sa survie et à sa croissance (Chapitre 3). Les champignons à AM qui sont nécessaires à la bonne performance de l'érable à sucre devront être pris en compte dans un potentiel plan de migration assistée. L'inoculation des

sites de migration en forêt boréale pourrait se faire avec du sol de l'écotone tempéré-boréal qui lui sont bénéfiques (Chapitre 3), ce qui serait potentiellement suffisant à la réussite d'une telle opération d'un point de vue technique. Cependant, cette migration nordique assistée se ferait au dépend de la forêt boréale et de sa biodiversité. De plus, les grandes quantités de carbone séquestré sous forme organique depuis des centaines d'année dans les sols boréaux pourraient être relâchées dans l'atmosphère après exposition aux organismes décomposeurs associés aux érablières. Au contraire, l'avenir de nos forêts, qui sont toutes sous l'influence de perturbations anthropiques, résiderait dans leur diversité. Les forêts composées de différentes espèces d'arbres sont connues pour favoriser la stabilité de nombreux processus écologiques telle que la productivité primaire (Jucker *et al.*, 2014). En foresterie, la plantation de mélanges d'espèces est considérée comme l'une des principales options pour réduire les risques liés au dérèglement climatique (Bauhus *et al.*, 2017). Cependant, la promotion de la diversité devrait aussi se faire au niveau souterrain, où la coexistence de plusieurs stratégies d'acquisition des nutriments pourrait agir comme un moteur de la diversité végétale et des services écosystémiques associés (Chapitre 4). L'étude des forêts présentant un mélange de plusieurs stratégies mycorhiziennes est parfois négligée car elles sont considérées comme moins courantes, mais cela ne semble pas être le cas à l'échelle de la parcelle forestière, du moins à travers l'Amérique du Nord (Chapitres 1 à 4). En outre, même si la diversité mycorhizienne peut être déterminée à plusieurs échelles, cette thèse souligne l'importance de considérer l'impact des mycorhizes et de la mixité des stratégies souterraines d'une forêt sur les processus écologiques à l'échelle locale de la parcelle forestière.

Dans son ensemble, cette thèse améliore la connaissance de la biodiversité et de la dynamique microbienne des sols de forêts dominées et codominées par différents types mycorhiziens, permettant ainsi de mieux appréhender l'importance de la symbiose mycorhizienne dans les écosystèmes forestiers. La combinaison de différentes approches basées sur la description, l'expérimentation et la modélisation a permis d'innover dans un domaine de l'écologie encore peu exploré. La fameuse « boîte noire » que constitue le compartiment souterrain des écosystèmes terrestres se dévoile à mesure qu'augmente la compréhension du rôle des interactions plantes-sols dans le fonctionnement des écosystèmes et dans les services naturels qu'ils nous rendent. De plus, la diversité des approches choisies dans cette thèse fortifie les acquis avec l'amélioration des connaissances spécifiques utiles pour la gestion et la conservation de forêts telles que les érablières, qui sont d'une importance économique et culturelle toute particulière au sein de la société

québécoise. Cette thèse a permis de démontrer que les interactions souterraines entre plantes, sols et microbes sont à l'origine de nombreux processus écologiques, mais qu'elles doivent néanmoins être quantifiées à des échelles pertinentes. Les différences éco-physiologiques clés entre AM et EcM peuvent se traduire par des impacts locaux de la dominance mycorhizienne sur les communautés forestières et leurs réponses face aux conditions environnementales. Ainsi, il est primordial d'intégrer les mycorhizes dans les modèles de fonctionnements écosystémiques et globaux (Treseder *et al.*, 2012; Brzostek *et al.*, 2017). Finalement, cette thèse met en évidence une certaine vulnérabilité des écosystèmes forestiers face aux pressions anthropiques dont les changements climatiques, mais elle nous permet par ailleurs d'améliorer nos capacités d'adaptation face à ces changements qui sont de plus en plus sévères.

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