UNIVERSITÉ DU QUÉBEC EN OUTAOUAIS

LEGS DES COUPES FORESTIÈRES SUR LE SOL ET LES PLANTES EN FORÊT TEMPÉRÉE

THÈSE PRÉSENTÉE COMME EXIGENCE PARTIELLE DU DOCTORAT SUR MESURE 2080

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

AI, Aménagement générant une forêt de structure inéquienne

AÉ, Aménagement générant une forêt de structure équienne

FRQNT, Fonds de recherche du Québec – Nature et technologies

ECM, Ectomycorhize

CMA, Champignon mycorhizien arbusculaire

PCR, Réaction de polymérisation en chaîne

q-PCR, PCR quantitative

MO, Matière organique

Ratio C/N, ratio carbone sur azote

Ratio C/B, ratio champignon sur bactérie

Ca, Calcium

Ca^{2+}, Cation calcium

K, Potassium

K^{+}, Cation potassium

P, Phosphore

Al, Aluminium

Al^{3+}, Cation aluminium

Mg, Magnésium

Mg^{2+}, Cation magnésium

Na, Sodium

Na^{+}, Cation sodium

O, Oxygène

N, Azote

NO^{3-}, Ion nitrate

NH^{4+}, Ion ammonium

C, Carbone

CO^{2}, Dioxyde de carbone

H, Hydrogène

pH, Potentiel hydrogène

LISTE DES SYMBOLES ET DES UNITÉS

°C, Degré Celcius

m^2, Mètre carré

%, Pourcentage

RÉSUMÉ

Dans l'est de l'Amérique du Nord, les forêts tempérées sont aménagées de manière à générer des forêts sous aménagement inéquienne (AI) ou équienne (AÉ). Cependant, les connaissances concernant les effets temporels de ces types d'aménagements forestiers sur les sols et la dynamique de la végétation du sous-bois demeurent limitées. Le premier objectif de cette thèse était de comparer la diversité alpha et beta (spécifique, fonctionnelle et phylogénétique) des communautés de plantes dans des peuplements sous AI et AÉ le long d'une chronoséquence après coupe. Le deuxième objectif était d'analyser la variation des propriétés physico-chimiques du sol, des débris ligneux et de la productivité du sol après coupe. Le troisième objectif était d'évaluer les effets de la coupe sur les communautés microbiennes du sol, avec un regard particulier sur la diversité des champignons. Le quatrième objectif était de comparer différents indices communément utilisés pour mesurer la diversité des communautés dans les écosystèmes forestiers en utilisant des simulations théoriques. L'hypothèse générale de cette thèse est que les coupes en AÉ, en modifiant plus fortement les conditions biotiques et abiotiques, vont entraîner des effets plus importants à court, moyen et long terme sur les plantes, les propriétés du sol et les microorganismes du sol que les coupes en AI. Pour répondre à nos objectifs, différentes variables ont été mesurées dans des forêts non-aménagées et dans des forêts aménagées (AÉ et AI) le long d'une chronoséquence de coupe (< 5 ans, 15 ans, 30 ans après coupe) dans 189 parcelles. Nous avons mesuré la composition et la diversité (taxonomique, fonctionnelle et phylogénétique) des plantes du sous-bois, l'abondance des débris ligneux, plusieurs propriétés physico-chimiques du sol (horizons organique et minéral), l'abondance des champignons et des bactéries et la composition et diversité des champignons du sol (dissimilarité entre communautés, phylogénétique et proportion des guildes fonctionnelles et des modes trophiques). Une expérience en serre a également été réalisée afin d'évaluer la croissance de semis de trois espèces d'arbres dans des sols issus des forêts non-aménagées et de forêts après coupe. L'approche théorique en lien avec notre quatrième objectif a simulé une situation typique d'évaluation de la diversité en comparant différentes mesures de diversité (richesse, uniformité, disparité et composantes spatiales alpha et beta) obtenues dans différents sous-échantillons de communautés théoriques connues. Dans les forêts sous AÉ et AI, la diminution significative de la diversité phylogénétique des plantes de la state de sous-bois mesurée à court terme persistait 30 ans après coupe. Cette perte de diversité était associée entre autres à la persistance de plantes avec des traits fonctionnels particuliers (*e.g.*, très petites graines) et de plantes plus anciennes qui se reproduisent par spore. Seules les forêts non-aménagées étaient associées à une forte densité forestière, un couvert d'herbacées abondant et une grande diversité de plantes de sous-bois. Les coupes ont entrainé une diminution de l'abondance de certaines classes de bois mort et de la litière. Peu de temps après la coupe (< 5 ans), plusieurs propriétés du sol différaient significativement de celles dans les forêts non-aménagées. Bien qu'un rétablissement de la dynamique temporelle de certaines propriétés chimiques du sol (*e.g.*, le pH, l'azote minéralisable, le N total, le ratio C/N et l'Al^{3+}) ait été mesuré à plus long terme (> 30 ans après coupe), d'autres propriétés (*e.g.*, l'abondance de bois mort) continuaient d'être affectées significativement. Une augmentation de l'abondance des bactéries, de la dissimilarité dans la communauté des champignons et de la proportion de champignons

pathogènes et parasitaires au détriment des symbiotiques a été mesurée peu de temps après coupe de plus forte intensité (AÉ). La structure et la densité forestière ainsi que le pH du sol sont apparus comme des déterminants importants afin de comprendre le rôle de la coupe forestière sur les communautés microbiennes du sol. L'analyse théorique des mesures de diversité a démontré l'importance d'utiliser la diversité phylogénétique ou fonctionnelle ainsi que les deux composantes spatiales (alpha et beta) afin de détecter les modifications engendrées par la récolte forestière dans les communautés végétales. Cette thèse a montré l'importance de considérer les forêts non-aménagées dans les études visant à quantifier les effets temporels de différents types de coupes sur la biodiversité et les fonctions écosystémiques dans les forêts aménagées.

Mots clés : diversité, sol, plantes, microbiome, coupe, forêt tempérée

INTRODUCTION GÉNÉRALE

Problématique

Les forêts sont des écosystèmes terrestres essentiels qui couvrent plus de 30% de la surface terrestre et qui fournissent de nombreux services clés tels que le carburant, les matériaux de construction, la séquestration du carbone (C), la conservation de la biodiversité et la régulation de la qualité de l'eau (FAO & UNEP, 2020). Les plantes de ces forêts sont essentielles au maintien d'un bon nombre de ces services (Augusto *et al*., 2003; Lorenz *et al*., 2006). Les sols forestiers, avec leur microbiome, soutiennent les processus cruciaux de flux de nutriments et d'énergie tout en régulant la productivité primaire (Read & Perez-Moreno, 2003; Uroz *et al*., 2016). Les sols forestiers constituent aussi un important puits de C (Lladó *et al*., 2018).

Il est donc d'intérêt planétaire d'avoir des écosystèmes forestiers en santé. Or, la biosphère fait face à un taux exceptionnellement élevé d'extinction des espèces en raison de perturbations anthropiques croissantes (Pereira *et al*., 2010; Pimm & Raven, 2017). De grandes surfaces forestières peuvent perdre de leur efficacité à séquestrer du C suite à des perturbations d'origine anthropique comme l'aménagement forestier (Gauthier *et al*., 2015). De plus, les forêts décidues tempérées de l'est de l'Amérique du Nord ne font pas exception à la liste des écosystèmes forestiers dont les sols sont vulnérables à l'exploitation forestière (Marshall, 2000; Cleavitt *et al*., 2018).

En forêt décidue tempérée, plusieurs travaux suggèrent que les coupes peuvent avoir des effets à plus ou moins long terme sur les propriétés physiques et chimiques des sols (e.g., Tritton, 1987; Federer *et al*., 1989; Dyck *et al*., 2012). De plus, il est connu que les coupes

forestières peuvent altérer de façon drastique la diversité des communautés de plantes et de microorganismes du sol (Hartmann *et al*., 2012; Bell *et al*., 2016). Or, ces deux groupes taxonomiques sont essentiels au fonctionnement des écosystèmes forestiers, notamment en contribuant au recyclage et à l'entreposage des nutriments (Elkins & Whitford, 1982; Augusto *et al*., 2003; Lorenz *et al*., 2006). Comme la grande majorité des écosystèmes forestiers est aménagée pour la récolte (FAO 2007; Likens & Franklin, 2009) et que, face aux changements globaux, une pression supplémentaire est mise sur la ressource forestière pour substituer à d'autres produits plus polluants, il est essentiel de connaître et de minimiser les impacts écologiques négatifs de l'exploitation forestière. Ainsi, il apparait légitime de poser la question suivante : comment aménager les forêts tout en minimisant les impacts négatifs de la récolte sur les sols, les plantes et les microorganismes du sol?

La majorité des forêts tempérées sont aménagées à l'aide de deux systèmes sylvicoles, l'aménagement équienne (AÉ, structure d'âge des arbres homogène à l'échelle du peuplement) et l'aménagement inéquienne (AI, structure d'âge hétérogène) (Nolet *et al*., 2018). Dans les forêts feuillues de l'est de l'Amérique du Nord, l'AI est l'approche la plus communément adoptées par les aménagistes forestiers. Dans une moindre mesure, l'AÉ est aussi préconisé. Sur la base d'une revue de la littérature, Nolet *et al*. (2018) ont montré que la perception selon laquelle l'AI est mieux adaptée que l'AÉ pour maintenir la diversité et les processus écologiques des forêts n'est pas bien documentée. Les auteurs ont fait valoir que les deux approches seraient nécessaires à l'échelle du paysage pour minimiser les impacts écologiques négatifs des coupes sur les services écosystémiques fournis par les forêts. Des résultats contradictoires rapportés dans la littérature suggèrent que des travaux supplémentaires sont nécessaires pour évaluer les effets à long terme de ces différents

systèmes sylvicoles sur les fonctions des forêts feuillues tempérées (Thiffault *et al*., 2011; Hume *et al*., 2018; Nolet *et al*., 2018).

Ainsi, la présente thèse s'intéresse à étudier les effets de la coupe forestière dans un contexte d'AÉ et d'AI sur les plantes, plusieurs propriétés du sol et les communautés microbiennes du sol, ainsi que les mécanismes qui régulent ces effets. Pour mesurer la direction et l'importance des effets, deux éléments nous apparaissent particulièrement importants : 1) le temps depuis la coupe, et 2) la prise en compte de forêts témoins non-aménagées. De plus, il est primordial de mieux comprendre les échanges de matière entre le sol et les plantes.

Les plantes et le microbiome du sol, des liens entre ciel et terre

Il est difficile de dissocier le rôle des plantes de ceux du microbiome du sol et des propriétés physico-chimiques du sol, étant donné leurs nombreuses interactions dans l'écosystème forestier. Ainsi, la présente section s'attarde à décrire très brièvement ces interactions afin de pouvoir, par la suite, s'interroger sur les effets écologiques potentiels de la coupe forestière.

Le bois mort, la litière et les racines des végétaux

Premièrement, le CO_2 de l'air, qui est fixé par les végétaux, entre dans les sols à partir de la litière aérienne (*i.e.*, les feuilles qui tombent), le bois mort et les racines (*e.g.*, la rhizodéposition). La litière aérienne et le bois mort sont, entre autres, une source d'énergie et de nutriments pour plusieurs organismes qui habitent le sol (Lambert *et al*., 1980; Feller, 2003), ainsi qu'un habitat procurant différentes conditions micro-climatiques pour la

croissance des plantes et d'autres organismes forestiers (Xiong et Nilsson, 1999; Karst *et al*., 2005). Par exemple, le bois mort, qui emmagasine de l'eau et des nutriments, procure des conditions facilitant la germination et la survie de graines ou de propagules de nombreuses espèces floristiques. De plus, la concentration des cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) dans le sol va varier, entre autres, selon la fréquence et l'importance des apports de matière organique (MO) provenant des plantes (*e.g.,* la litière et le bois mort), du lessivage, ainsi que des conditions microclimatiques du sol. Les propriétés biochimiques de la litière et du bois mort (*e.g.,* composition en cellulose, lignine, sucres, protéines et tanins), propre à chaque espèce, influencent grandement leur taux de décomposition (Berg & McClaugherty, 2008). Ainsi, certaines espèces en forêt tempérée, comme le hêtre à grandes feuilles (*Fagus grandifolia*), sont connues pour avoir de la litière acide et à faible vitesse de décomposition (Neirynck *et al*., 2000; Aubert *et al*., 2004; Molder *et al*., 2008).

Les racines des arbres ont aussi un rôle clé pour le sol et son microbiome. En forêt boréale, Clemmensen *et al*., (2013) ont déterminé que plus de la moitié du C accumulé dans l'humus forestier proviendrait de la décomposition des racines. Le C provenant des exsudats racinaires est particulièrement important pour stimuler la croissance des hyphes des champignons symbiotiques (Bécard & Piché, 1989; Clemmensen *et al*., 2015). On estime que jusqu'à 21% des produits de la photosynthèse sont relâchés dans le sol sous forme d'exsudats racinaires composés, entre autres, de substances carbonées, d'acide aminées, d'enzymes, d'hormones, de H^{+}, d'ions inorganiques, d'eau et d'électrons (Bertin *et al*., 2003; Prescott & Grayston, 2013). Les exsudats racinaires, variant selon l'âge de la plante, peuvent altérer les propriétés chimiques et les conditions abiotiques du sol (Bertin *et al*., 2003, Singh *et al*., 2017) ainsi que son microbiome (Chapparro *et al*., 2014). Les racines

fines des plantes influencent aussi indirectement le microbiome en augmentant la macroporosité et la disponibilité de l'oxygène du sol (Tivet *et al*., 2013).

Le microbiome du sol

Le microbiome du sol forestier inclut plusieurs organismes, dont les bactéries et les champignons. Il existe de multiples interactions intraspécifiques et interspécifiques au sein du microbiome et celles-ci sont dites responsables du filtre fin des différences observées dans les communautés microbiennes (Wu *et al*., 2018). La surface des sols forestiers peut être dominée par des Proteobactéries, des Acidobactéries et des Actinobactéries (Kumar *et al*., 2017; Zhang *et al*., 2018). Les champignons du sol peuvent être divisés en trois modes trophiques qui sont basés sur les stratégies d'acquisition de C dans le sol, les champignons symbiotiques, saprophytiques et parasitiques/pathogènes (Nguyen *et al*., 2016a). Chacun de ces modes trophiques a un rôle dans différentes parties du sol ; les saprophytes colonisent massivement la litière, tandis que les symbiotiques vont échanger avec l'arbre de l'eau et des nutriments en retour de sucres générés par la photosynthèse (Sterkenburg *et al*., 2018). Les champignons symbiotiques sont aussi reconnus pour leurs capacités à emmagasiner le C dans le sol, contrairement à plusieurs espèces de champignons saprophytiques ou parasitiques qui, eux, entraînent un net relâchement de CO_2 dans l'atmosphère (Pan *et al*., 2011; Clemmensen *et al.*, 2013; Keller *et al*., 2021). Baldrian (2017) a décrit que les champignons ectomycorhiziens (ECM) sont responsables de près de la moitié du C organique dissout dans les sols en forêts tempérées et boréales. Chez les saprophytes, essentiels à la décomposition, les différentes guildes de champignons peuvent être associées aux ressources qu'elles décomposent (*e.g.,* le bois mort, la litière, les feuilles ou d'autres molécules directement dans le sol) (Nguyen *et al*., 2016a).

Le destin des sols forestiers

Dans les sols, la dynamique de formation et de décomposition de la MO en forêts feuillues est assez complexe (Natelhoffer & Fry, 1988). Le C dans les sols forestiers peut être rapidement relâché dans l'atmosphère sous forme de CO_2 suite à la décomposition de la MO fraîche et facilement décomposable. À l'opposé, le C peut être stabilisé à long terme dans les sols sous la forme de substances humiques complexes (Martin *et al*., 2011; Augusto *et al*., 2015). Les champignons et les bactéries du sol sont responsables de la transformation, de la stabilisation et du stockage du C organique dans les sols (Kalbitz *et al*. 2000; Baldrian 2017). Les substrats, les enzymes et les produits de ces microorganismes régulent l'avenir de la MO dans le sol (Malik *et al*., 2016) dépendamment des conditions microclimatiques du milieu, de l'accessibilité physique à la MO (Tivet *et al*., 2013) et de sa récalcitrance qui peut être appréciée par différentes variables (*e.g.,* ratio C/N, contenu en lignine et polyphenols) (Lauber *et al*., 2008; Kraus *et al*., 2003). De plus, l'importance du C utilisé par les microorganismes pour synthétiser leurs propres biomasses est de plus en plus reconnu dans la dynamique de la MO (Kallenbach *et al*., 2016; Keller *et al*., 2021).

De même que le C, l'azote (N) libéré lors de la décomposition de la matière organique peut être stabilisé ou utilisé dans les sols. Le N du sol se retrouve principalement sous forme organique. Les plantes vont généralement prélever le N sous une forme inorganique suite à sa minéralisation par les bactéries (Schimel & Bennett, 2004). Sans entrer dans les détails, on peut mentionner que la dépolymérisation, l'ammonification, la nitrification et la dénitrification sont des processus importants dans le cycle de l'azote en sol forestier (Barton *et al*., 1999) et que dans ces écosystèmes, la principale source d'azote disponible

pour les plantes est l'ammonium (Nadelhoffer *et al*., 1983; Larcher, 2003; Vernimmen *et al.*, 2007).

Ensemble, les plantes et le microbiome du sol vont produire et transformer une importante proportion de la MO des sols forestiers (Kallenbach *et al*., 2016). Généralement, un ratio C/N plutôt bas dans le sol traduit une utilisation rapide de la MO et un retour rapide des éléments nutritifs pour les organismes du sol, ainsi qu'une forte activité microbienne. Les flux de la MO dans le sol sont aussi grandement influencés par la structure du sol. Le microbiome (notamment les champignons mycorhiziens qui produisent de la glomaline) et les racines des plantes influencent grandement l'agrégation des particules du sol et sa structure (Tivet *et al*., 2013; Kallenbach *et al*., 2016).

Le sol, un socle pour le microbiome et les plantes

Les nutriments du sol sont utilisés sous différentes formes pour assurer le fonctionnement des plantes et du microbiome (*e.g*., métabolisme basal et activité enzymatique). Les sols ayant une forte capacité d'échange de cations et une forte saturation en bases (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) sont considérés comme riches et favorables à la productivité forestière (Organisation des Nations Unies pour l'alimentation et l'agriculture, 2010). Les propriétés physiques du sol (*e.g.*, la texture et la stabilité des agrégats) sont reconnues pour influencer les conditions hydriques (*e.g.,* la capacité de rétention de l'eau), la croissance et la nutrition des plantes (Brady & Weil, 2013). Comme les plantes, le microbiome du sol a des conditions optimales de croissance qui dépendent aussi de l'humidité du sol, du pH et de la concentration en oxygène et en nutriments.

Le pH a un rôle crucial dans les sols forestiers. En forêt feuillue tempérée, l'acidification du sol est connue pour entraîner le lessivage de cations, ainsi que l'accumulation de minéraux (*e.g.,* Al^{3+}) pouvant devenir toxique pour les plantes et le microbiome (MAAARO, 2006). Sur un gradient environnemental ou à l'échelle continentale, le pH est connu pour jouer un rôle majeur sur la composition (Lauber *et al*., 2009; Bulgarelli *et al*., 2012; Tedersoo *et al*., 2014) et la diversité (*i.e.* plus de diversité bactérienne sur sol neutre) (Fierer & Jackson, 2006; Rousk *et al*., 2010) du microbiome du sol. La diminution du pH des sols forestiers est aussi associée à une réduction de la diversité des plantes et de l'abondance d'espèces rares (Barbier *et al*., 2008).

Un équilibre plante-sol fragile ?

En somme, il existe de multiples interactions dynamiques entre les plantes, les microorganismes du sol et les conditions physiques et chimiques dans les sols. Quels sont les effets du retrait des arbres (*i.e.,* la litière, le bois mort, les exsudats racinaires) et de la modification des conditions abiotiques suite aux coupes forestières de différente intensité sur les sols et les plantes ? Pendant combien de temps ces effets peuvent-ils se manifester ? Voilà des questions auxquelles cette thèse tentera de répondre.

Effets des coupes qui génèrent des structures inéquienne ou équienne en forêt feuillue tempérée sur les plantes, le microbiome et les propriétés physico-chimiques du sol

Le régime de perturbation naturelle par trouées caractérise les forêts feuillues tempérées d'Amérique du Nord (Runkle, 1985). Ainsi, dans ces écosystèmes, les aménagements qui génèrent des forêts de structure inéquienne sont fortement utilisés. L'utilisation d'un aménagement plus intensif, qui génère des forêts de structure équienne, bien que moins intuitive, pourrait cependant avoir l'avantage de perturber moins fréquemment le paysage.

Il apparaît donc important de bien connaître les effets de ces deux types d'aménagements en forêt feuillues tempérées.

Les effets directs de l'aménagement forestier

L'AI est caractérisée par des petites trouées qui augmentent la disponibilité de la lumière et affectent d'autres conditions microclimatiques au sol (Beaudet *et al*., 2004). Suite à ce type d'aménagement, la simplification de la structure forestière (Hale *et al.*, 1999), ainsi que la diminution de la quantité de bois mort selon leur stade de décomposition (Angers *et al*., 2005) ont été observées, par rapport à des forêts témoins. L'AI est une perturbation qui peut aussi modifier les propriétés physico-chimiques du sol ainsi que la composition et la diversité des communautés microbiennes du sol et végétales. Par exemple, l'AI, connu pour favoriser l'envahissement des peuplements par le hêtre à grandes feuilles en sous-étage (Roy & Nolet, 2018), pourrait nuire à plusieurs espèces végétales (Mölder *et al.,* 2008; Gasser *et al*., 2010).

D'un autre côté, l'AÉ crée des grandes ouvertures modifiant de manière plus importante que l'AI la disponibilité de la lumière et les conditions microclimatiques du sol (Moroni & Zhu, 2012). Aussi, l'AÉ peut contribuer à diminuer largement la densité forestière et la diversité en structure forestière, à réduire l'abondance de bois mort (Humphery, 2014) et à favoriser la régénération d'espèces d'arbres intolérantes à l'ombre. L'AÉ est une perturbation qui peut ainsi avoir des effets à court et moyen terme plus importants que l'AI sur les plantes de sous-bois, le microbiome et les variables physico-chimique du sol.

La présente thèse s'intéresse à l'effet de différents types de coupes forestières (*i.e.,* AÉ *vs* AI) sur plusieurs variables pouvant être directement ou indirectement modifiées par celle-ci, le long d'une chronoséquence de coupe (Figure 1).

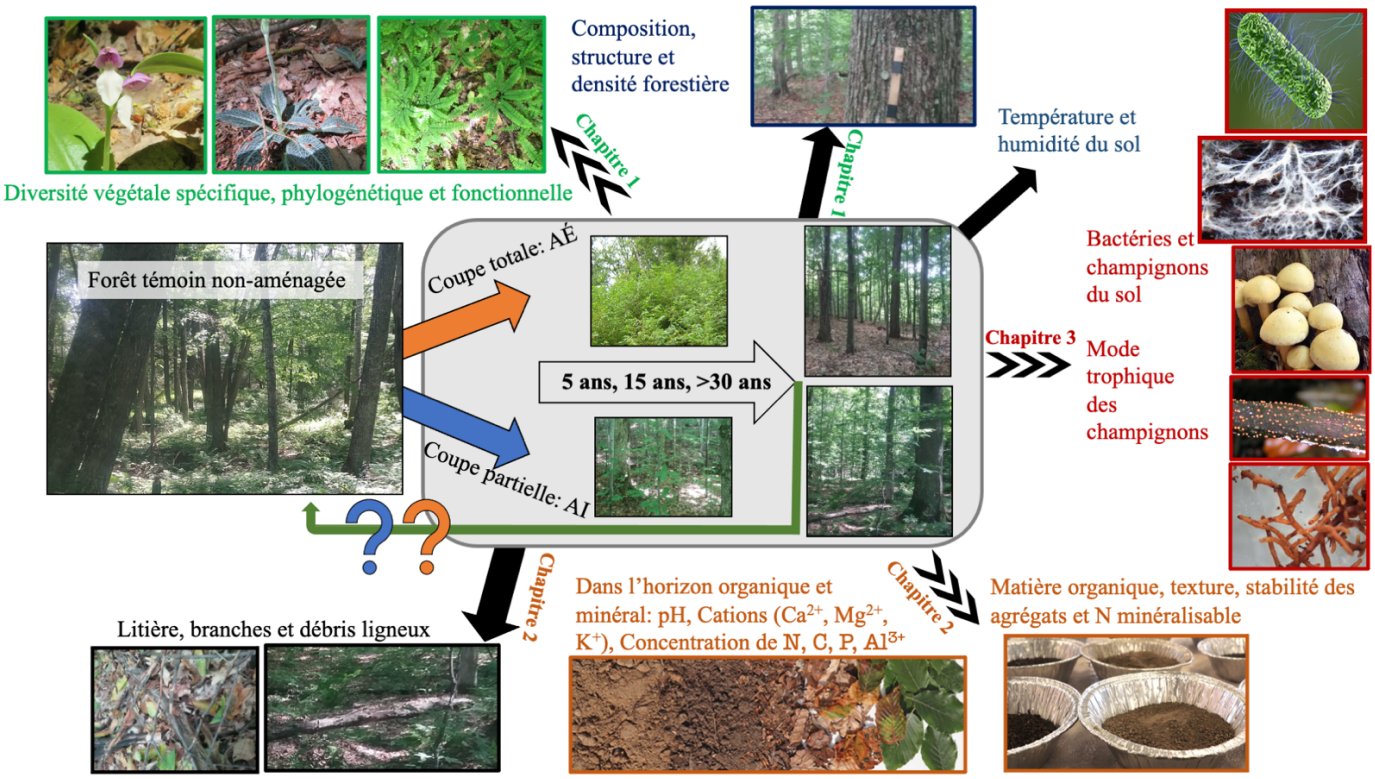

Figure 1. Représentation des différentes variables pouvant être affectées par les coupes forestières (*i.e.*, aménagements entraînant des forêts de structure équienne (AÉ) ou inéquienne (AI)) le long d'une chronoséquence de coupe, comparativement à des forêts non-aménagées. Les flèches pleines et les flèches discontinues représentent des variables qui sont anticipées comme étant, dans l'ordre, directement et indirectement modifiées par la coupe forestière. Les chapitres 1, 2 et 3 s'intéressent à chacune de ces variables, ainsi qu'à certaines de leurs interactions. La photo des différents horizons de sol est tirée de Walser et al. (2018).

Les effets de l'aménagement forestier sur les plantes de sous-bois

La transmission de la lumière, la composition du couvert forestier, la concentration des nutriments dans le sol, la quantité et l'état du bois mort, ainsi que la quantité et la composition des feuilles de la litière sont des déterminants importants de la diversité des plantes de sous-bois (Aussenac, 2000; Miller *et al.,* 2002; Barbier *et al*., 2008). Les effets potentiels de la coupe sur certaines de ces variables, comme la perte de cations et la diminution du pH, peuvent être associés à une réduction de la diversité des plantes et de l'abondance d'espèces rares (Barbier *et al*., 2008).

Contrairement à ce qui était attendu, plusieurs études en forêt tempérée mixte ou feuillue, dont la comparaison a été faite avec des forêts dites non-aménagées relativement jeunes (*e.g.,* 70 ou 80 ans), n'ont pas constaté d'effet significatif de la coupe forestière (AÉ et AI) sur la richesse et la diversité des communautés de plantes (Gilliam *et al*., 1995; Fredericksen *et al.*, 1999; Elliott & Knoepp, 2005; Lenoir *et al*., 2010; James, 2012). D'un autre côté, Meier *et al*. (1995) et Elliott *et al*. (1997) ont montré que la diversité et la richesse des plantes après coupe totale étaient inférieures à celles dans des forêts réellement non aménagées depuis plusieurs centaines d'années. Il semblerait que certains attributs, comme l'accumulation de bois mort, qu'on retrouve dans des forêts non-aménagées depuis longtemps (*e.g.,* plus de 100 ans), serait nécessaire pour maintenir une forte diversité et richesse en espèces vasculaires.

Les perturbations naturelles permettent aux forêts feuillues tempérées d'être diversifiées, notamment en démontrant de la variabilité en termes de structure forestière, mais aussi en termes de composition végétale. De plus, plusieurs facteurs tels le stade de succession, la disponibilité à la lumière et la concentration en nutriment étant connu pour influencer les

traits fonctionnels (*e.g.,* longévité, profondeur d'enracinement, densité des tiges, masse de graine) des plantes habitant ces forêts (Garnier & Navas, 2013). La modification de la structure et de la composition du couvert forestier suite aux interventions sylvicoles (Hale *et al.,* 1999; Lenière & Houle, 2006; Moola & Vasseur, 2008) est aussi connue pour affecter différents traits des plantes reliés à la capacité de dispersion des graines, la tolérance à la lumière et l'adaptation aux micro-conditions du sol (Scheller & Mladenoff, 2002; Aubin *et al.,* 2007; Tremlova & Munzbergova, 2007; Depauw *et al*., 2020). L'ouverture du couvert après coupe, même sous une forme partielle (*e.g*., l'AI), est susceptible de favoriser les espèces pionnières, les espèces envahissantes (Deconchat & Baient, 2001; Shields & Webster, 2007; Petzold *et al*., 2018), une densification des arbustes (Royo & Carson, 2006) et les espèces peu sensibles aux perturbations. Cette ouverture risque aussi de générer une homogénéisation des traits fonctionnels des plantes, ainsi qu'une diminution des espèces de fin de succession, comparativement aux forêts non-aménagées. Un des dangers de la coupe forestière est de modifier les traits fonctionnels des communautés de plantes de façon à générer des communautés moins diversifiées et résilientes.

De nombreuses études ont émis l'hypothèse que les effets de l'AÉ seraient plus importants que ceux de l'AI sur la diversité des plantes de sous-bois ; cependant, cette conclusion est toujours débattue (Duguid & Ashton, 2013). En forêt tempérée, des coupes plus intensives (i.e., AÉ) devraient modifier la composition et la structure de la forêt plus fortement, mais moins fréquemment que des coupes moins intensives (i.e., AI). Cependant, en raison des différences naturelles dans les besoins en lumière des plantes, la fréquence de l'aménagement forestier, plutôt que l'intensité des interventions qui lui sont associées, a été suggérée comme un facteur défavorable à certains groupes fonctionnels de plantes

(Decocq *et al*., 2004), ce qui alimente le débat concernant le type d'aménagement à prioriser.

À court terme, certaines études ont observé des effets négatifs plus importants de l'aménagement AÉ, comparativement à AI, sur la diversité fonctionnelle des plantes de la strate de sous-bois (Haeussler *et al*., 2007; Decocq *et al*., 2004). Outre la diversité fonctionnelle, les systèmes sylvicoles peuvent aussi affecter différemment différentes espèces, voire différentes familles qui sont moins aptes à persister après coupe (Brewer, 1980; Reader, 1987; Klironomos *et al.,* 1993; Baldocchi *et al*., 2002). Par exemple, de nombreuses espèces de fougères et de bryophytes deviennent plus rares dans les peuplements aménagés, où les conditions de transport, de germination et de survie de leurs propagules peuvent être altérées (Karst *et al*., 2005). Ainsi, la diversité phylogénétique pourrait être moindre après coupe. Alors que l'effet de la lumière sur la diversité fonctionnelle des plantes de sous-bois a été bien étudié, l'effet du temps depuis la coupe forestière sur différent aspects de la diversité (*e.g.,* diversité fonctionnelle et phylogénétique) demeure moins bien documenté.

Les effets de l'aménagement forestier sur le bois mort, la litière et les variables physico-chimique du sol

Certaines propriétés du sol, de la litière et du bois mort sont connues pour être particulièrement affectées par la coupe forestière. Par exemple, en forêt tempérée, la récolte forestière peut entraîner une perte en cations basiques ou en N, tout en contribuant à diminuer le pH du sol (Tritton, 1987; Federer *et al*., 1989, Siemion *et al*., 2011) et l'abondance et l'hétérogénéité des débris ligneux au sol (Angers *et al*., 2005; McGee *et al*., 2007; Vanderwel *et al*., 2008). Bien évidemment, les effets de la coupe forestière sur les

propriétés du sol vont varier selon l'intensité de la coupe (Grigal, 2000; Jerabkova *et al*., 2011; Dyck *et al*., 2012). Les coupes plus intensives sont généralement ciblées comme ayant les effets négatifs les plus importants (Grigal, 2000; Lindo & Visser, 2003; Siemon *et al*., 2011). Des études en forêt tempérée et boréale ont montré un effet plus important de l'AÉ, comparativement à l'AI, sur la réduction de débris ligneux au sol (notamment l'entrée moins progressive des débris ligneux de forte dimension) et des litières à décomposition lente (Humphery, 2014) et du C du sol (Elliott & Knoepp, 2005; Nilsen & Strand, 2013).

Comme les propriétés du sol peuvent varier dans le temps suivant la coupe (Jonard *et al*., 2017), il est d'intérêt de mieux connaître, si, et en combien de temps, ces variables vont revenir à leur état « avant coupe » ou à un état semblable à celui des forêts dites non-aménagées. Par exemple, dans une méta-analyse en forêts tempérées et boréales, Hume *et al.* (2018) ont déterminé que la concentration de N et de C totaux dans la couche superficielle du sol forestier diminuait rapidement après coupe puis elle augmentait lentement avec le vieillissement des peuplements forestiers. Afin de mieux comprendre les effets des coupes forestières sur le sol, il est donc crucial d'étudier la variabilité temporelle de ses propriétés.

Certains effets de la coupe forestière sont connus à court terme, comme l'augmentation des taux de nitrification et du lessivage des cations basiques, ainsi que la libération d'Al^{3+} et l'acidification du sol (Adams *et al*., 2000; Jerabkova *et al*., 2011). À court terme, la coupe forestière, et en particulier la coupe totale dans un contexte d'AÉ, pourrait aussi engendrer des pertes considérables en nutriments dans la couche superficielle du sol forestier (Yanai

et al., 1999; Jenkins *et al*., 2004; Thiffault *et al*., 2011). Après coupes, suivant les phases d'accumulation de biomasse ou la re-végétation, la disponibilité en nutriments dans le sol peut varier (Lovett *et al*., 2018); une baisse de plusieurs éléments en raison de la forte séquestration par les végétaux étant attendue. À moyen terme, les propriétés physiques du sol telles que la porosité et la stabilité des agrégats, importantes dans le cycle des nutriments, peuvent également être affectée par les coupes forestières (Zhou *et al*., 2015; Siebers & Kruse, 2019). À long terme, notre compréhension empirique de la façon dont les différentes intensités de coupes affectent les propriétés des sols forestiers reste limitée (Clarke *et al*., 2015). Il est cependant documenté que le rétablissement complet de certaines propriétés du sol après coupe peut nécessiter plusieurs décennies (Lal *et al*., 2005; Diochon *et al*., 2009; Prest *et al*., 2014; Bowd *et al*., 2019).

L'effet de l'aménagement forestier sur le microbiome du sol

Dans les forêts feuillues tempérées non-aménagées, les processus naturels entraînent généralement des peuplements végétaux étagés avec une forte abondance et diversité structurelle de débris ligneux au sol. Cette diversité structurelle contribue à la formation d'une variété de micro-habitats pour le microbiome du sol incluant les diverses communautés fongiques qui se succèdent lors de la décomposition du bois mort (Baldrian, 2017).

L'impact de la coupe forestière sur ce microbiome peut être attribué à plusieurs facteurs dont l'altération des propriétés chimiques (*e.g.*, le pH) et physiques du sol (Jeanbille *et al*., 2016), la modification de la composition et de la structure de la forêt (Uroz *et al*., 2016; Llado *et al*., 2018), la réduction de l'accumulation de bois mort et de la litière (Purahong *et*

al., 2015) et les modifications microclimatiques du sol (Brockett *et al*., 2012). En outre, la coupe forestière, en modifiant les facteurs abiotiques du sol, pourraient influencer la biomasse, la structure et la diversité des champignons et des bactéries (Hartmann *et al*., 2009; Zhang *et al*., 2010; Lewandowski *et al*., 2019). Les facteurs biotiques liés aux plantes mortes (*e.g*., la litière forestière, les débris ligneux) ou vivantes (*e.g.*, la composition de la forêt ou sa diversité) sont aussi des déterminants importants des communautés de champignons (Nguyen *et al*., 2016b; Sun *et al*., 2016; Sun *et al*., 2017; Hiiesalu *et al.*, 2017) et de bactéries du sol (Uroz *et al.*, 2016; Lewandowski *et al*., 2019; Dukunde *et al.*, 2019). Il parait ainsi clair que les facteurs biotiques et abiotiques modifiés par la coupe forestière peuvent influencer les communautés microbiennes du sol. De plus, ces facteurs ne sont pas indépendants. Par exemple, la modification de la composition forestière peut avoir des effets directs ou indirects sur la concentration en divers nutriments, le ratio C/N et le pH du sol (Dukunde *et al.*, 2019). Généralement, l'AÉ entraîne des changements plus importants dans le ratio champignon/bactérie et la dynamique des communautés microbiennes que la coupe partielle (AI) (Bailey *et al.*, 2002; Wu *et al*., 2011; Holden & Treseder, 2013).

Parlade *et al*., (2019) mentionnent que les modes trophiques des champignons moins dépendant des exsudats racinaires, comme les champignons parasites, pathogènes et saprophytes pourraient être moins affectés à court terme par la coupe que ceux qui en dépendent comme les champignons mycorhiziens. De plus, plusieurs études, principalement en forêt boréale ou en forêt de conifères, ont observé une diminution de l'abondance des champignons symbiotiques suite aux coupes forestières (Simard *et al*., 1997; Marshall, 2000; Durall *et al*., 2006; Hartmann *et al*., 2012); l'effet néfaste de la coupe

pouvant augmenter avec l'intensité de la coupe (Kropp & Albee, 1996; Dahlberg *et al*., 2001; Parlade *et al*., 2019). Les coupes forestières, en modifiant la quantité et la qualité du bois mort et des apports de litière, sont également connues pour modifier l'abondance des champignons saprophytiques (Hiiesalu *et al.*, 2017; Lewandowski *et al.*, 2019). En forêt tempérée, Purahong *et al.*, (2015) ont observé des différences significatives dans les communautés microbiennes spécialisées dans la décomposition de la litière, selon le type d'aménagement forestier (AÉ, AI et forêts non-aménagées).

Pour étudier l'effet des coupes sur le microbiome du sol, il est important de bien cibler l'échelle spatiale et la profondeur du sol dans laquelle le microbiome sera échantillonnée. Par exemple, l'étude du microbiome du sol à l'échelle locale (*i.e*., à multiples endroits dans le sol d'une parcelle forestière) devrait permettre de cibler le rôle de la composition forestière et des propriétés physico-chimiques du sol sur celui-ci (Llado *et al*., 2018). Pour sa part, la profondeur du sol influence l'abondance des bactéries ainsi que la proportion de plusieurs guildes de champignons (Carteron *et al*. 2020); la couche superficielle du sol étant particulièrement affectée par la coupe forestière (Hartmann *et al*. 2009).

Comme peu d'études ont comparé les communautés de champignons et de bactéries du sol entre des AÉ et des AI en forêt tempérée feuillue le long d'une chronoséquence de coupe (Nolet, 2016), des études supplémentaires sont nécessaires afin d'en évaluer les effets à long terme.

Comment mesurer la diversité des communautés ?

La préservation de la biodiversité, telle que désignée par l'ONU, nécessite le maintien de toutes les formes de vie sur Terre et des caractéristiques naturelles qu'elles présentent

(Convention sur la diversité biologique, 2008). Ce besoin se traduit à plus petite échelle (*e.g.,* à l'échelle d'un domaine bioclimatique) par la nécessité de conserver la biodiversité qui lui est propre. Ainsi, la mesure de cette diversité ne devrait pas uniquement s'intéresser au nombre et à l'abondance des espèces, mais aussi à leur identité, leurs caractéristiques et même leur degré de naturalité (tel que défini dans Limoges *et al*., 2013) dans l'écosystème. Cependant, la littérature abonde d'études à petite échelle (*e.g.,* Vellend *et al*., 2013) dont les conclusions sur la diversité se basent uniquement sur le nombre d'espèce.

Le sens donné aux termes « diversité » ou « biodiversité » varie grandement selon le domaine d'activité, ce qui peut aller jusqu'à compromettre l'atteinte des objectifs fixés en conservation (Limoges *et al*., 2013). Ainsi, dans un objectif de préservation de l'écosystème, l'étude des effets des perturbations sur les communautés animales, végétales et microbiennes nécessite de choisir des mesures de diversité qui permettront de discerner leurs effets réels sur la conservation et le rétablissement de leurs diversités et leurs fonctions. Selon Jost (2006), il y a une nuance marquée entre la diversité biologique et les indices fréquemment utilisés pour l'estimer (*e.g.,* richesse spécifique et indice de Shannon-Wiener). De plus, tenter d'évaluer la diversité sans une compréhension claire et fondamentale de ses métriques pourrait conduire à des conclusions trompeuses, voire erronées (Willis, 2019). D'un autre côté, l'obtention d'une métrique représentative de la diversité peut apparaître comme un défi mathématique ou un choix difficile parmi une multitude d'options (Daly *et al.*, 2018). Réduire l'écart entre l'évaluation de la biodiversité utilisée en écologie théorique et celle utilisée par des praticiens pourrait conduire à de

meilleures décisions et à une gestion plus durable des ressources. Pour y parvenir plusieurs éléments peuvent être considérés.

Premièrement, Daly *et al.* (2018) ont identifié la richesse (c'est-à-dire le nombre d'espèces), l'uniformité (leur abondance relative) et la disparité (importance relative contrastée de chaque espèce sur une base génétique, phylogénétique ou fonctionnelle) comme les trois composantes critiques et éprouvées de la diversité. Deuxièmement, la diversité peut être analysée selon trois composantes spatiales, alpha (locale), beta (entre sites) et gamma (régionale).

La diversité alpha peut être calculée en utilisant soit une composante indépendante de l'espèce (*i.e.*, qui ne prend pas en compte la disparité entre les espèces), soit une composante dépendante de l'espèce (*i.e.*, qui prend en compte la disparité entre les espèces en définissant une importance relative contrastée entre elles). L'indice de Shannon (H) est une métrique de diversité alpha classique, indépendante de l'espèce et largement utilisée. D'autre part, les diversités phylogénétique et fonctionnelle sont des exemples de métriques dépendantes des espèces (Scheiner *et al*., 2017a), puisqu'elles reconnaissent les différences entre elles, selon leur histoire évolutive ou de leurs traits, respectivement (Scheiner *et al*., 2017b). Ces mesures prennent en compte le fait que, dans les écosystèmes, de nombreuses espèces peuvent être fonctionnellement redondantes (*i.e.*, espèces qui contribuent de façon similaire à une fonction), ou phylogénétiquement étroitement liées (Cadotte, 2011). L'utilisation de métriques dépendantes des espèces permettrait donc de considérer non seulement la composition des espèces, mais aussi l'étendue de leur histoire évolutive et de

leurs fonctions (Hillebrand *et al*., 2009), la diversité de leurs niches écologiques, ainsi que des processus des écosystèmes (Cornelissen *et al*., 2003).

La diversité beta peut aussi être utilisée pour détecter des pertes de diversité ou de fonctions dans l'écosystème. Par exemple, la diversité beta (intra-traitement) mesure la similarité entre les sites dans un même traitement et renseigne ainsi sur l'homogénéisation des communautés. De plus, si l'intérêt est de comparer la similarité entre les communautés soumises à différents traitements (inter-traitement), la diversité beta est également très instructive (Verhoef & Morin, 2010). Comme pour la diversité alpha, plusieurs équations permettent de calculer la diversité beta en utilisant les composantes indépendante ou dépendante des espèces (Pellens & Grandcolas, 2016).

Il est important de déterminer la ou les questions précises reliées au calcul de la diversité. En effet, si l'on s'intéresse à l'effet de la coupe sur la diversité, le choix de la question peut conduire à des réponses très différentes. De plus, un choix de question comme « Est-ce qu'il y a moins d'espèces après une coupe forestière ? » renferme plusieurs pièges et ne permettra pas nécessairement de comprendre ou de bien évaluer l'effet de la coupe sur la diversité. Avant de formuler une question, certaines réflexions devraient être apportées, notamment en ce qui concerne : 1) les processus écologiques impliquées dans la question (*e.g.*, disparition d'espèces rares, homogénéisation des communautés ou des traits), 2) les contextes de comparaison de la diversité (*e.g.*, types de forêts aménagées et l'échelle temporelle) et 3) l'échelle spatiale à laquelle les données ont été prises. Ces différents points seront abordés dans le Chapitre IV.

OBJECTIFS ET HYPOTHÈSES

L'objectif général de cette thèse est d'analyser les effets de deux aménagements sylvicoles contrastés pratiqués en forêt tempérée sur les communautés de plantes de la strate de sous-bois, le microbiome du sol (champignons et bactéries) et les propriétés physico-chimiques du sol, le long d'une chronoséquence (5, 15 et 30 ans après la coupe). La thèse vise aussi à explorer les relations entre les communautés étudiées et les propriétés du sol et du couvert forestier. La thèse est composée de quatre objectifs spécifiques qui représentent chacun un chapitre. Pour les trois premiers objectifs spécifiques (O), différentes hypothèses (H) sont testées.

Le **premier objectif** est d'évaluer la diversité (spécifique, phylogénétique et fonctionnelle) des communautés de plantes de la strate de sous-bois (basée sur l'identité et les traits) dans des peuplements aménagés de façon équienne et inéquienne le long d'une chronoséquence de 30 ans, ainsi que dans des peuplements non aménagés. **O1H1.** En modifiant plus considérablement les filtres environnementaux abiotiques, l'AÉ (plus intensif) modifie plus fortement que l'AI les traits fonctionnels des communautés des plantes de sous-bois. En se basant sur l'analyse des traits fonctionnels, nous nous attendons à détecter un rétablissement de la communauté (*i.e*., rapprochement de celle de la forêt non-aménagée) plus on avance dans le temps le long de la chronoséquence (similarité des communautés : 30 ans > 15 ans > 5 ans après la coupe). **O1H2**. La seconde hypothèse testée est qu'en modifiant les variables abiotiques (*e.g*., la chimie du sol) et biotiques (*e.g*., la végétation), les deux types d'aménagement (AÉ, plus intensive ; AI, plus fréquente), ne permettent pas de conserver la diversité phylogénétique des plantes après coupe, comparativement à la

forêt non-aménagée. La prédiction est donc que des pertes de diversité phylogénétique seront détectées tout au long de la chronoséquence.

Le **deuxième objectif** est de déterminer l'effet de l'AÉ et de l'AI sur les propriétés physico-chimiques du sol 5, 15 et 30 ans après coupe. **O2H1**. L'hypothèse est que parce qu'ils modifient les caractéristiques des sites forestiers (*e.g.*, la végétation, le bois mort, la litière), l'AÉ et l'AI affectent négativement les propriétés clés du sol relativement à des sols de forêts non-aménagées. Notre prédiction est que l'ampleur des réponses du sol à la coupe serait plus grande à court terme et dans les forêts sous AÉ. **O2H2**. La deuxième hypothèse est que les différences de productivité du sol générées par la coupe auraient un effet significatif sur la croissance des semis d'arbres. Notre prédiction est que les sols moins riches associés à des sites de coupe induisent des effets négatifs sur la croissance des semis d'arbres comparativement aux sols plus riches de forêts témoin non-coupées.

Le **troisième objectif** vise à analyser l'effet de l'aménagement forestier sur les bactéries et les champignons du sol (notamment la proportion des différentes guildes et modes trophiques). Nous visons aussi à explorer les relations entre le microbiome du sol et les variables abiotiques et biotiques modifiées après coupes. **O3H1**. L'hypothèse testée est que la modification des variables biotiques et abiotiques après coupe affecte la structure, la composition et la diversité des communautés microbiennes. Une diminution plus importante du ratio champignon/bactérie et une modification de plus forte ampleur des communautés de champignons sont attendues peu de temps (< 5 ans) après AÉ (plus intensif) comparativement aux forêts non-aménagées. **O3H2**. Une autre hypothèse émise est que la modification de la chimie du sol après coupe est associée à la modification de

l'abondance des bactéries dans le sol et que la modification des caractéristiques de la végétation après coupe est associée à la modification des guildes ou modes trophiques de champignons. Due à l'importance des exsudats racinaires pour les champignons symbiotiques (comparativement aux autres modes trophiques) on s'attend à ce que leur proportion diminue avec la diminution de la densité forestière.

Le **quatrième objectif** est de comparer l'efficacité de plusieurs indices de diversité afin de répondre à la question générale : « Est-ce que la diversité est différente entre les communautés soumises à différents traitements ? », à l'aide de simulations théoriques de communautés de plante. Cet objectif découle des besoins et des lacunes observés dans les chapitres I et III lors des comparaisons des communautés soumises à divers traitements.

CHAPITRE I. Legacies of forest harvesting on plant diversity and plant community composition in temperate deciduous forest

Abstract

To conserve forest natural heritage, sustainable forest harvesting requires the recovery of plant diversity and ecosystem functions following management. There is a need to clarify the temporal dynamics of plant diversity following harvesting, for both even-aged or uneven-aged silvicultural systems. To achieve this goal, the temporal dynamics of plant diversity in the herb layer was measured in unmanaged forests (control) and along a chronosequence (< 5 years, 15 years, 30 years after harvesting) for even-aged (EA) and uneven-aged (UA) managed forests in a hardwood forest in southern Quebec, Canada. Plant diversity, plant community composition, and ecosystem functioning were investigated using metrics exploring richness, evenness and disparity diversity components, and included two scales of diversity partitioning (alpha and beta). Shrub-canopy layer, forest tree species composition and structure, and total forest basal area were also measured. We found 1) a substantial decrease in mean plant phylogenetic diversity in UA and EA managed forest stands compared to unmanaged forest, even 30 years after harvesting (*i.e.*, decrease of 16% and 22%, respectively), and 2) greater total numbers of plant species in unmanaged forest herb layer. Lowest plant alpha-diversity in the herb layer was observed 15 years after EA and UA harvesting. For forest composition and structure, plant community and plant traits, dissimilarity (beta-diversity) relative to the unmanaged control was highest 5 years after EA management. Trait-based community were more similar to unmanaged forest at intermediate levels of forest density (*i.e.*, ~20 m^2 ha^{-1}) that were found 30 years after EA and 5 years after UA management. Forest management clearly affected diversity, community composition and ecosystem functions, along the chronosequence, highlighting the strongest effects of more intensive management (*i.e.*, EA) and the need to improve the sustainability of forest management.

Key words, Plant diversity, Management, Legacies, Chronosequence, Forest

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Introduction

Forests are essential ecosystems that cover more than 30% of the world's land surface, and which provide many key services, such as fuel, building materials, carbon sequestration, and water purification (FAO and UNEP, 2020). Forest species are essential for maintaining many of these key services (Augusto *et al*., 2003; Lorenz *et al*., 2006). However, plant diversity continues to decrease worldwide, with exceptionally high rates of species extinction due to increases in anthropogenic perturbations, including forest management (Pereira *et al.,* 2010; Pimm and Raven, 2017). In addition to affecting plant diversity, forest management could also alter forest services through modification of plant community composition (based upon identity or functional traits) or forest composition and structure. It seems clear that conservation of unmanaged forests, which represent less than one-third of global forest cover (Likens and Franklin, 2009; FAO and UNEP, 2020), is one way of preserving plant diversity and community composition. Yet, it is less clear how different forest management practices affect plant diversity (Duguid and Ashton, 2013) and how to test whether management is done in an ecologically sustainable manner (Lindenmayer *et al*., 2000). This emphasizes the importance of an approach that considers both conservation of diversity and ecosystem function in questions that are at the core of assessing the performance of different forms of forest management.

In temperate forests of North America, forest management is generally based upon uneven-aged (UA) silvicultural systems that favour regrowth of a stand that is dominated by at least three age classes (Nolet *et al*., 2017). Even-aged (EA) silvicultural systems that favour the regrowth of a stand that is dominated by trees mostly of the same age are also used in many situations at a smaller scale in North America, but these are more commonly used in

other parts of the world. Analysis of both EA and UA silvicultural systems ensures a broader spectrum of response for detecting timber harvesting effects. Many studies have hypothesized that the effects of EA management would be more important than those of UA management on understory plant diversity; however, this conclusion is still debated (Duguid and Ashton, 2013). In temperate forest, severe silvicultural prescriptions like EA management are expected to modify forest composition and structure more strongly than a less severe, but more frequent silvicultural intervention, such as UA management. Due to natural differences in plant light requirements, the frequency rather than the severity of forest management has been suggested to put some plant functional groups at a disadvantage (Decocq *et al.,* 2004).

Some studies suggest that both UA and EA forest management can alter diversity of plant communities (Bell *et al*., 2016). In contrast, other studies in temperate forests did not find significant effects of EA and UA management relative to unmanaged forest, on the diversity of plant communities (Gilliam *et al*., 1995; Fredericksen *et al.,* 1999; Elliott & Knoepp, 2005; James, 2012). These contrasting results are more likely due to methodological problems than to a real absence of effects of forest management on diversity. For instance, some studies that failed to detect a management effect used relatively young forest controls (*e.g*., 70- or 80-years-old; Duguid & Ashton, 2013). Yet, forests that did not reach a stage of senescence that favours dead wood accumulation could be less diverse or rich in vascular plant species than old unmanaged forests (Graae & Heskjær, 1997). For instance, Meier *et al*., (1995) used old (> 100-years-old) unmanaged forests as controls and showed that clear-cutting (EA system) substantially reduced plant

diversity and richness. Because forests are complex ecosystems (Kuuluvainen, 2009), the use of an appropriate unmanaged forest as a control is required.

The temporal scale of studies investigating the effects of forest management is often limited. Forests are complex ecosystems with long-lived species, and focusing on one point in time after harvesting can only provide partial answers. As plant species recover after management, the conclusions of studies that were performed immediately after or many years following harvest would lead to different conclusions about plant diversity. Since high species richness is often associated with intermediate levels of disturbance or forest succession (Berkes *et al.*, 2003), the absence of long-term data would be inappropriate for studying the effects of disturbances on forest plant diversity. Temporal dynamics could be evaluated using time interval resurveys, however, in many cases, a space-for-time substitution is the only practical method that is available to infer long-term dynamics. The importance of studying the temporal dynamics of ecosystems following disturbance has been noted by several authors (*e.g.*, Orwin & Wardle, 2005; Orwin *et al.,* 2006; Bengtsson & Berg, 2005; Verhoef & Morin, 2010), but these dynamics are often ignored in studies regarding the impacts of forest management on plant diversity.

Another common methodological problem that is encountered in the literature is the type of metric that is used to measure diversity. Most studies use relatively simple metrics such as species richness or Shannon diversity, which consider all species to be equal. Regardless of whether the number of species can be maintained or even increased following tree harvesting, plant community structure and composition can change drastically with major consequences for ecosystem functioning or for the conservation of rare plants. For instance,

the before-after study of Falk *et al*., (2008) found that management increased plant species richness of the herb-layer, compared to unmanaged temperate forest. Yet, canopy opening following tree harvesting is likely to favour pioneer species; moreover, an increase in local species richness is commonly observed, due to an increase in the number and abundance of invasive species (Deconchat & Baient, 2001; Shields & Webster, 2007), together with an increase in shrub density (Royo & Carson, 2006; Decocq *et al*., 2004). To accurately reflect the effect of management on plant diversity, the functional role (*i.e*., functional diversity) and the evolutionary history (*i.e.*, phylogenetic diversity) of species should be considered when measuring diversity changes. For instance, phylogenetic diversity might indicate set of taxa, which is more likely to be affected by ecological changes, such as forest management (Veron *et al*., 2019) while helping to predict branches where diversity decreases are to be feared. For these purposes, alpha-diversity metrics that are based upon species-dependent measures (*i.e*., disparity, which can only be measured relative to the identity of other species, like functional and phylogenetic diversity) could be used (Scheiner *et al.,* 2017a,b; Faith, 2018). Variation of selected species traits, as well as forest density or plant percentage cover could inform about important ecological function of a forest, such as carbon sequestration (Imai *et al*., 2009) and nutrient retention (Larcher, 2003).

Beta-diversity metrics that are used to compare community composition could also be implemented in addition to species-independent measures (*e.g*., plant identity and abundance) or species-dependent measures (*e.g*., plant functional traits) (Scheiner *et al*., 2017b). Homogenization of both the plant community and traits (*i.e.*, functional homogenization) or forest composition and structure, which is measured with beta diversity

(Anderson *et al*., 2011), could be a concern that is associated with biodiversity losses or alteration of ecosystem functions (Zambrano *et al*., 2020). Depending upon the selected traits, variation of those traits following disturbances could provide insight into how disturbance alters abiotic and biotic filters governing community assembly (Zambrano *et al*., 2020). Finally, the recovery of plant functional traits, forest composition and structure, and forest density following management are important for the maintenance of ecological functions of a forest.

The objective of this study is to compare the effects of two forest management methods, *i.e*., EA and UA, on plant communities by comparing forests that were harvested at different times in the past to old unmanaged forests. We used a wide range of diversity metrics and community comparisons (Table 1). Given that EA management is more intensive (than UA) and could substantially modify abiotic environmental filters, we expected that plant community composition, plant traits, and forest composition and structure would be very dissimilar to unmanaged controls following this treatment. We expected that both management types (EA: more intensive; UA: more frequent) would decrease plant diversity compared to unmanaged forest. We expected to detect a recovery pattern of plant diversity, and more similar communities compared to unmanaged forest, with time-since-harvesting for both management types.

Table 1. Selected questions and the metrics used for assessing the effects of forest management at the herb layer (plant community, plant diversity, plant traits and percentage cover) and at the shrub-canopy layer (forest composition and structure and forest basal area) along a chronosequence.

	Selected questions	Metrics
Diversity	How did **plant diversity** change over time after forest harvesting? Can we encounter the same number of species as in unmanaged forest?	**Alpha Richness, Shannon Index and Disparity (Phylogenetic diversity)** and **Total species richness** at different times after forest harvesting in EA and UA forests compared to the unmanaged control
Community composition	Are **plant species, plant traits** and **forest composition and structure** in EA and UA more similar to unmanaged forest over 30 years following forest harvesting?	**Beta diversity (inter-treatment) based upon identity-independent and identity-dependent (trait community dissimilarity) metrics** at different times after forest harvesting in EA and UA forests compared to the unmanaged control
	Do the differences in UA and EA effects decrease over time after harvesting?	**Beta diversity (inter-treatment)** between paired sites (EA vs. UA) at each time-since-management
	Are **plant community, plant traits and forest composition and structure** more homogenous after treatment? If so, when?	**Beta diversity (intra-treatment) based upon identity-independent and identity-dependent (trait community dissimilarity) metrics** between sites of the same treatment-year
Ecosystem functioning	How do different management treatments change plant traits?	PCA on selected plant traits
	Do **forest basal area & percentage cover of the herb layer** recover after forest harvesting?	Abundance and density at different times after forest harvesting in EA and UA forests compared to the unmanaged control

Methodology

Study sites, experimental design and vegetation data collection

Plant community composition and abundance were assessed in unmanaged forests (12 sites of old-growth forest > 100 years, with dominant and co-dominant trees older than 200 years, and no obvious sign of past harvesting), and in even-aged (27 sites) and uneven-aged (27 sites) managed forests along a chronosequence (< 5 years, 15 years, 30 years after forest harvesting) (Figure 1). The chronosequence that was used fit a complete UA management rotation period (*i.e.,* around 30 years), which represented about one-third of the complete EA management rotation period (*i.e.,* around 90 years). In total, 66 sites were selected based upon random stratification (for each treatment at least two sites were

selected in each of the four zones that were determined following latitude and longitude) of a deciduous forest that was located in the sugar maple (*Acer saccharum*)-basswood (*Tilia americana*) bioclimatic subdomain of southern Quebec (Canada). The natural gap-disturbance regime that created uneven-aged structure stands characterizes these temperate deciduous forests (Runkle, 1985). The sites were located within a 26 500 ha private forest (Kenauk Nature site network; 45.71 to 45.84 N, 74.95 to 74.77 W). Over the last 40 years, harvesting in Kenauk Nature private forest has consisted mainly of strip cutting, where 50-metre-wide strips are clear-cut (EA), while the intercut strip is managed using selection cuts (UA) (30% basal area removed). In both EA and UA forests, trees were felled by chainsaw, delimbed on site and skidded tree-length to the landings. This management method has been used in different locations of the territory and has resulted in even-aged and uneven-aged areas of contrasting harvest ages, from < 5 years to > 30 years, which are located nearby. Prior to this 40-year period of strip cutting, the Kenauk Nature private forest has been used for many purposes, including conservation and management activities (*i.e.,* historical harvesting activity including the cutting of large eastern white pine [*Pinus strobus*]). With the aim of isolating harvesting impact and drawing temporal conclusion using a chronosequence, sites were selected by satisfying a concern that they have similar soil characteristics (slope, soil texture) and past harvesting histories prior to this 40-year period. We selected paired even-aged and uneven-aged sites that were close to one another (*i.e.*, < 200 m apart) to minimize differences in soil and potential vegetation types (tolerant hardwoods) (Robitaille & Saucier, 1998). An unmanaged forest reference site with a common history (based upon available information and sites observations, *e.g.*, absence of large white pines) was selected relatively close to each paired site (*i.e.,* 300 to 900 m

distance). Selected sites were restricted to minimal slopes and stand areas > 0.52 ha (*i.e.*, continuous groups of trees that were sufficiently uniform in terms of age-class distribution, composition and structure). Soil, site characteristics and locales of sites and plots that were used to study the legacies of forest harvesting along the chronosequence (with space-for-time substitution) are described in greater detail by Roy *et al*., (2021).

In each site (1200 m²), three circular plots (400 m²) were established (total of 198 plots). In each plot, species identity, diameter at breast height (DBH, 1.3 m) and locations of each tree > 9.1 cm DBH were determined. In the herb layer, total plant species identity and abundance (percentage cover) were sampled in each plot using eight circular micro-plots of 4 m². In each plot, species identity and DBH of shrubs and small trees (DBH range: 1.0 to 9.1 cm) were measured in three circular micro-plots of 25 m². Data were collected in 2016 and 2017, between June and August. To minimize seasonal variability and allow detection of early spring species, plants (identity and abundance) in the herb layer were measured twice (once in June to early-July, and once in late-July to August).

The climate is cold temperate, with an average annual temperature of 4.5 ºC, ranging from an average minimum of -12.5 ºC in January to an average maximum of 18.9 ºC in July (Environment et Changement climatique Canada, 2020). Average annual precipitation is 1091.1 mm. Soils in the study area are classified as Dystric Brunisols (USDA: Typic Dystrochrepts) with moder-type humus, which developed on glacial till deposits mainly composed of gneiss, quartzite and granite (Lajoie 1967; Soil Classification Working Group 1998). Forest soils had mean pH values ranging from 4.2 to 6.1. The average (± SD) percent sand, silt and clay in the different treatments was analyzed for each site (pooling samples

from the three plots) and were respectively: EA: 51% ± 1.9, 40% ± 1.6 and 9% ± 0.6; UA: 49% ± 1.7, 44% ± 1.3 and 7% ± 0.7; and Unmanaged control: 44% ± 2.9, 47% ± 1.9 and 9% ± 1.6.

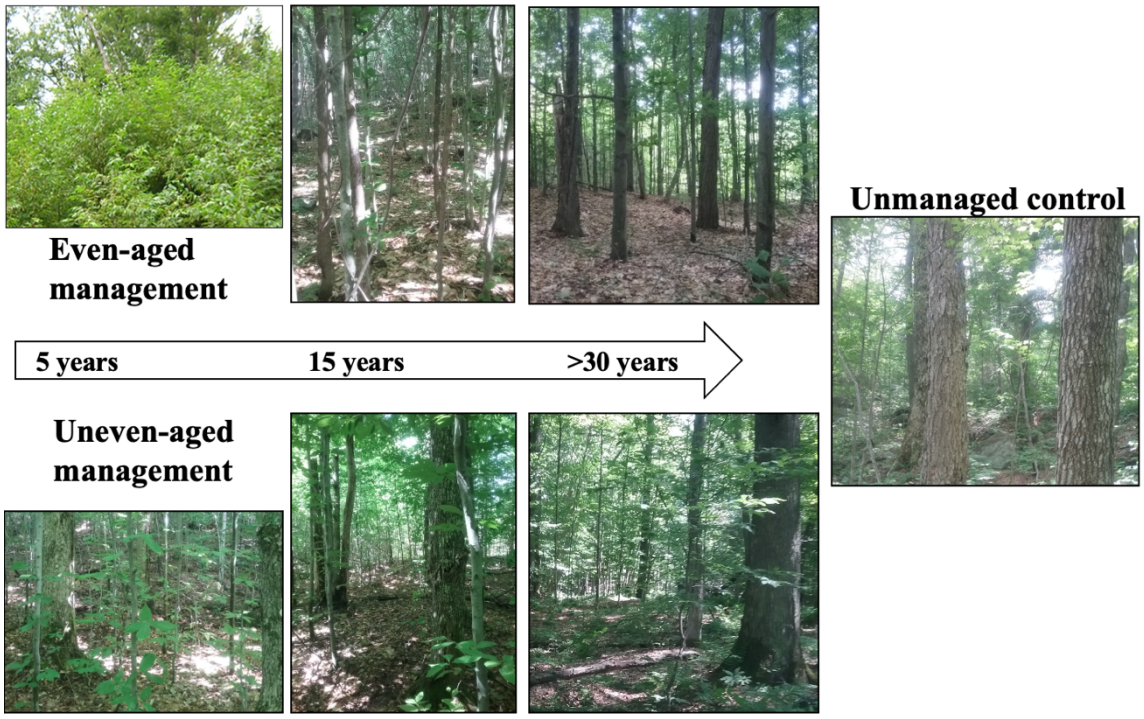

Figure 1. Photographs of plots from the experimental design following even-aged and uneven-aged management along the selected chronosequence, together with the unmanaged control.

Herb layer, plant community, plant diversity, plant traits and percentage cover

For the herb layer, the abundance and taxonomic identity of 212 inventoried plant species were used to calculate phylogenetic diversity, Shannon index (Alpha diversity), plant trait frequency metrics, and plant community dissimilarity (Beta diversity). Scientific nomenclature was provided according to the VasCan database (data.canadensys.net) (Brouillet *et al*., 2010). For phylogenetic diversity, to cope with the lack of phylogenetic resolution for some genera or families, we extrapolated data from phylogenetically related

species with available information using TimeTree (Kumar *et al*., 2017) and APG III (Angiosperm Phylogeny Group, 2009) (Table S1 for species replacement).

Plant traits that are related to forest perturbation at small scales were selected for each species (de Bello *et al*., 2010). We included two traits that were related to seeds (*i.e*., seed mass and seed dispersal mode) and two traits that were related to roots (*i.e*., rooting depth and vegetative propagation). For quantitative data such as seed mass or root length, mean values for each species were calculated using multiple studies that were available from the TOPIC database for functional traits (Aubin *et al*., 2012). Trait values were grouped into meaningful categories to cope with inclusion of both qualitative and quantitative trait values. When a species had multiple associations with a qualitative value, it was represented by the matrix of proportions of trait values (*i.e.*, relative proportion of the available data from the TOPIC database that recorded this trait value) for this species (sum of values for a species = 1). For species with missing data, we used data from phylogenetically or physiologically related species using information available from the TOPIC database or the Angiosperm Phylogeny Group (2009) (Table S1).

Shrub-canopy layer, forest composition and structure and forest basal area

Data that were related to the shrub-canopy layer included all trees and shrubs of DBH > 1.1 cm. In each site, dissimilarity in forest composition and structure (intra- and inter-treatments) was calculated based on a matrix where columns represented different combinations of DBH classes (1.1-4 cm, 4-9.1 cm, 9.1-20 cm, 20-35 cm, >35 cm) and species (total of 89 combinations). Forest basal area (m^2 ha^{-1}) in each site was calculated as the total cross-sectional area at 1.30 m of all shrub and tree stems with a DBH > 1.1 cm.

Diversity metric calculations

Metrics were used exploring richness, relative abundance (e.g., Shannon Index) or disparity components, and two scales of diversity partitioning, more familiarly known as alpha and beta diversity (Table 1). In each plot, we calculated mean species richness, Shannon index, and Faith's phylogenetic diversity using abundance of species (PD) (Scheiner *et al.,* 2017a; Faith, 2018). PD ranged from 0 to 1, where 1 represented the highest diversity. For the same sampling area, the total number of plant species that were encountered was recorded for each treatment, producing a species accumulation curve by randomizing the sample. Dissimilarity between plots (Beta diversity) was measured using the Bray-Curtis index of dissimilarity (Anderson *et al*., 2011). First, for each comparison between a managed forest site and an unmanaged forest site, beta diversity was calculated using all pairs of sites. Second, beta diversity was calculated between adjacent paired sites (from strip cutting; same zones) with the same time-since-management, but with different silvicultural treatments (EA vs. UA), with nine paired sites for each time-since-management. Last, to assess the compositional dissimilarity between sites for the same forest management type and same time-since-harvesting (intra-treatment), mean beta diversity was calculated using all randomly selected paired sites that had the same treatment and years.

Statistical analysis

All statistical analyses were performed in R (version 4.0.2.). Effects of forest management at different times-since-harvesting on plant species richness, Shannon diversity, PD and percentage cover of the herb layer (calculated at the plot level) were analyzed using a linear mixed model (*lme4* package, function *lmer*) with site and zone as random effects. Effects of forest management at different times-since-harvesting on forest basal area of the shrub-

canopy layer (calculated at the site level) were analyzed using a linear mixed model with zone as a random effect. Significantly different means among treatments were separated using post-hoc Tukey's tests. For all these analyses, homogeneity of variance was verified using Levene's tests, normality was tested using Shapiro-Wilk tests, and Durbin-Watson tests for autocorrelation among residuals. Percentage cover of the herb layer was log-transformed to improve normality. Statistical significance was declared at $\alpha = 0.05$. Analyses of group similarities (ANOSIM) with 999 permutations using Bray-Curtis index of dissimilarity (BC_{ij}) was used to illustrate intra-treatment mean dissimilarity. Means dissimilarity between treatments (inter-treatment) was evaluated using pairwise comparisons (*vegan* package, function *pairwise.adonis*) with adjusted *P*-values (Holm step-down method). Non-metric multidimensional scaling (NMDS) was used to ordinate communities. Permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (*vegan* package, function *adonis2*) was used in variation partitioning (considering the matrix of plant traits), which is explained by the treatments and the sites. Principal component analysis (*FactoMineR* package, function *PCA*) revealed the structure of dependence and correlation among plant traits. To summarize changes that were induced by different management treatments, PCA results were illustrated for both EA and UA management types along the chronosequences and the unmanaged control.

Results

Impact of forest harvesting on plant diversity along a chronosequence

The total number of plant species that were surveyed in the herb layer was 212 (total of 187 species in the EA and UA managed forests along the chronosequence and 185 species in the unmanaged forests). In managed forest, very common species such as *Dennstaedtia*

punctilobula, *Acer pensylvanicum, Rubus idaeus* and *Viburnum lantanoides* were abundant. Rare plants species such as *Galearis spectabilis* and *Goodyera pubescens* were only found in unmanaged forests, while species that are threatened by unsustainable harvesting like *Adiantum pedatum* and *Uvularia grandiflora* were more abundant in unmanaged forests (Figure S2).

Mean species richness (Figure 2a) and Shannon diversity (Figure 2a) in the herb layer were lowest in EA and UA forests 15 years after forest harvesting compared to the unmanaged control. Plant phylogenetic diversity (PD) also was significantly lower 15 years after EA and UA forest harvesting ($P < 0.01$) compared to the unmanaged control (Figure 2c). Thirty years after UA and EA management, we still observed significantly ($P < 0.05$) lower mean plant phylogenetic diversity (PD) (0.77 and 0.72, respectively), compared to the unmanaged control (mean PD, 0.93). Many species with a long phylogenetic history that reproduce by spores like *Dryopteris goldieana*, *Botrypus virginianus* and *Adiantum pedatum* (Figure S3) were more abundant in unmanaged forest. Proportions of plant abundances in the order *Poales* and order *Fagales* in the herb layer were both high shortly after EA and UA management (Figure S4). Total species richness for each treatment, evaluated for the same sampling area, demonstrate that more species are found in unmanaged stands (*i.e.*, 142 species) compared to forest stands at each point in time after management (*e.g.*, lower than 103 species after each UA management) (Figure 2d). Alpha identity-independent metrics demonstrate a peak in plant richness or diversity 5 years after harvesting, followed by a major decrease 15 years after harvesting and a tendency toward converging on the unmanaged control 30 years after harvesting (Figures 2b and 2c). Five years after EA management, the 28 species in the order *Poales*, the 18 species from the

order *Asterales* and the 12 species in the order *Rosales*, are an important component of abundance (*i.e.*, 38.8%; Figure S4) and plant richness (*i.e.*, 45%) that were observed in this treatment. All plant diversity measures that were used in this study showed a tendency of recovering (converging on unmanaged forests) plant diversity in the herb layer 30 years after forest harvesting, compared to 15 years after harvesting (Figures 2a, b, c).

Impact of forest harvesting on community composition along a chronosequence

Results demonstrate a statistically significant difference (all significances values $P = 0.001$) in plant community composition, forest composition and structure and plant trait communities (*i.e.*, all plant traits for seeds and roots) between treatments (*i.e.*, forest management and time-since-harvesting). ANOSIM *R*-statistics are 0.194, 0.345 and 0.142 for plant composition, forest composition and structure, and plant trait communities, respectively, suggesting a slightly higher dissimilarity inter-treatment than intra-treatment. Dissimilarity in plant community composition, forest composition and structure, and plant trait communities with treatment are illustrated in Figure 3.

Considering comparisons between managed and unmanaged forests, plant species community composition in the herb layer were significantly dissimilar from the unmanaged control, 5 years after EA ($P < 0.05$) and UA ($P < 0.05$) forest harvesting (adjusted p-values from pairwise PERMANOVA). Community composition in EA forests 5 years after harvesting was the most dissimilar to the unmanaged control. Bray-Curtis dissimilarity index ($BC_{ij} = 0.79$) was higher than in all other managed forests (BC_{ij} ranging from 0.66 to 0.68) (Figure 4a). For forest composition and structure, 30 years after UA forest harvesting treatment was not significantly dissimilar to the unmanaged control ($P > 0.05$).

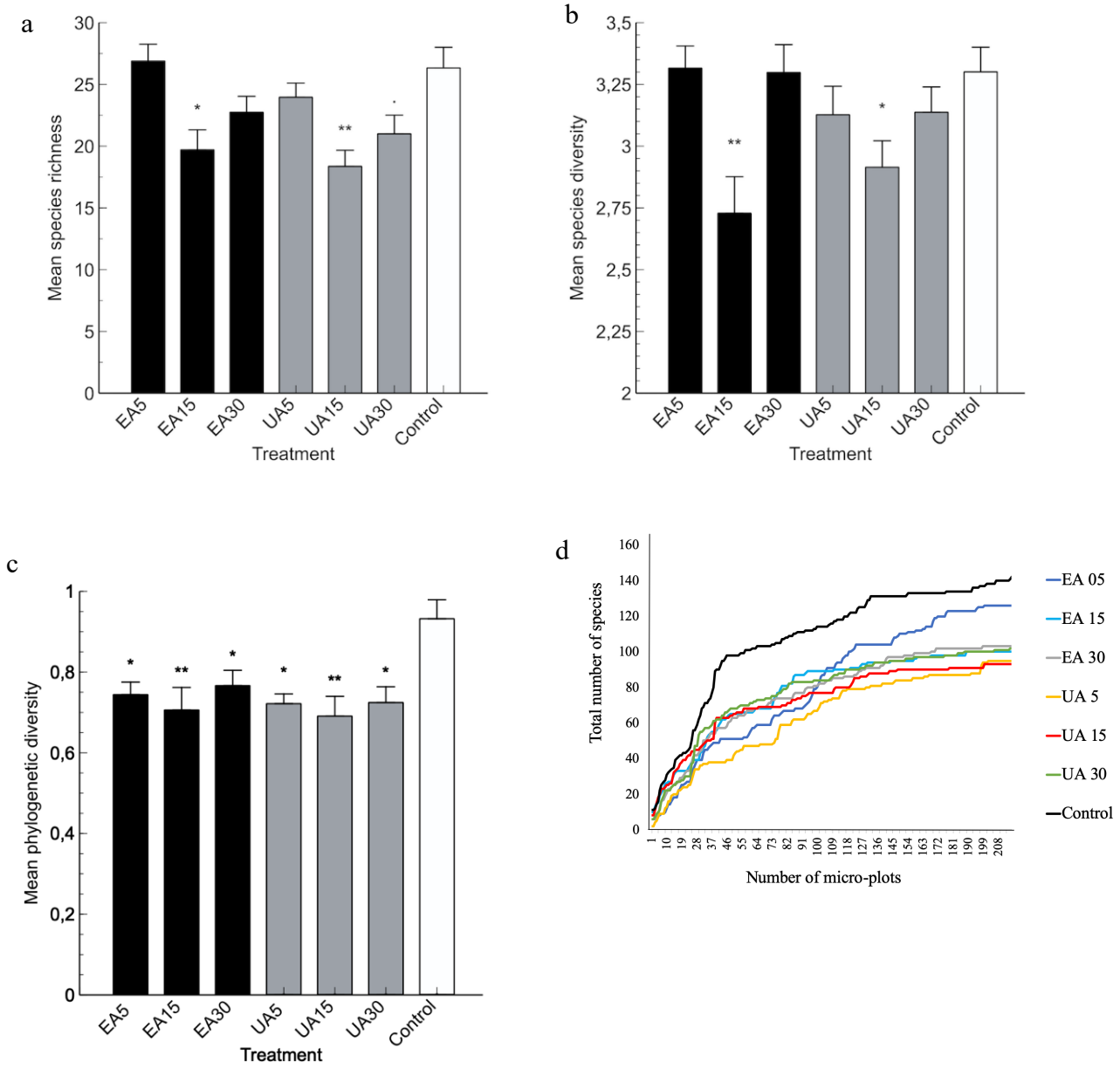

Figure 2. Variation in (a) mean alpha-species richness, (b) mean alpha-species diversity (Shannon), and (c) alpha phylogenetic plant diversity (identity-dependent measure) in the herb layer in even-aged (EA) and uneven-aged (UA) forests over 30 years following forest harvesting. For EA and UA, n = 27; for unmanaged forests (control), n = 36. The number following the treatment represents the number of years after forest harvesting. Error bars are standard errors. Treatment means were compared to the unmanaged control. Means that are significantly different from the control are represented by ** ($P < 0.01$), * ($P < 0.05$), · ($P \approx 0.05$). (d) Total plant species richness (for the same sampling area (*i.e.*, 216 micro-plots or 864 m^2)) are presented for each treatment.

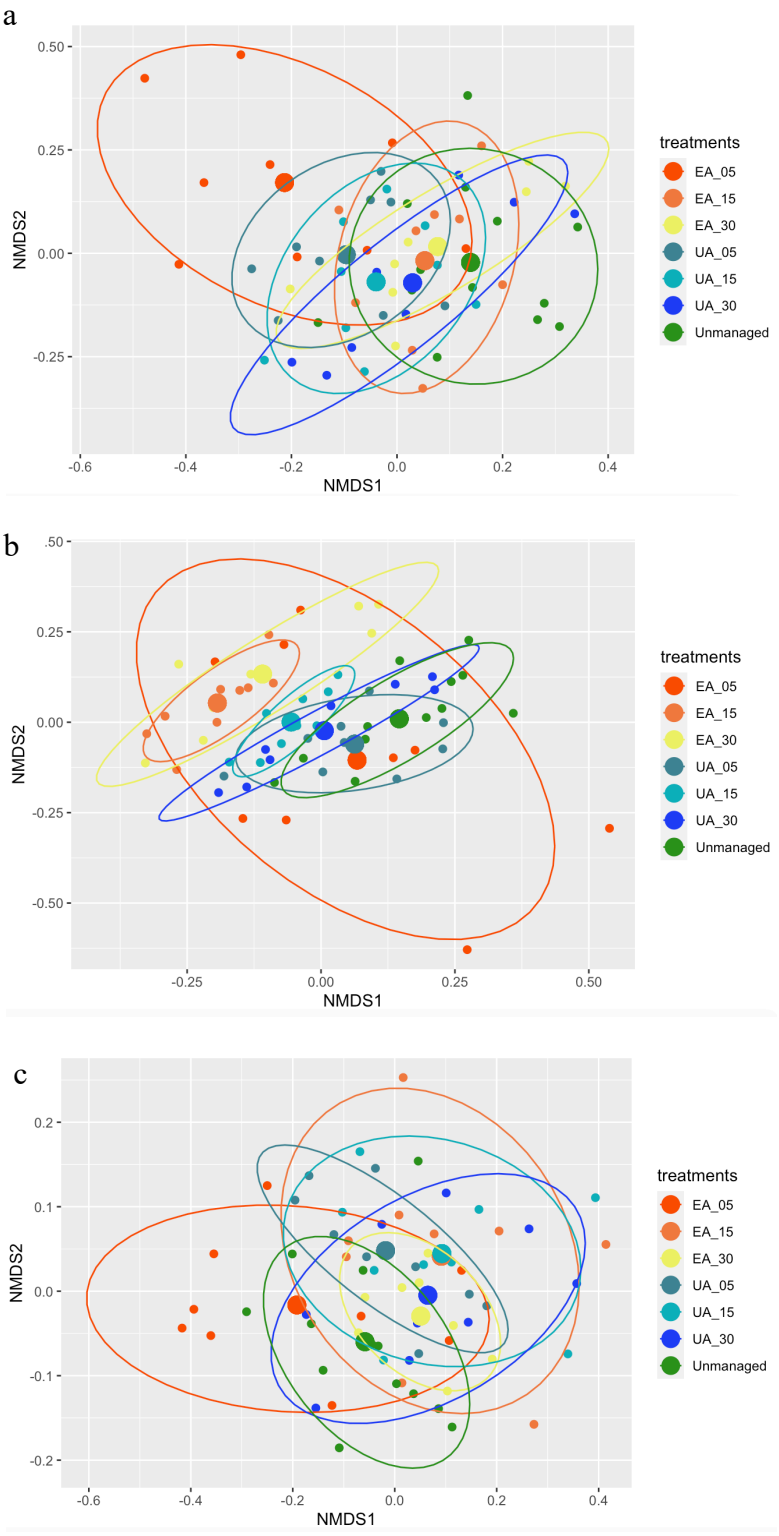

Figure 3. NMDS results of community comparison for a) plant species in the herb layer, b) forest composition and structure in the shrub-canopy layer and c) total plant traits, between sites following even-aged (EA) and uneven-aged (UA) management along a chronosequence (5, 15, 30 years after harvesting), as well as unmanaged forest sites. The larger circles represent the position of mean centroid for each treatment along these dimensions.

Forest composition and structure was more dissimilar to unmanaged controls in EA forests (BC_{ij} ranging from 0.76 to 0.79) compared to UA forests (BC_{ij} ranging from 0.62 to 0.67), regardless of the year after harvesting (Figure 4b). Dissimilarity in trait-based community to the unmanaged control was significantly different between treatments ($P < 0.001$). Trait-based community were more dissimilar to unmanaged forest 5 and 15 years after EA management (Figure 4c). Association between traits and treatment are described in greater detail in Figure S4.

For selected plant traits community, according to the multivariate variation partitioning test (PERMANOVA), the treatments (management type and time-since-harvesting) explained a considerable portion of the variation ($R^2 = 0.22$, $P < 0.001$). The first and second components of PCA (Dimensions 1 and 2; Figure 5) explained respectively 39.9 and 21.9% of plant trait variation. Dimension 1 was positively associated with, 1) Seed mass, seed light (8.5%) and seed medium light (9.5%); 2) Seed propagation, water (8.3%), animal (8.1%), unassisted (7.1%), wind (8.6%); 3) Rooting depth, rd_1m (8.9%) and rd_3m (6.0%); 4) Vegetative propagation, collar (9.3%), rhizome (9.7%) and stump (9.4%). Dimension 2 was positively associated with 1) Seed mass, seed very light (18.4%), 2) Seed propagation, explosive (18.0%), bulb (11.7), 3) Rooting depth, rd_intermediate (14.1%). The quality of representation for the first two dimensions was highest for rhizome, stump, and explosive and very light seed (Cos 2 analysis, data not shown). The first dimension clearly segregated recently harvested (> 5 years) EA management sites from all remaining treatments (Figure 5). For UA management, the second dimension demonstrates the recovery of plant traits community (closer to unmanaged forest) with time-since-harvesting (Figure 5).

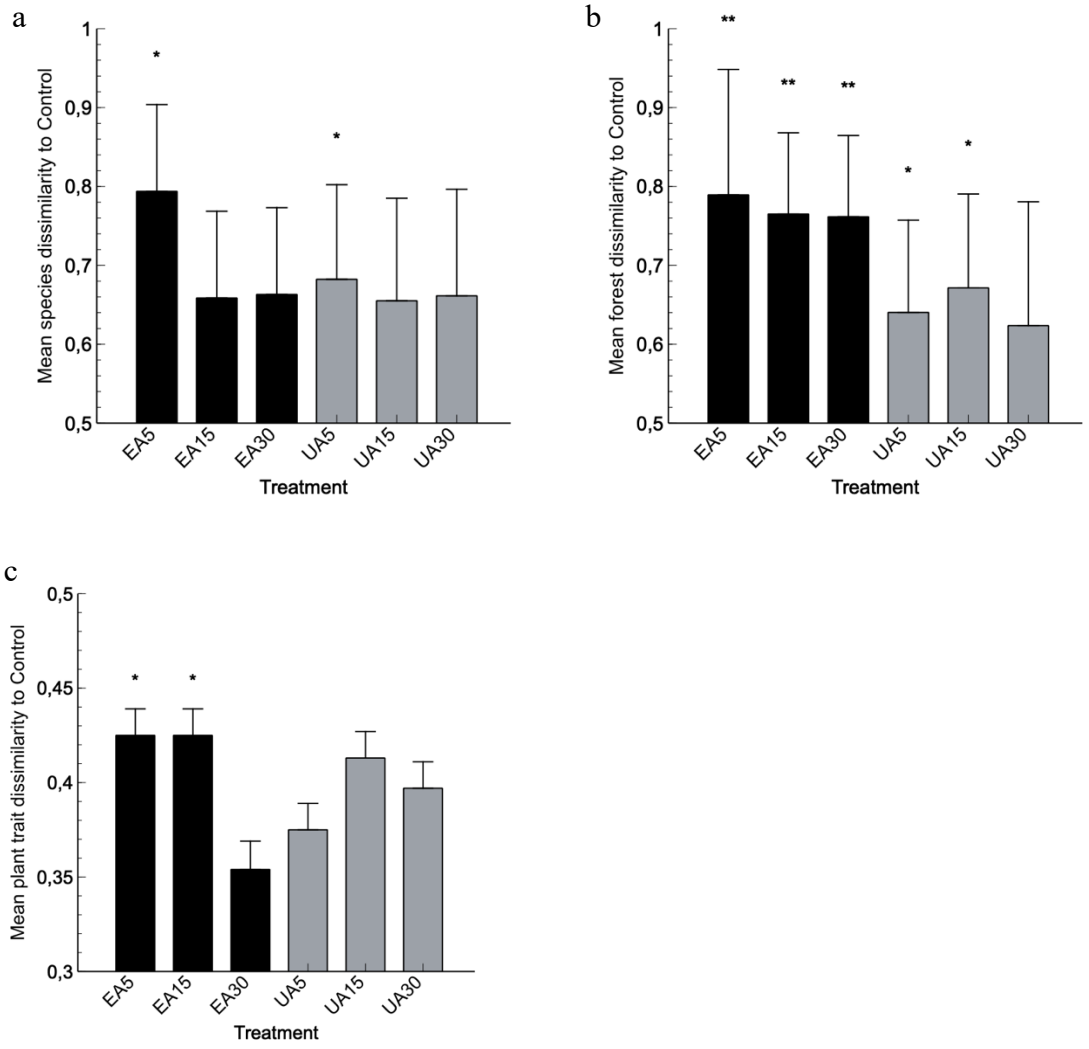

Figure 4. Variation in beta diversity (Bray-Curtis dissimilarity between managed and unmanaged forests (control)) in even-aged (EA) and uneven-aged (UA) forests over 30 years following forest harvesting for a) plant species in the herb layer, b) forest composition and structure in the shrub-canopy layer, and c) plant traits. Each value is the mean of all possible combinations (n = 108) between managed and unmanaged forest for a specific year after forest harvesting. The number following EA or UA represents years after forest harvesting. Error bars are standard errors. All linear mixed models were statistically significant ($P < 0.001$). Means were compared between different treatments using pairwise comparisons with adjusted *P*-values (Holm step-down method). Means differing significantly from the control are represented by ** ($P < 0.01$), * ($P < 0.05$).

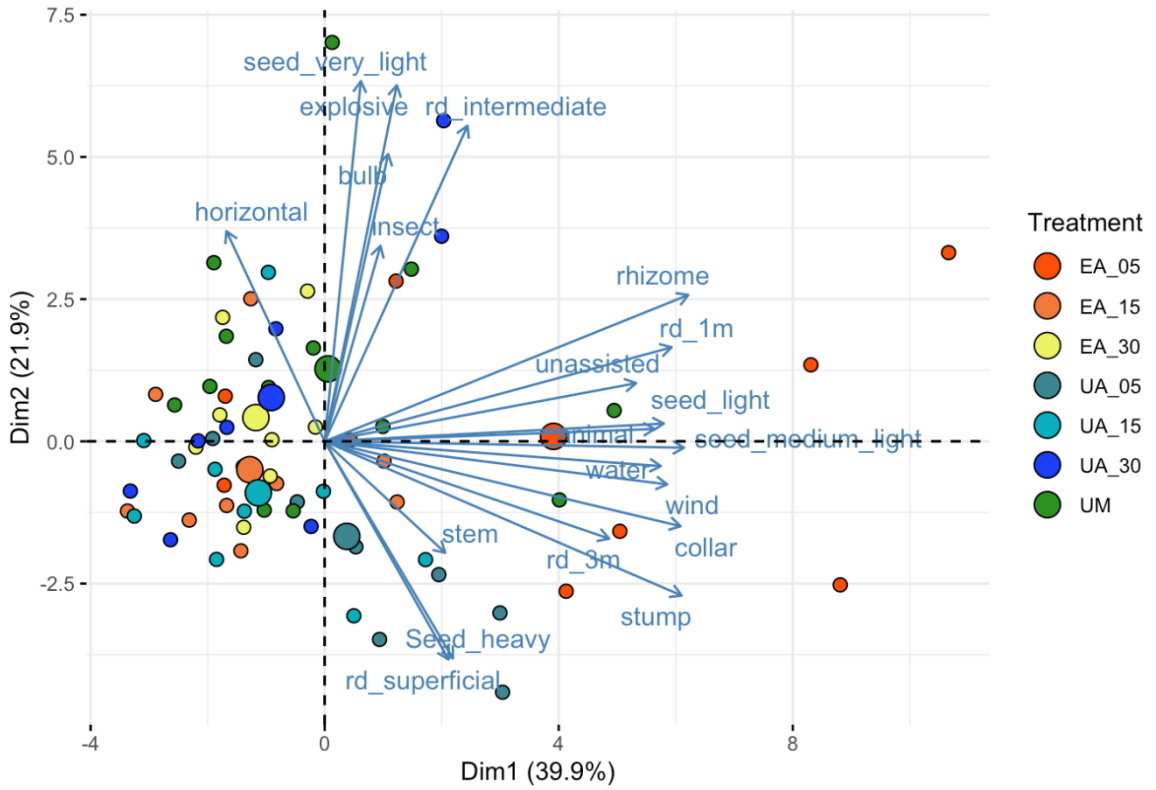

Figure 5. Principal component analysis (PCA) of selected plant traits after uneven-aged (*i.e.*, UA), even-aged (*i.e.*, EA) management, together with unmanaged forest (UM). The larger circles represent the position of each treatment along the first two dimensions. The number after the management type (*i.e.*, EA or UA) represents time-since-harvesting, 5, 15 or 30 years. The biplot (blue vectors) indicates the magnitude and direction of the correlations among selected variables (plant traits), which are described as follows. Seed mass, *seed_very_light*, < 0.02 mg; *seed_light*, between 0.02 and 4 mg; *seed_medium_light*, between 4 and 20 mg; *seed_heavy,* between 50 and 100 mg. Seed dispersal mode, *Insect* (mostly ants; myrmecochorous); *Water* (hydrochorous); *Explosive* (*i.e.*, explosive discharged, ballistichorous); *Unassisted* (autochorous); *Wind* (anemochorous); and *Animal* (Animal carried externally, exo-zoochorous). Rooting depth, *rd_1m*, Long (100-200 cm); *rd_intermediate*, Medium (30-100 cm); *rd_3m,* Short (10-30 cm); *rd_superficial*, as superficial phanerophyte (includes shallow roots spreading through soil). Vegetative propagation, *bulb*, *stump, stem; horizontal,* horizontal stem rooting; *rhizome,* rhizome, suckering root and stolon; and *collar,* collar and sprout.

In considering a comparison between site intra-treatments, the lower degree of heterogeneity in both plant communities (*i.e.*, rank dissimilarity < 750), and forest composition and structure and (*i.e.*, rank dissimilarity < 500) was observed 5 years after UA forest management and 15 years after both UA and EA forest management (Figure S5). For plant communities, the lower heterogeneity (*i.e.*, rank dissimilarity < 750) was

observed 5 years after UA forest management and 30 years after EA management (Figure S5).

In comparisons between paired EA and UA, species dissimilarity in the herb layer 5 years after harvesting was significantly higher than that 15 and 30 years after forest harvesting ($P < 0.01$) (Figure 6). Likewise, forest structure dissimilarity between UA and EA 5 years after harvesting was significantly higher than that 15 and 30 years after forest harvesting ($P < 0.05$) (Figure 6).

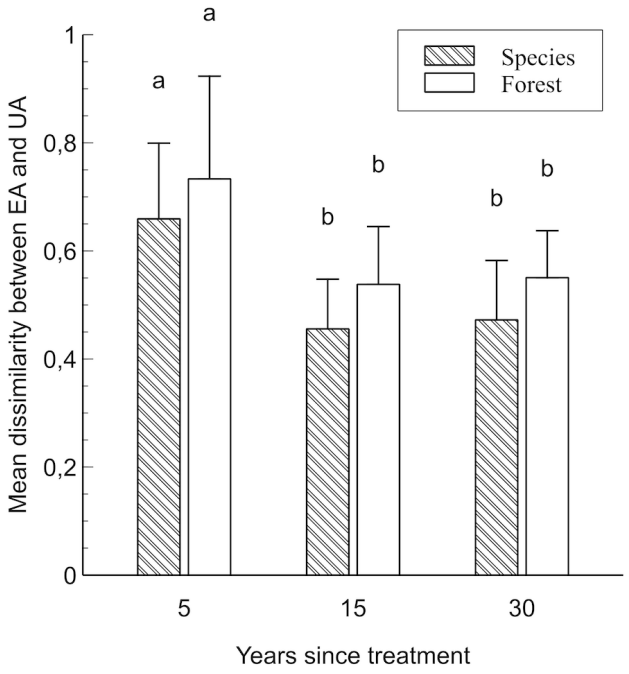

Figure 6. Variation of beta diversity (Bray-Curtis dissimilarity between EA and UA) over time after forest harvesting for A) plant species of the herb layer and B) forest composition and structure of the shrub-canopy layer. Each value is the mean of all paired treatments (EA and UA; in the same strip cutting). Error bars are standard errors. Means were compared between different treatments. Means not sharing the same letter significantly differ at $P < 0.05$ (Tukey's tests).

Impact of forest management on forest basal area and percentage cover of the herb layer along a chronosequence

Unmanaged forests have a significantly higher percentage cover of the herb layer (mean of 55.8 %) than forests 15 or 30 years after EA or UA management (means ranging from 37.6 % to 41.1 %; $P < 0.05$; Figure 7). In EA forests along the study chronosequence, percentage cover of the herb layer was the highest 5 years after EA forest harvesting (mean of 84.3 %) and was the lowest 15 years after EA forest harvesting (mean of 37.6%; Figure 7). In EA and UA, forest basal area tended to increase over time-since-harvesting (Figure 8). Forest basal area was significantly highest in the unmanaged forests compared to EA management at every time along the chronosequence (all $P < 0.001$) and compared to UA forests 5 and 15 years after forest harvesting ($P < 0.001$ and $P < 0.05$, respectively).

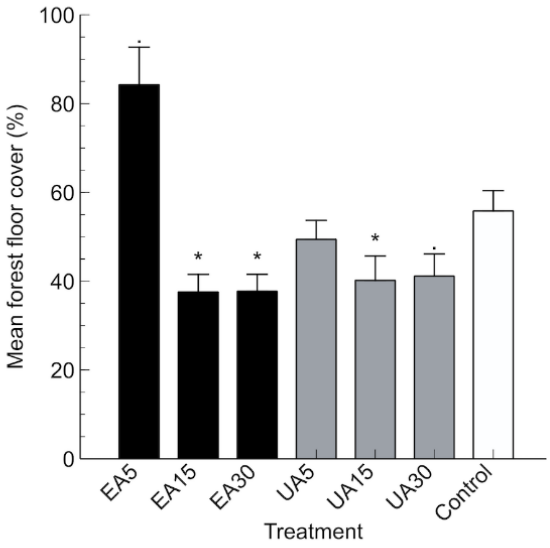

Figure 7. Variation in percentage forest floor cover in the herb layer of even-aged (EA) and uneven-aged (UA) forests over 30 years following forest harvesting. For EA and UA, n = 27; for unmanaged forests (control), n = 36. The number following the treatment represents the number of years after forest harvesting. Error bars are standard errors. Treatment means were compared to the unmanaged control. Means significantly differing from the control are represented by * ($P < 0.05$), · ($P \approx 0.05$).

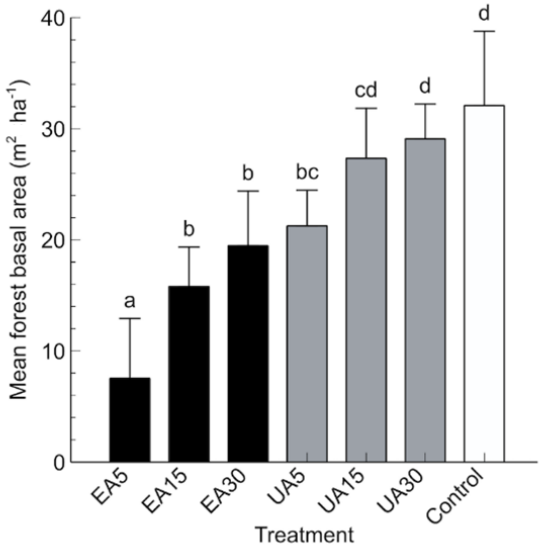

Figure 8. Variation in mean forest basal area of the shrub-canopy layer (m^2/ha) at the site level. For EA and UA, n = 9; for unmanaged forests (control), n = 12. The number following the treatment represents the number of years after forest harvesting. Error bars are standard errors. Means were compared between different treatments. Means not sharing the same letter significantly differ at $P < 0.05$ (Tukey's tests).

Discussion

Using metrics that were related to diversity, community composition and ecosystem functioning, we revealed the legacy of forest harvesting all along the chronosequence (Table 2). For both EA and UA management, the negative impacts of forest harvesting were highest 15 years after harvesting (Table 2). With respect to plant diversity of the herb layer, phylogenetic diversity metrics highlight long-lasting impacts of both EA and UA management (*i.e.*, significant decrease in diversity). As expected, we detected more numerous effects of the most intensive management (*i.e.*, EA) on community dissimilarity, compared to the less intensive one (*i.e.*, UA) (Table 2). Analysis of community composition reveal 1) a short-lasting but strong dissimilarity in plant traits and plant species community of the herb layer 5 years after EA harvesting and 2) more dissimilar forest

composition and structure that was acquired using EA management compared to unmanaged forest along the test chronosequence.

Table 2. Summary of legacies of forest harvesting on plant diversity of the herb layer and forest composition and structure along a chronosequence for even-aged (EA) and uneven-aged (UA) management, obtained from answers to questions that are related community composition, diversity and ecosystem functioning.

Management type	Metrics	5 years since harvesting	15 years since harvesting	30 years since harvesting
EA	Diversity		Lower total plant richness Lower alpha plant richness Lower alpha plant diversity Lower plant phylogenetic diversity	Lower total plant richness Lower plant phylogenetic diversity
	Community composition	Dissimilar plant species* Dissimilar forest composition and structure* Dissimilar trait-based community*	Dissimilar forest composition and structure* Dissimilar trait-based community* Tendency of more homogenous community for plant species and forest composition and structure	Dissimilar forest composition and structure* Tendency of more homogenous community for plant traits
	Ecosystem functioning	Stronger modification of plant trait Lower forest basal area	Lower forest basal area Lower % forest floor cover	Lower forest basal area Lower % forest floor cover
UA	Diversity	Lower total plant richness Lower plant phylogenetic diversity	Lower total plant richness Lower alpha plant richness Lower alpha plant diversity Lower plant phylogenetic diversity	Lower total plant richness Lower plant phylogenetic diversity
	Community composition	Dissimilar plant species* Dissimilar forest composition and structure* Tendency of more homogenous forest composition and structure and community for plant species and plant traits	Dissimilar forest composition and structure* Tendency of more homogenous forest composition and structure and community for plant species	
	Ecosystem functioning	Lower forest basal area	Lower % forest floor cover	

*Compared to unmanaged control

In addition, diminution of percentage cover of the herb layer and forest basal area compared to unmanaged forest targets forest harvesting as a disturbance that could affect forest functions at some point along the chronosequence. Given that we did not perform plant surveys of the same sites over time, the substitution of time-for-space is a limitation of our study (*e.g.*, Johnson & Miyanishi, 2008). Yet, the sampling effort was substantial, and care was taken to select close, paired sites with similar soil, topography, and management histories (Roy *et al.,* 2021).

Loss of species and long-lasting decrease in plant phylogenetic diversity of the herb layer

Contrary to many studies in temperate forests that are not based upon a chronosequence or which used limited diversity metrics (*e.g.*, Fredericksen *et al.,* 1999; Elliott & Knoepp, 2005; James, 2012), we did observe significant effects of EA or UA management on plant species diversity. Total species richness by treatment (for the same sampling area) captured the total decrease in richness of more than 28% in managed stands compared to unmanaged stands (excluding 5 years after EA). Also, using both identity-dependent PD and identity-independent metrics (species richness, Shannon Index), the period of 15 years after both EA and UA harvesting was identified as displaying the lowest plant alpha-diversity (Figure 2). In UA managed forest, with a harvesting rotation around 30 years, many temperate forests appear to be actually experiencing a major decrease in plant species diversity.

Phylogenetic diversity was more sensitive to long-lasting impacts of forest harvesting than species richness and Shannon diversity. In fact, significant differences between unmanaged forest and managed forest 30 years after forest harvesting were observed for PD but not for species richness and Shannon Index. The substantial decrease of more than 22% in PD

within UA forests 30 years after forest harvesting compared to unmanaged forests is an important legacy of forest harvesting. This result might illustrate the targeted filtering role of forest harvesting as seen in the plant phylogenetic tree that led to decreases in plant taxa, which are poorly suited to such management practices.

As has been observed by Dinnage (2009), many plant species were clustered in the phylogenetic tree of disturbed area, temporally free from biotic competition, compared to undisturbed one. For example, around 45% of total richness that we found shortly after EA harvesting was represented by only three of 36 orders (*i.e.*, *Poales, Asterales* and *Rosales*), which represent 17.8% of the total richness for unmanaged forests. Shortly after clear-cutting, plant species with adapted dispersal capacity and similar abiotic requirements, which could also be closely related phylogenetically, could all colonize this new environment. It seems that more than 5 years since EA harvesting are required to observe a phylogenetic tree with less clustering, possibly due to biotic filtering (*e.g.*, competition between species with similar niches that are also phylogenetically related). Silvicultural management could differentially affect species or even families, depending upon their abilities to persist after forest harvesting (Brewer, 1980; Reader, 1987; Decocq *et al*., 2004). For example, many fern and bryophyte species that have long phylogenetic histories are becoming rare in managed stands (Caners *et al*., 2010), where the conditions of transport, germination and survival of their propagules are altered (Karst *et al*., 2005). In the present study, we identified many species, including spore-bearing species, monocot species (*i.e*., both having a long phylogenetic history) and species at risk, which were more abundant in unmanaged forest (*e.g*., Figure S2). This behaviour reinforces the requirement for a diversity measure that takes phylogenetic relationships among species or disparity

into consideration. Yet, meta-analyses (*e.g*., Duguid & Ashton, 2013; Fedrowitz *et al*., 2014; Chaudhary *et al*., 2016), which lend support to some types of harvesting methods, are still based upon observations of mean species richness. We argue that even if PD along a chronosequence is a complex diversity metric to measure, it could be a more accurate method for evaluating species diversity that is related to conservation concerns.

Given that EA and UA management are largely implemented in temperate forest ecosystems, this decrease of phylogenetic diversity could raise many concerns (Srivastava *et al*., 2012). For biodiversity conservation, it would be important to evaluate the time that is needed to recover PD after forest harvesting in diverse ecosystems. Yet, we do not have a clear answer about limiting plant PD loss in temperate forest ecosystems.

Community composition: more important effects of even-aged management

Our results highlight important modifications to the plant species community in the herb layer that occurred 5 to 15 years after forest harvesting in EA forests (Figures 3a, 4a), thereby leading to a plant community assemblage that was more similar to that of unmanaged forests. This shift is consistent with the effects on pioneer species, such as increases in the genus *Rubus*, on plant community that were observed shortly after intensive forest management (Duguid & Ashton, 2013). Such pioneers are no longer abundant 15 years after harvesting. The recovery pattern of the plant community after EA management also could be observed through the increase in similarity of EA to its paired UA forest sites 15 or 30 years after harvesting (Figure 6).

Given that unmanaged forests contribute greatly to biodiversity conservation and are becoming scarce, variation in trait-based community in managed forests could simply be interpreted as how close they are to the unmanaged forests (*i.e*., integrity of trait-based community; dissimilarity of frequency or relative proportion of trait values) and whether they are closer with time-since-harvesting. In the present study, trait-based community was more similar to unmanaged forest at intermediate levels of canopy opening or forest density (*i.e*., about 20-22 $m^2 ha^{-1}$) that were found 30 years after EA management and 5 years after UA management (Figures 3c, 4c). It reinforces the fact that in deciduous forest, which is regulated by medium- and small-scale disturbances, such as gap formation (Runkle & Yetter, 1987), the light regime plays an important role in the distribution of plant traits (Tremlová & Münzbergová, 2007) and probably in the integrity of trait-based community. In the present study, trait-based community found in unmanaged forests are associated with high-density stands (Figure 8). This capacity to maintain both high forest density and integrity of trait-based community, which is only observed in unmanaged forest, could be partially due to the presence of large trees and the abundance of dead wood. In fact, large-diameter trees and abundance of dead wood provides plant species of the herb layer both heterogeneity in forest structure and light regimes (Lenière & Houle, 2006; Lutz *et al*., 2013), which are important for maintaining the integrity of trait-based community.

Like Aubin *et al.,* (2007 & 2009), we found plant traits that were associated with light requirements were related to effects of forest management. Plant traits in the herb layer, such as seed mass, seed propagation, root depth and root propagation were modified in different ways with time and type of silvicultural management (Figures 3c and 5, Figure S3). In the present study, 5 years following EA management and with greater canopy

openings, seed and root plant trait frequency values more strongly contrasted with unmanaged forest plant trait values. Similar observations have been made by Haeussler *et al*., (2007) and Decocq *et al*., (2004). The greater difference in plant traits could lead to temporary modification of ecosystem biodiversity and functioning (Garnier & Navas, 2013). More precisely, the association of the first dimension in PCA with forest stands less than 5 years after EA management would suggest a more substantial proportion of plants with 1) light and medium light seed, 2) seeds that were dispersed by water, animals and wind, 3) a rooting depth that was either shallow (10-30 cm) or deep (100-200 cm), and 4) vegetative propagation by the root collar, rhizome or stump (Figure 5). Without going in details, it is known that plant traits, such as plant-rooting depth, influence forest primary productivity, together with soil nutrients and hydrology (Nepstad *et al*., 1994; Jackson *et al*., 1997). Our results also highlight the importance of unmanaged forests in the conservation of plants with 1) vegetative propagation by bulbs, 2) a medium rooting depth (30-100 cm), and 3) very light seeds (< 0.02 mg $seed^{-1}$), which are usually found in spore-bearing plants (with old phylogenetic histories), such as bryophytes, ferns, lycopods and small-seeded families of angiosperms (*e.g*., *Orchidaceae*) (Figure 5). Whitney and Foster (1988) also found more plant species with low seed mass and limited litter penetration capacity in unmanaged forests.

As expected, forest structural dissimilarity to unmanaged forests was significantly higher in EA forests compared to UA forests along the study chronosequence (Figure 3b). This result agrees with the meta-analysis of Chaudhary *et al*., (2016), who ranked clear-cutting as a management prescription having a stronger negative effect than did selective logging on forest structure. At the stand level or higher spatial scales, homogenization of the forest

composition and structure following forest harvesting, especially through clear-cutting, is a concern that is raised in many studies of forest biodiversity (*e.g.*, Hale *et al.,* 1999; Moola & Vasseur, 2008; Rosenvald & Lohmus, 2008). Yet, this legacy of EA forest harvesting might be diminished if we consider a whole forest rotation period that is associated with EA management. In fact, the chronosequence that was used in the present study is more adapted to fitting a UA management rotation period; indeed, a longer period would be needed to anticipate more precisely the legacies of EA management.

With regard to UA forest management, the low heterogeneity that was observed 5 years after harvesting (Figure S5) accords with studies in temperate forests that observed homogenization of plant composition after partial forest harvesting (Scheller & Mladenoff, 2002).

Percentage cover of the herb layer and forest basal area related to forest functions

The percentage cover of the herb-layer and forest basal area in the shrub-canopy layer, which were highest in unmanaged stands (except percentage cover 5 years after EA harvesting; Figures 7 and 8), may have important implications for forest ecosystem functioning. In temperate forests, a high percentage cover of the herb-layer is usually associated with high nutrient turnover rates from plant biomass to the soil (Larcher, 2003). Obviously, the temporary high percentage cover of the herb layer 5 years after EA harvesting was likely related to very low forest basal area at the shrub-canopy layer (Figure 8), as has been observed in other studies (*e.g.*, Chavez & Macdonald, 2010). The presence of large-diameter deciduous trees in unmanaged forest could lead to both high forest basal area (Sist *et al*., 2014) and heterogeneity of light availability in the herb layer (Nicotra *et*

al., 1999). These forest conditions can lead to increased ecosystem resilience to disturbances (Orwin & Wardle, 2005) and aboveground carbon sequestration (Torres & Lovett, 2012; Lutz *et al*., 2018). For example, Imai *et al*., (2009) found that carbon density of forest stands (sum of aboveground, fine roots, and soil organic carbon) was more than two-fold higher in unmanaged forest compared to degraded forest that had been harvested by conventional logging. With the very low forest basal area that was observed shortly after EA management, we would expect to have less carbon fixation by plants and lower nutrient inputs to the soil.

Conclusion

The present study suggests that the studied chronosequences for either EA or UA management are shorter than the recovery time that is needed to conserve plant diversity. We can anticipate long-term decreases in total species richness and plant species phylogenetic diversity (*e.g*., decrease in abundance of many spore-bearing and very small-seeded plant species). Along the studied chronosequence, the 15-year period after harvesting for both EA and UA management had the highest list of detected negative impacts. Modification of community composition based upon dissimilarity metrics demonstrated more numerous effects of EA management than UA management. A strong, but short-lasting dissimilarity in trait-based community of the herb layer 5 years after EA harvesting relative to unmanaged forest suggests a modification of forest ecosystem functioning. Moreover, decreases in forest basal area compared to unmanaged forest pointed forest harvesting as a disturbance that could affect forest functions at some point along the chronosequence.

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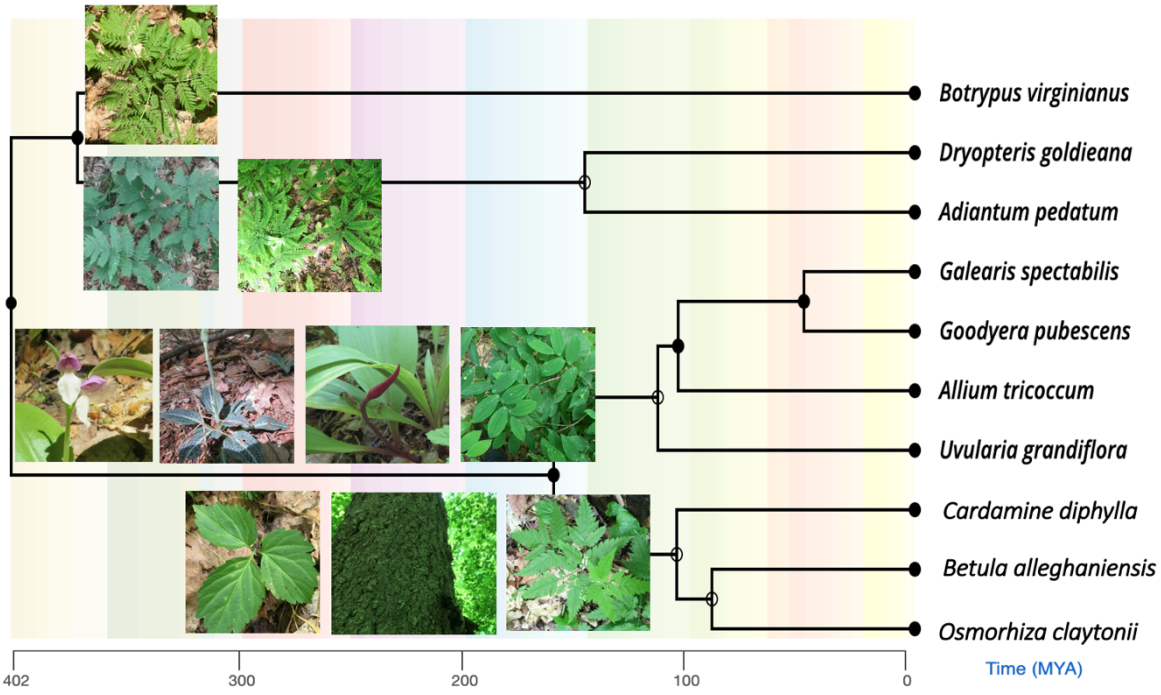
Supplementary information I

Table S1. List of species used to replace the actual plant species when trait data are missing for specific plant trait values or phylogeny. Plant traits are from TOPIC, Aubin *et al*., 2012.

Species name	Replacement species	**Species name**	Replacement species
Actaea pachypoda	*Actaea rubra*	***Fragaria vesca***	*Agrimonia gryposepala*
Adiantum pedatum	*Dryopteris marginalis*	***Galéaris spectabilis***	*Orchis spectabilis, Cypripedium acaule*
Agrostis alba	*Agrostis capillaris, Agrostis scabra*	***Galeopis tetrahit***	*Apocynum androsaemifolium, Lycopus uniflorus*
Allium tricoccum	*Trillium erectum*	***Galium triflorum***	*Apocynum androsaemifolium*
Alnus rugosa	*Alnus incana*		
Amelanchier canadensis	*Prunus pensylvanica, Prunus virginiana*	***Goodyera pubescens***	*Cypripedium acaul*e
Amphicarpa bracteata	*Viola canadensis*	***Gymnocarpium dryopteris***	*Dryopteris marginalis, Dryopteris intermedia*
Aralia racemosa	*Aralia nudicaulis*	***Hydrophyllum virginianum***	*Solidago canadensis*
Arisaema atrorubens	*Medeola virginiana*	***Impatiens capensis***	*Pyrola elliptica*
Asarum canadense	*Medeola virginiana*	***Juncus effusus***	*Poa pratensis* ssp. *pratensis*
Aster acuminatus	*Aster lanceolatus*	***Lactua biennis***	Taraxacum officinale
Aster lowrieanus	*Aster lanceolatus*	***Lycopus uniflorus***	*Apocynum androsaemifolium*
Athyrium thelypteroides	*Athyrium filix-femina*	***Maianthemum racemosum***	*Medeola virginiana*
Botrychium virginianum	*Dryopteris intermedia*	***Onoclea sensibilis***	*Osmunda cinnamomea*
Brachelytrum erectum	*Poa pratensis*	***Oryzopsis asperifolia***	*Poa compressa, Poa pratensis*
Cardamine diphylla	*Cardamine pratensis*	***Osmorhiza claytoni***	*Aralia nudicaulis*
Carex aperta	*Carex arctata, Carex annectens*	***Osmunda cinnamomea***	*Dryopteris intermedia*
Carex arctata	*Carex albursina*	***Osmunda claytoniana***	*Dryopteris intermedia*
Carex debilis	*Carex deweyana*	***Oxalis montana***	*Oxalis acetosella* ssp. *montana*
Carex novae-angliae	*Carex normalis*	***Panicum canadensis***	*Panicum capillare*
Carex peckii	*Carex pedunculata*	***Poa alsodes***	*Poa palustris*
Carex praticola	*Carex prasina*	***Polygonatum pubescens***	*Streptopus roseus*
Carex scabrata	*Carex rostrata*	***Polygonum cilinode***	*Achillea millefolium*
Carex synocephala	*Carex stricta*	***Polypodium virginianum***	*Dryopteris marginalis*
Circaea canadensis	*Circaea alpina*	***Polystichum acrostichoides***	*Dryopteris marginalis*
Circaea lutetiana	*Circaea alpina*	***Potentilla norvegica***	*Anaphalis margaritacea, Fragaria vesca*
Claytonia caroliniana	*Claytonia virginica*	***Prenanthes altissima***	*Anaphalis margaritacea*
Claytonia virginica	*Trillium erectum*	***Pyrola elliptica***	*Pyrola asarifolia*
Coptis groenlandica	*Coptis trifolia*	***Ranunculus abortive***	*Ranunculus repens*
Cornus stolonifera	*Cornus sericea*	***Ribes americanum***	*Ribes glandulosum*
Cypripedium acaule	*Orchideae*	***Ribes cynosbati***	*Ribes glandulosum*
Danthonia spicata	*Poa pratensis*	***Sambucus pubens***	*Sambucus canadensis*
Dennstaedtia punctilobula	*Dryopteris intermedia*	***Sanguinaria canadensis***	*Ranunculus abortivus*
Desmodium glutinosum	*Amphicarpaea bracteata*	***Solidago altissima***	*Solidago caesia*
Dicentra canadensis	Papaveraceae	***Sonchus arvensis***	*Taraxacum officinale*
Dirca palustris	*Lonicera canadensis*	***Symphiotrichum puniceum***	*Solidago canadensis*
Dryopteris goldiana	*Dryopteris marginalis*	***Thelypteris palustris***	*Thelypteris noveboracensis*
Dryopteris spinulosa	*Dryopteris marginalis*	***Tiarella cordifolia***	*Mitella nuda*
Epifagus virginiana	*Lycopus uniflorus*	***Uvularia grandiflora***	*Trillium grandiflorum*
Epipactis helleborine	*Cypripedium acaule*	***Viburnum trilobum***	*Viburnum opulus*
Equisetum arvense	*Equisetum sylvaticum*		
Eurybia macrophylla	*Aster macrophyllus*		

Figure S2. Photographs and phylogenetic tree of species that were observed to be more abundant or only present in unmanaged forest in the current study sites.



The first three species reproduce by spores. Galearis spectabilis and *Goodyera pubescens* are rare orchids and *Allium tricoccum* has vulnerable status in Quebec. *Adiantum pedatum*, a fern that is vulnerable to unsustainable harvesting, was abundant in unmanaged forest but experienced a major decrease in managed forest. *Uvularia grandiflora* is also vulnerable to unsustainable harvesting in Quebec.

Figure S3. Proportion of plant abundance in the herb layer that was found for each order (ranked by phylogeny) following each treatment.

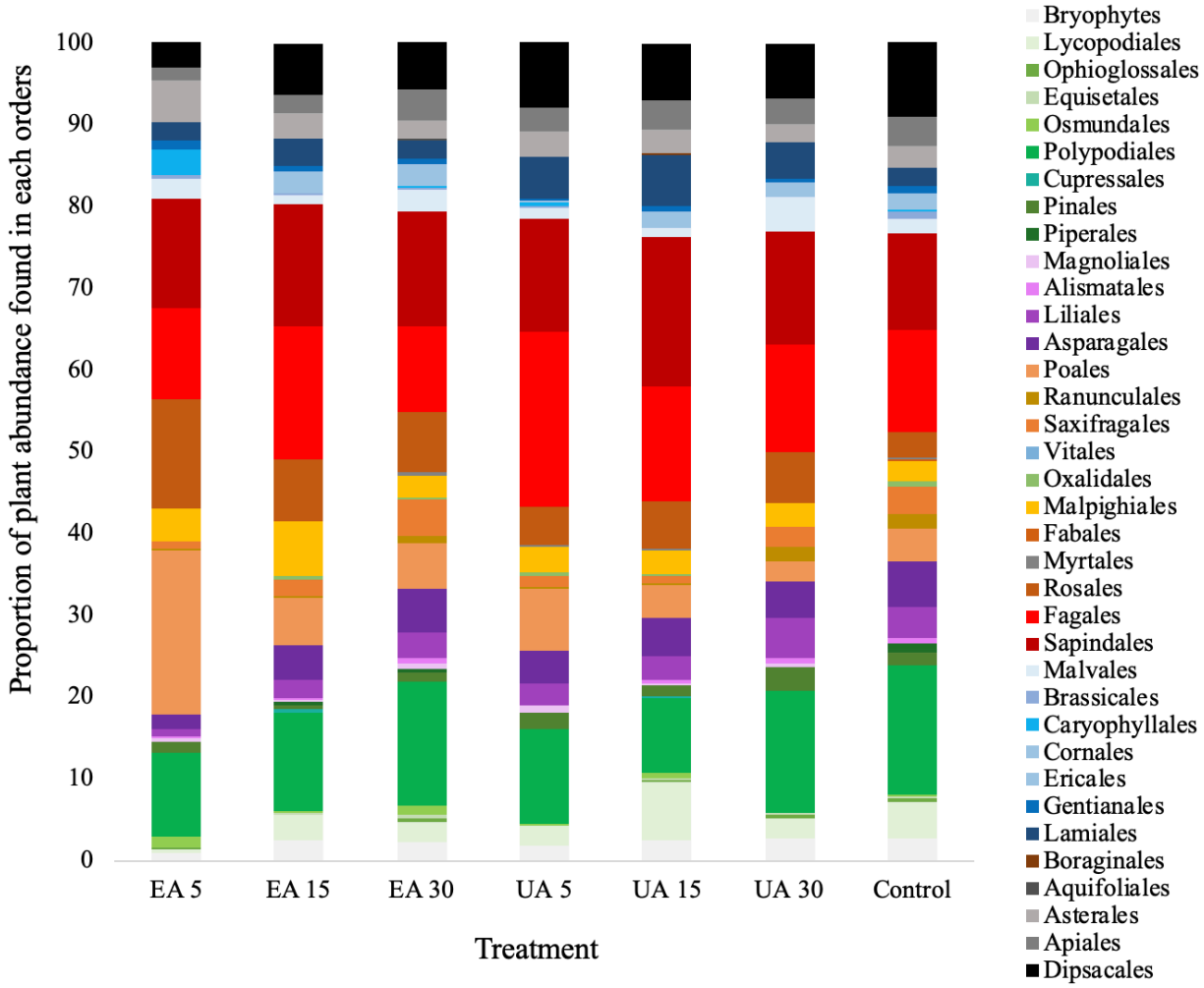
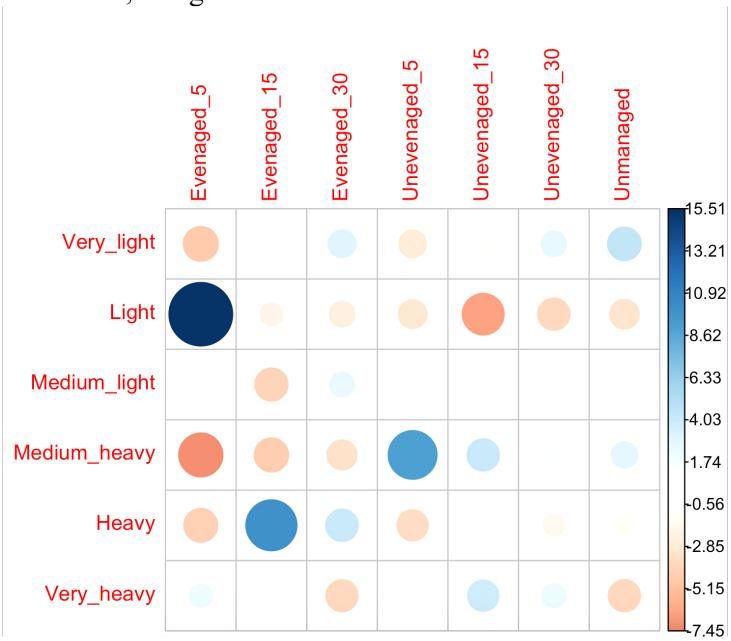
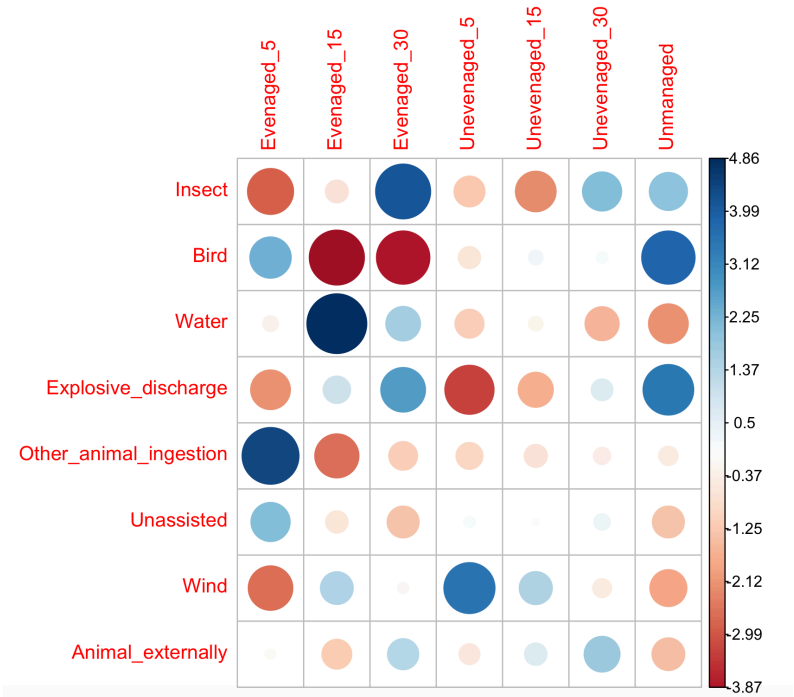


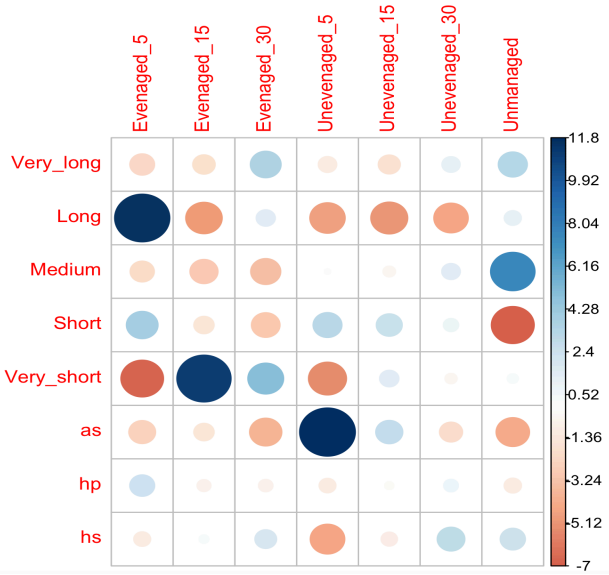
Figure S4. Association between trait values of the four plant traits in the herb layer and the treatments, using Pearson residuals.



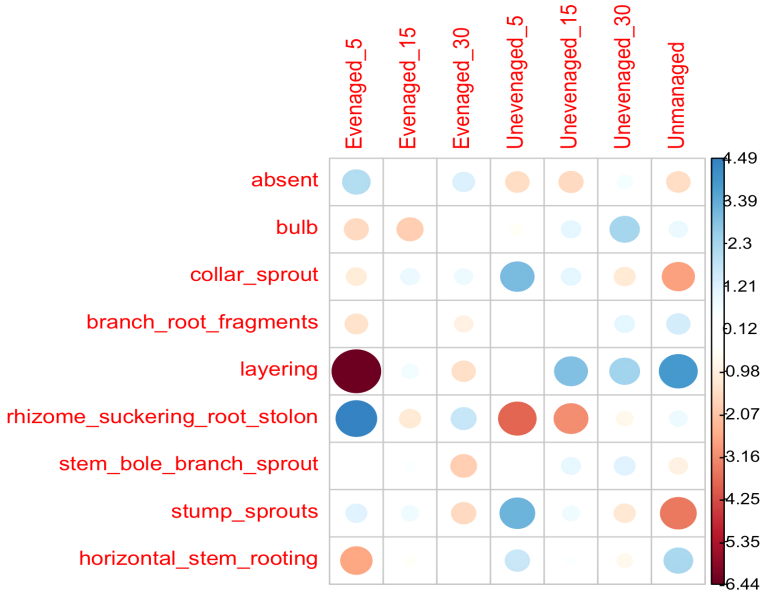
a) Seed mass (*Very light*, < 0.02 mg; *Light*, < 4 mg; *Medium Light*, < 20 mg; *Medium Heavy*, < 50 mg; *Heavy*, < 100 mg; *Very Heavy*, > 100 mg).



b) Seed dispersal mode (*Insect* (mostly ants; myrmecochorous), *Bird* (ingestion; endo-zoochorous), *Water* (hydrochorous), *Explosive discharge* (ballistichorous), *Other animal ingestion* (endo-zoochorous), *Unassisted* (autochorous), *Wind* (anemochorous) and *Animal carried externally* (exo-zoochorous)).



c) Rooting depth, *Very long*, >200 cm; *Long*, 100-200 cm; *Medium*, 30-100 cm; *Short*, 10-30 cm; *Very short*, <10 cm; *as*, superficial phanerophyte (includes shallow roots spreading through soil); *hp*, other deep Raunkier life forms (includes tap roots); *hs*, other superficial Raunkier life forms (includes shallow roots spreading through soil).



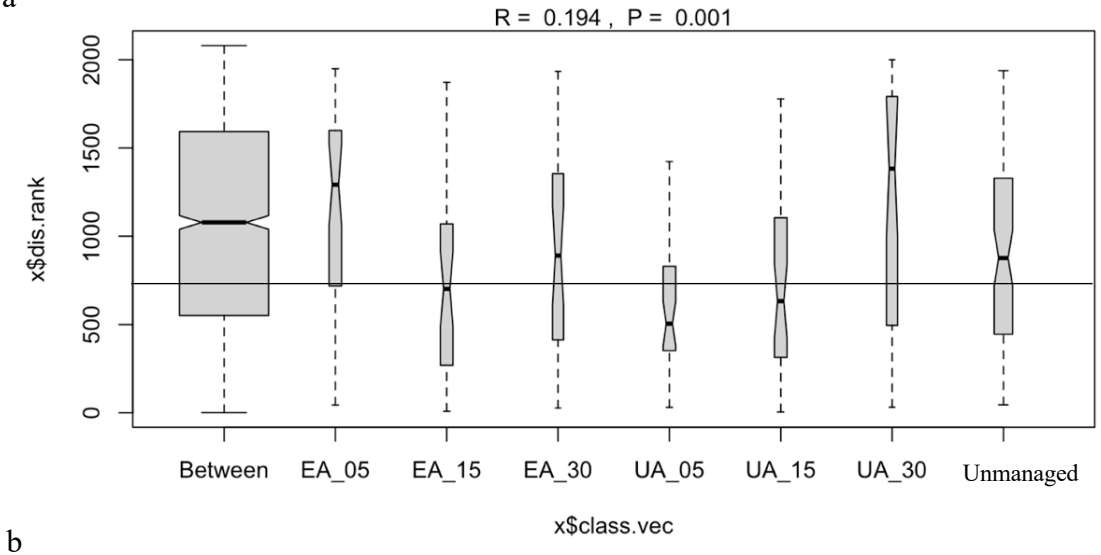
d) Vegetative propagation

Description Figure S4. The size of the circle is proportional to the cell contribution to the Chi-Square score. Positive residuals (in blue) specify a positive association and negative residuals (in red), a negative association between trait values and treatment-years. EA; even-aged stand, UA; uneven-aged stand. The number following the treatment represents the number of years after forest harvesting. Differences in trait frequency were estimated at different times after forest harvesting in EA and UA forests compared to the unmanaged control. The Chi-Squared test of independence was used to evaluate whether there was a significant association between traits and the treatment-years (including control). Under the null hypothesis (H_0), the trait values and the treatment-years variables of the contingency table are independent. If the trait values and the treatment-years variable were statistically significantly associated ($P < 0.05$), the contribution of each value of traits to the Chi-square score could be evaluated with Pearson's (standardized) residuals.

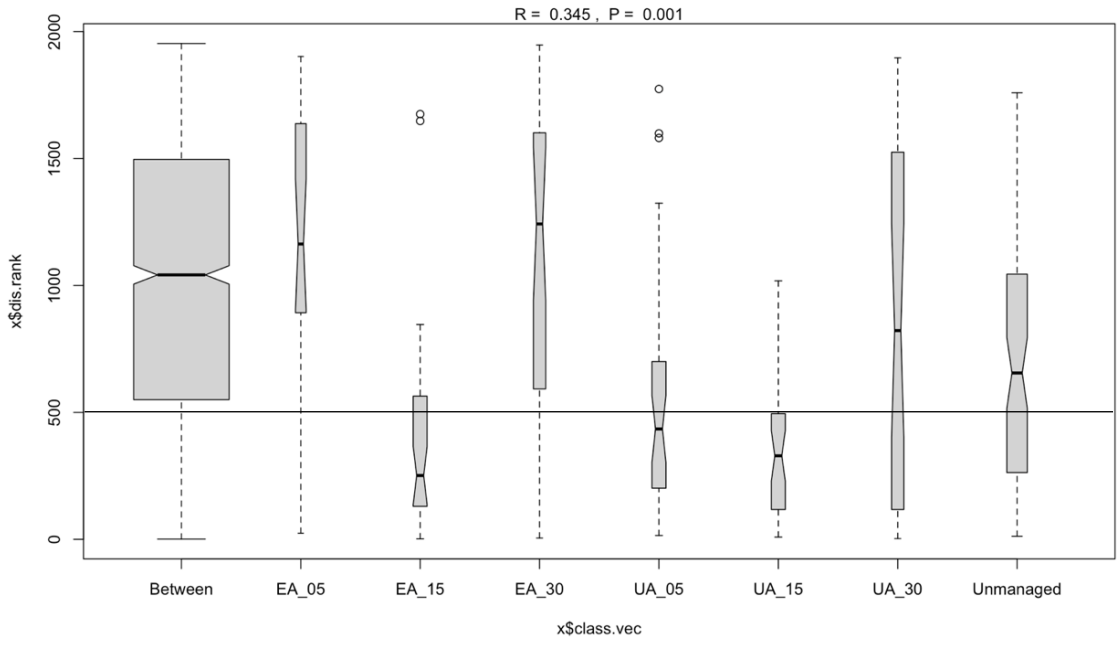
For all traits that were tested in this study, trait values were significantly associated ($P < 0.05$) with the different forest management treatments (Seed mass $X^2 = 832$, df = 30, Seed dispersal mode $X^2 = 242$, df = 42, Rooting depth $X^2 = 922$, df = 42 and Vegetative propagation $X^2 = 232$, df = 48). Important associations are described here. Very light seeds (< 0.02 mg seed^{-1}) that are found in spore-bearing plants, such as ferns and lycopods, and small-seeded angiosperm families, such as *Orchidaceae*, were positively associated with unmanaged forest (+5.0) and negatively associated with EA forests 5 years after forest harvesting (-5.0) (a). Light seeds (between 0.02 to 4 mg seed^{-1}) were strongly and positively associated with EA forests 5 years after forest harvesting (+16.0) and negatively associated with UA forests 15 years after forest harvesting (-7.0). Five years after forest harvesting, medium-heavy seeds (between 20 to 50 mg seed^{-1}), which are found in some species of genera *Fraxinus* and *Acer*, and in herb species such as *Maianthemum racemosa*, were positively associated with UA forests (+9.0) and negatively associated with EA forests (-7.0). Finally, heavy seeds (between 50 to 100 mg seed^{-1}) that were found mostly in shrub or tree species were positively associated with EA forests 15 years after forest harvesting (+10). Seed propagation strategies varied among forest management treatments (b). Seed propagation by animal ingestion (+4.4) and by wind (+3.5) was positively associated with EA forests 5 years after forest harvesting. Plant root depth of medium length was positively associated with unmanaged forests (+7.5) (c). EA forests 5 years after forest harvesting were positively associated with long root (+11.6). In contrast, EA forests 15 years after forest harvesting was negatively associated with long roots (-5.0) and positively associated with very-short roots (+11.2). Root propagation by layering was negatively associated with EA forests 5 years after forest harvesting (-6.4) (d). Root propagation by rhizome, suckering root or stolon was positively associated with EA forests 5 years after forest harvesting (+4.5).

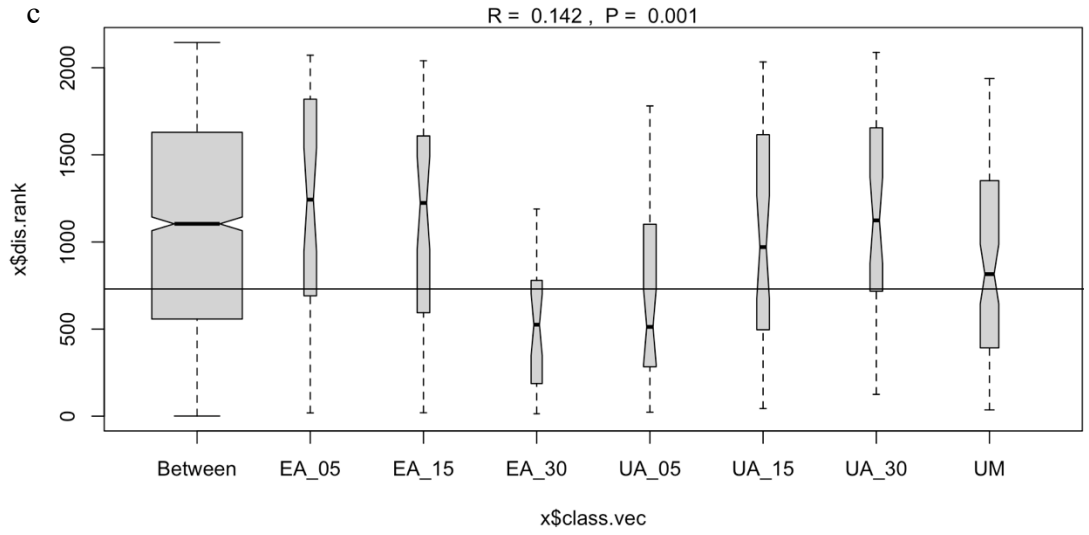
Figure S5. Box-and-whisker plots of the mean intra-treatment dissimilarity (BC_{ij}) in even-aged (EA) and uneven-aged (UA) forests over 30 years after forest harvesting. a) Mean intra-treatment dissimilarity (BC_{ij}) a) for plant species and in the herb layer, b) forest composition and structure at the shrub-canopy layer and c) plant traits.

a



b





Each value is the mean of all possible combination of site with the same treatment-years or unmanaged control. EA, even-aged stand; UA, uneven-aged stand. Between represent the mean inter-treatment dissimilarity. R = Statistic R refer to dissimilarity *between (inter-treatment)* compare to *within (intra-treatment)* and P refer to the statistically significance of within dissimilarity following ANOSIM analysis. The number following the treatment represents the number of years after forest harvesting.

Supplementary information II

Variable that explains plant diversity

Detection of variables associated with potential diversity loss due to forest management could help improving our understanding of forest ecology. In Kenauk Nature territory, we analyze if there are important variables associated with plant diversity? The relationship between fixed continuous variables and plant diversity was evaluated in the present experimental design. More precisely, in order to evaluate the importance of selected forest parameter on plant diversity, litter weight and soil physico-chemical parameters concentration were measured in each plot.

Selection of variable used to explain plant diversity of the herb layer

Aside from management, the importance of other variable on plant diversity of the herb layer were tested. In order to evaluate the relationship between plant diversity of the herb layer and fixed continuous variable related to litter, soil and forest canopy, model comparison approach based upon the Kullback–Leibler information quantity as presented by Anderson *et al*., (2000) using the package AICcmodavg. We first compared the performance (using the Akaike information criterion, AIC_C) of all logical model combinations, which ranged from single effects to double and triple interactions among our predictor variables, with management included in the model (Table SII 1). The predictor variables included soil pH (organic and mineral), American beech litter abundance (g/m^2), exchangeable bases (cmol kg^{-1}), ammonification rate (mg $kg^{-1}d^{-1}$) and forest basal area (m^2 ha^{-1}). Only American beech litter was selected due to the known potential negative impact of this litter on understory plant establishment maple-basswood bioclimatic domain. Based on this preliminary analysis, total soil pH and American beech litter abundance were selected. Two linear mixed model (lme4 package, function lmer) were used to explore the relationship between 1) soil pH and 2) American beech litter weight (fixed continuous variables) on plant phylogenetic diversity, with forest management included in those models.

Is their important variable associated with plant diversity in the herb layer?

The best tested model to explain plant PD in the herb layer (with management type included in the model; random factor) was soil pH, follow by the null model (Table SII 1). Soil pH was significantly ($p=0.003$) positively correlated (Corr= 0.978) to plant PD (slope 0.17 and intercept -0.21) with management type included in the model. In the present study plant PD in the herb layer was significantly ($p=0.002$) but not strongly correlated with beech litter abundance (the third best model Table SII 1). The output of the mixed model suggests that there was a negative correlation (Corr = -0.592) between beech litter abundance (slope -0.78) and plant PD (intercept 0.7276) with management type included in the model (data not shown).

pH and American beech litter abundance as explanatory variable for plant diversity of the herb layer

The relation between soil or other forest variable on plant diversity demonstrate a negative correlation between plant PD and beech litter abundance as well has a positive correlation with soil pH. Not surprisingly, pH was the best predictor variable to explain plant PD (Table SII 1). In fact, at large scale, in temperate and boreal forest, where most of the soils are acidic, soil pH has a strong positive association with plant diversity (Pärtel *et al*., 2004; Lenière & Houle, 2006). This could be due to the important pool of plant species that prefer soil with medium and high pH (Pärtel *et al*., 2004) and the scarcity of those soil in temperate forest. Beech litter abundance was the third best model to explain mean plant PD. It has been demonstrated that the dominance of Fagus species could be associated with a reduction in plant diversity of the herb layer (Barbier *et al*., 2008, Molder *et al*., 2008). In fact, beech produces a weakly decomposable and acidic litter that could have negative impacts (physical, chemical or allelopathic) on propagules establishment (Pellissier & Souto, 1999; Hane, 2003) and ability of the roots to penetrate the litter depending on seeds reserves and sizes (Xiong & Nilsson, 1999; Leishman *et al*., 2000). In temperate forest, a special care on soil pH and beech (or other tree species with weakly decomposable and acidic litter) abundance are recommended for manager interested in the recovery of plant diversity.

Table SII 1. Model comparisons for plant phylogenetic diversity (PD) in the herb layer.

Model	Model no.	*k*	AICc	Weight (ω, %)
pH+(1|management)	2	4	0.61	69
(1|management)	8	3	2.63	25
Beech litter abundance+(1|management)	4	4	5.87	5
pH+ Beech litter abundance +(1|management)	6	5	9.71	1
Ammonification rate+(1|management)	5	4	12.55	0
Base exchangeable+(1|management)	3	4	14.54	0
Forest basal area+(1|management)	1	4	14.72	0

An underline predictor variable indicates its negative effect on the response variable (plant PD in the herb layer) in lmer model with management as random factor. K number of parameters estimated in the model, AICc Akaike information criterion, corrected for small sample sizes. Simple model (1 predictor) and other models with $\omega > 1\%$ are shown.

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CHAPITRE II. Legacies of forest harvesting on soil properties along a chronosequence in a hardwood temperate forest

Abstract

Understanding long-lasting effects of different silvicultural systems on soil properties is critical to sustainable forest management. We determined even-aged (EA, clearcuts) and uneven-aged (UA, partial harvests; 30% by single-tree selection) management effects on soil properties 5, 15 and 30 years after harvesting, relative to unmanaged old-growth forests, in a hardwood forest in southern Quebec, Canada. In total, 198 plots were sampled in 66 randomly selected sites. We measured coarse woody debris (CWD) and examined key soil physico-chemical properties in the forest floor and mineral horizon (0-20 cm). CWD volume strongly decreased in the forest floor of EA managed forests compared to unmanaged forests; no recovery pattern was observed 30 years post-harvest. Following UA management, CWD volume only significantly decreased 5 years after harvesting. Relative to old-growth forests, sites that were subject to forest harvesting were characterized by soils with lower values for key chemical properties that drive soil fertility, including pH, available K, Ca and Mg, and base saturation. Five years after harvesting, both EA and UA managed forests had higher rates of nitrification than unmanaged forests. Overall, EA management had stronger and longer lasting harvest effects on soil chemical properties than forest sites involving UA management. We also assessed, in a greenhouse pot experiment, whether a hypothetical gradient of decreasing soil fertility would affect seedling growth of three tree species (trembling aspen, white birch, yellow birch). Soil originating from EA managed forests with lower soil fertility resulted in lower height growth rates and total dry biomass for the three species, relative to soil from the unmanaged forest (higher soil fertility). Forest harvesting can have major detrimental effects on soil fertility and productivity, over both the short- and long-term, and impacts may increase with harvest intensity.

Key words, Soil productivity, Even- and uneven-aged silviculture, Forest harvesting legacies, Chronosequence, Tree growth, Northern hardwood forest

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Introduction

Forest soils facilitate crucial nutrient and energy flow processes that support primary production, regulate climate and sustain biodiversity. Yet, these ecosystem processes and services may be altered by forest harvesting over the short- to long-term (Hume *et al*., 2018; Bowd *et al*., 2019). Soils of hardwood forests in eastern North America are vulnerable to forest harvesting (Marshall, 2000; Cleavitt *et al*., 2018). In these temperate forests, sylvicultural systems may be based upon partial harvesting (*e.g.*, group to single tree selection cutting) and uneven-aged (UA) management, which promote a permanent forest cover and the regrowth of stands with multiple age classes. Shelterwood systems that are based upon total harvesting of varying form and extent (*e.g.*, patch clearcuts, strip clearcuts) and even-aged (EA) management are used to reset forest stands to a regeneration stage. Based upon a literature review, Nolet *et al*. (2018) showed that the common perception of UA management being better suited than EA management to maintaining ecological diversity and processes cannot be substantiated. The authors argued that both approaches are needed at the landscape level to ensure a greater number of positive ecological impacts. Contradictory results reported in previous studies suggest that further work is clearly required to assess the long-lasting effects of different silvicultural systems on soil properties in northern temperate hardwood forests (Thiffault *et al*., 2011; Hume *et al*., 2018; Nolet *et al*., 2018).

Evaluating the legacies of forest harvesting on soil physical and biochemical properties is methodologically challenging. First, there are few remaining old-growth forest stands in northeastern North America in which making inferences regarding the effects of forest

harvesting on soil properties is arduous (Diochon *et al*., 2009). Nevertheless, when soil attributes following harvesting are compared to the unmanaged forest reference, information about recovery time or shifts towards natural conditions may be obtained, which is critical in designing sustainable forestry. Second, the effects of harvesting on soil properties can strongly vary among harvesting intensities and the type of forest management that is involved (Federer *et al*., 1989; Grigal, 2000; Jerabkova *et al*., 2011; Dyck *et al*., 2012). Detrimental effects of harvesting on soil physical, chemical and biological properties and on soil productivity are expected to increase with harvest intensity (Grigal, 2000; Lindo & Visser, 2003; Siemons *et al*., 2011). Third, the impacts of harvesting on soil properties may be dependent upon soil layers. For example, the negative effects of harvesting on soil nutrient pools (*e.g.*, N, P and base cations) and soil acid-base status tend to be more frequent and evident in the forest floor than in the mineral soil (Thiffault *et al*., 2011; Hume *et al*., 2018). Last, soil properties may vary through time following harvesting (Jonard *et al*., 2017). For example, in a meta-analysis of studies that were conducted in northern forest soils (*i.e*., temperate and boreal), Hume *et al*. (2018) determined that N concentration (forest floor and mineral horizons) and C concentration (forest floor only) declined rapidly after harvesting and increased slowly as stands aged. In the short-term, harvesting may export large quantities of biomass from the forest, especially after clearcutting (EA management), which can lead to considerable depletion of coarse woody debris, and soil carbon and nutrients (Yanai *et al*., 1999; Jenkins *et al*., 2004; Thiffault *et al*., 2011). Forest harvesting may also promote short-term increases in nitrification rates, base cation leaching, release of Al and soil acidification through microclimate effects, such as increased soil temperature and moisture (Adams *et al*., 2000;

Jerabkova *et al*., 2011). Harvesting can also cause short- and mid-term degradation of soil physical properties, such as bulk density, porosity and aggregate stability, which in turn may alter nutrient cycling (Zhou *et al*., 2015; Siebers and Kruse, 2019). Accordingly, any important short-term effects of forest harvesting on soil nutrient availability would affect tree regeneration growth. Over the long-term, our empirical understanding of how different harvesting intensities affect forest soil properties, however, remains limited (Clarke *et al*., 2015). Such studies suggest that soil properties could take from multi-decadal to a century to recover from harvesting impacts (Lal *et al*., 2005; Diochon *et al*., 2009; Prest *et al*., 2014; Bowd *et al*., 2019). In the long- term, soils of hardwood forests seem especially vulnerable to base cation depletion (Tritton, 1987; Federer *et al*., 1989; Siemion *et al*., 2011) and decreases in abundance and heterogeneity of coarse woody debris (Angers *et al*., 2005; McGee *et al*., 2007; Vanderwel *et al*., 2008). Moreover, litter of different origins could modify cation cycling. For example, beech species are especially associated with decreases in soil cations and pH (Guckland *et al*., 2009). Although legacies of forest harvesting may vary between EA and UA management, both can modify inputs and quality of tree litter (Lindo & Visser, 2003). Yet, these soil legacies could also impair long-term site productivity and tree growth (Lambers, Chapin & Pons, 2008).

The first objective of this study was to determine the effects of EA and UA forest management on soil properties 5, 15 and 30 y after harvesting in a hardwood forest of southern Quebec, Canada. Because UA and EA forest management modified site characteristics, we hypothesized that relative to the unmanaged forest reference, they would affect key soil properties. We predicted that the magnitude of soil responses to forest harvesting would be greater over the short-term and in EA managed forest. The second

objective was to determine, in a greenhouse pot experiment, whether differences in soil productivity in EA managed forest and unmanaged forest reference would affect tree seedling growth. In the EA managed forests, soils were collected along a hypothetical gradient of decreasing soil fertility (*i.e.*, simulated decrease after one, two and three forest rotations). We hypothesized that this gradient of decreasing soil fertility would induce negative effects on tree seedling growth and that these effects would increase with the decreasing gradient.

Materials and methods

Study sites, experimental design and field sampling

Soil properties were assessed in unmanaged forests (reference, 12 sites of old-growth forest > 100 years, with dominant and co-dominant trees older than 200 years, and no obvious sign of past harvesting). These were compared with even-aged managed stands (EA, 27 sites) and in uneven-aged managed stands (UA, 27 sites) along a harvest chronosequence (< 5 years, 15 years, 30 years after forest harvesting; hereafter, EA5, EA15, EA30, UA5, UA15 and UA30). The sites were selected based upon random stratification (following latitude and longitude) of a deciduous forest in the sugar maple (*Acer saccharum* Marsh.) – basswood (*Tilia americana* L.) bioclimatic domain. This domain also contains other deciduous tree species, such as yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.) (Saucier *et al*., 2009). Mean basal area by tree species and percentage forest floor cover of the herb layer in the study sites are provided in Table 1. The sites were located within a 26 500 ha private forest (Kenauk Nature site network; 45.71° to 45.84° N, -74.95° to 74.77° W) (Figure 1). The climate is cold temperate, with an average annual temperature of 4.5 °C, ranging from an average minimum of –12.5 °C in

January to an average maximum of 18.9 ºC in July (Environment et Changement climatique Canada, 2020). Average annual precipitation is 1091.1 mm. Soils in the study area are classified as Dystric Brunisols (USDA, Typic Drystrocyepts), with moder-type humus (FH horizon of ca. 2 cm), which developed on glacial till deposits that are composed mainly of gneiss, quartzite and granite (Lajoie, 1967; Soil Classification Working Group, 1998). Soils in this region experienced acidification beginning in the mid-20th century given high S and N deposition exceeding soil critical loads (Ouimet *et al.*, 2006). For example, from 1999 to 2002, total dry and wet acid deposition rates were higher than 21 kg SO_4-S ha^{-1} yr^{-1} and about 10 kg N ha^{-1} yr^{-1} (Ouimet & Duchesne, 2009).

Table 1. Basal area by tree species and forest floor cover in even-aged and uneven-aged managed forests and in unmanaged forest reference sites along a chronosequence of forest harvesting.

	Even-aged management			Uneven-aged management			Reference
	5 years	15 years	30 years	5 years	15 years	30 years	
Mean basal area (m^2/ha)							
Acer pensylvanicum	0.8 (0.1)	2.1 (0.1)	0.9 (0.1)	1.0 (0.2)	1.2 (0.1)	0.4 (0.2)	0.4 (0.1)
Acer rubrum	0.2 (0.2)	0.5 (0.1)	2.4 (0.5)	2.0 (0.7)	1.9 (0.6)	3.1 (1.0)	0.9 (0.5)
Acer saccharum	2.3 (0.5)	1.7 (0.4)	4.2 (0.6)	10.5 (1.0)	13.5 (1.2)	11.7 (1.4)	15.0 (1.1)
Betula alleghaniensis	0.4 (0.1)	0.3 (0.1)	0.9 (0.2)	0.9 (0.5)	1.2 (0.7)	1.2 (0.3)	3.7 (1.0)
Fagus grandifolia	1.7 (0.3)	4.0 (0.4)	2.6 (0.4)	3.4 (0.8)	3.6 (0.4)	5.8 (0.8)	1.9 (0.5)
Fraxinus americana	1.9 (0.7)	1.4 (0.2)	2.2 (0.9)	0.5 (0.4)	0.6 (0.4)	0.5 (0.3)	0.8 (0.4)
Ostrya virginiana	0.7 (0.1)	0.9 (0.1)	1.2 (0.2)	1.8 (0.4)	1.1 (0.1)	0.5 (0.1)	0.4 (0.1)
Populus grandidentata	0.1 (0.0)	1.2 (0.7)	1.5 (1.1)		0.6 (0.2)	0.5 (0.1)	0.3 (0.4)
Prunus serotina	0.5 (0.1)	3.0 (0.3)	2.6 (0.5)	0.3 (0.1)	1.3 (2.3)	0.4 (0.4)	0.3 (0.6)
Quercus rubra	0.1 (0.1)	0.1 (0.0)	0.1 (0.1)	1.3 (1.5)	0.7 (0.6)	1.0 (1.4)	0.9 (1.8)
Tilia Americana		0.1 (0.2)	0.5 (0.2)	0.5 (0.4)	0.3 (0.5)	2.1 (0.9)	5.8 (1.0)
Tsuga canadensis	0.4 (0.2)	0.3 (0.8)		0.8 (1.1)	0.6 (0.9)	1.6 (0.8)	1.6 (0.5)
Other species	0.3 (0.1)	0.2 (0.1)	0.2 (0.1)	0.2 (0.1)	0.7 (0.4)	0.4 (0.2)	0.2 (0.1)
All species together	9.2 (1.4)	15.8 (1.2)	19.5 (1.9)	23.0 (1.6)	27.3 (2.4)	29.1 (1.7)	32.1 (2.9)
Mean forest floor cover (%)	84.3 (8.4)	37.6 (4.0)	37.8 (3.8)	49.4 (4.3)	40.2 (5.5)	41.1 (5.0)	55.8 (4.6)

Values in parentheses are standard deviations of the mean. For each EA and UA treatment, n = 27; for unmanaged forests (reference), n = 36. Mean forest floor cover includes herbaceous species, and shrubs and trees with diameters < 1.0 cm at 1.3 m height (DBH).

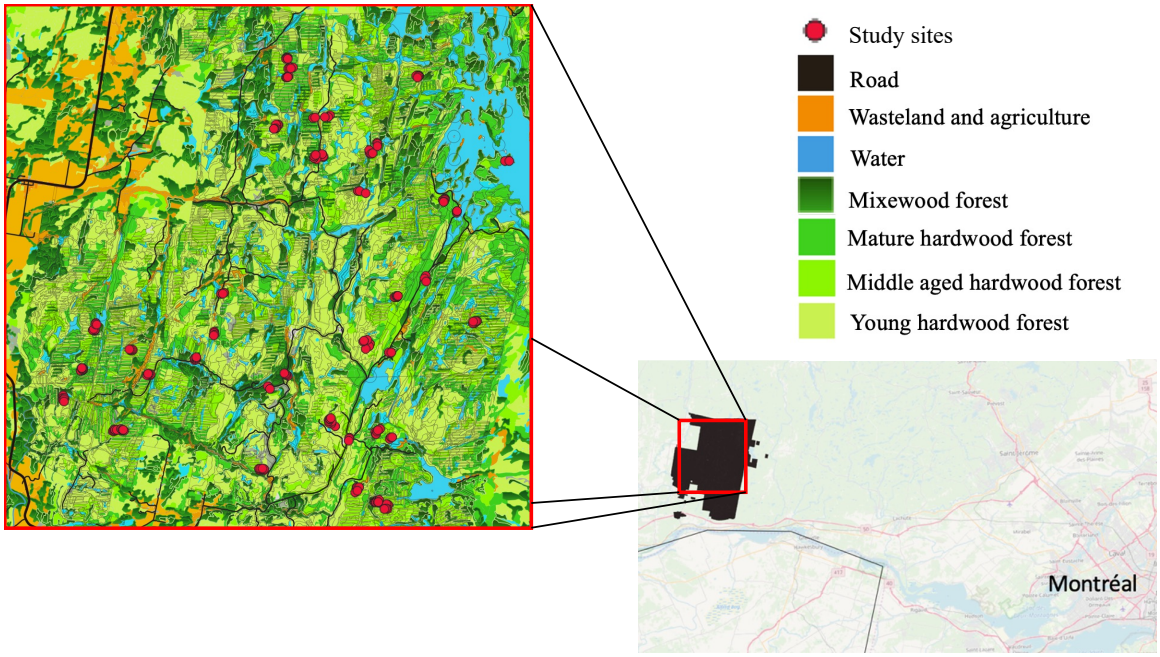

Figure 1. Localisation of sites and plots used to study the legacies of forest harvesting in southern Quebec, Canada.

In the last 40 years, harvesting in Kenauk Nature forest has consisted mainly of strip cutting, which included 50-meter-wide strips of clearcutting (EA management) alternating with 50 m-wide strips of partial cutting (30% basal area removed) through single-tree selection (UA management). This resulted in paired EA and UA areas of contrasting harvest ages, from < 5 years to more than 30 years. Paired EA and UA sites were close to one another (*i.e.*, less than 200 m apart), which were harvested concurrently, and selected to match similar soil types (exposure, slope, drainage, texture) and potential "tolerant hardwoods" vegetation types (Saucier *et al*., 2009). An unmanaged forest reference site was selected relatively close to each paired site (*i.e.,* 300 to 900 m). In both EA and UA forests, trees were felled by chainsaw, delimbed on site and skidded tree-length to the landings. The selected EA and UA sites were restricted to minimal slopes and stand areas of more than 0.52 ha. In each site, three circular plots (400 m²) were randomly selected.

In each circular plot, coarse woody debris (CWD) on the forest floor (minimum length of 1 m and diameter of more than 10 cm at both ends) was measured using a linear interception sampling method (Rondeux *et al*., 2012) along two perpendicular linear transects of 20 m. For each piece of CWD crossing the transect, the diameter and decay class was recorded using four decay classes that were based on the percentage of hard wood texture using a knife penetration method that is described by Rondeux *et al*. (2012). CWD volume was measured in m^3 of dead wood per ha using the aggregated aboveground volume of all pieces of coarse woody debris over a specified land area calculation that was described by Rondeux *et al*. (2012). For each plot, the volume of CWD was assigned to the four decay classes, Class 1, hard texture 90%; Class 2, hard texture 90–60%; Class 3, hard texture 60–30%; and Class 4, hard texture < 30%. In each plot, three litter samples (25 cm x 25 cm) were collected on the forest floor and pooled into one composite sample. Litter samples were dried at room temperature (ca. 22 ^oC). In June and July 2017, the forest floor (F- and H-horizons) and the 2–20 cm of underlying mineral soil (A and part of the B horizon) were sampled. Eight soil cores per plot (taken from each of the eight micro-plots for plant sampling (Chapter I)) were collected in each plot with a hand trowel and soil auger (7 cm diameter) that were pooled by layer (forest floor and mineral) and placed in separate plastic bags. Each composite sample of mineral soil was sieved (2 mm mesh) for subsequent soil physico-chemical analyses.

Soil physico-chemical analyses

A subsample of fresh soil (1 g of organic soil, 2.5 g of mineral soil) was dried at 105 °C for 24 h to determine gravimetric water content. Bulk pH was measured from deionized water, soil slurries with ratios of 10.1 for FH horizons and 5.1 for mineral soils,

respectively. Organic matter percentage was measured by gravimetric Loss-On-Ignition methods (Carter & Gregorich, 2007). Total C and N were measured by high-temperature combustion (1450 °C) on a TruMac CNS analyzer (Leco, St. Joseph, MI, USA). Exchangeable base cations (Ca^{2+}, Mg^{2+}, K^{+}), Al^{3+} and extractable P were extracted in Mehlich III solution, then were analyzed by flame photometry and atomic absorption spectrophotometry (Varian 220 FS, Agilent Technologies, Palo Alto, CA, USA). Duplicate subsamples were run within each batch for quality control. Percent base saturation was calculated in each plot by dividing the sum of exchangeable base cations by the effective CEC (sum of cations; Fe and Na were excluded given their trace concentrations in our samples) (Carter & Gregorich, 2007). Potentially mineralizable N was calculated as the difference between NO_3^- and NH_4^+ concentrations that were initially extracted and those extracted at the end of aerobic 28-day laboratory incubations at 22 °C (Curtin and Campbell, 2007). NO_3^- and NH_4^+ were extracted in aqueous 2 M potassium chloride both prior to and immediately following aerobic soil incubations in the laboratory. These available pools of inorganic N were quantified by flow-injection colorimetry (Lachat Instruments, Milwaukee, WI, USA). Aggregate stability and soil texture were analyzed for each site (pooling samples from the three plots). Stability of aggregates was estimated using disaggregation by agitation tests (sieve mesh-sizes of 0.05, 0.1, 0.2, 0.5, 1 and 2 mm) after both dry sieving and rapid moistening. For rapid moistening, the size distribution of water-stable aggregates of the entire soil was estimated after sieving in water (500 mL of water per 100 g of soil) (adapted from Carter & Gregorich, 2007). Aggregate stability was calculated using the distribution-size of aggregates for both dry- and wet-sieving methods. The equation of weighted mean diameter was used (*i.e.*, summed for each sieve of the mean

diameter between two sieves, multiplied by the proportion of the total sample retained on the sieve, where the lower limit of the smallest sieve class was set to zero) (Carter & Gregorich, 2007). Soil texture in each site was characterized with the hydrometer method (Bouyoucos, 1962). Litter samples were separated into leaves (American beech, other species) and branches (regardless of species); they were oven-dried (60 °C for 48 h). Tree leaf and branch subsamples were then weighed.

Greenhouse experiment

A pot experiment with three early successional tree species (*i.e.*, trembling aspen (*Populus tremuloides* Michx.), white or paper birch (*Betula papyrifera* Marsh.), and yellow birch and soil that had been collected from the study area was conducted in a greenhouse experiment located at the Institut des sciences de la forêt tempérée (Ripon, QC, Canada) from 4 June to 24 September 2018. Soil was collected from four forest sites (45.71^{o} to 45.90^{o} N, -75.14^{o} to -74.77^{o} W) corresponding to a hypothetical gradient of decreasing soil fertility, 1) an unmanaged forest reference (highest fertility); 2) a forest with characteristics of one impact of clearcutting (30 years after clearcutting; medium-high fertility); 3) a forest with characteristics of two impacts of clearcutting (15 years after the last clearcutting; medium-low fertility); and 4) a forest with characteristics of three impacts of clearcutting (recently harvested site; low fertility). Sites were selected in order to create a hypothetical gradient of decreasing soil fertility (*i.e.*, decreasing pH, total N and C concentration, and percentage base saturation with increasing harvesting rotations). Historical information on forest management was provided by the Kenauk Institute, a nonprofit charitable foundation located in Montebello, QC. The principal characteristics of the physico-chemical properties

of these soils have been summarized in Table 2. In each selected site, ca. 150 L of soil (mixture of FH layer and 0-20 cm of upper mineral layer) were collected.

Table 2. Principal physico-chemical properties of soils from different forest management histories including an unmanaged forest reference and forests with characteristics of one, two or three clear-cutting impacts forming a gradient of decreasing soil fertility.

Treatment	pH[1]	Organic matter[a] (%)	Sand (%)	Silt (%)	Clay (%)	Base saturation[b] (%)	Base saturation[a] (%)	N[b] (g kg^{-1})	C[b] (g kg^{-1})
Reference	5.55	2.64	53.9	42.6	3.5	82.0	49.0	2.5	41.1
1 impact	4.45	1.53	57.1	38.9	4.0	48.0	4.3	1.5	24.6
2 impacts	4.62	1.10	48.1	41.0	10.9	42.0	6.8	1.2	15.3
3 impacts	4.14	N.A.	69.6	28.4	2.0	38.6	3.8	N.A.	N.A.

[a] In the upper soil mineral (0-20 cm), [b] In the forest floor (FH horizons).

The greenhouse experiment included 144 pots (4 forest soil origins x 3 tree species x 12 replicates) to test for differences in soil productivity among the four management history treatments. For each forest soil origin treatment, 36 free-draining pots (12.7 cm diameter, 16.5 cm depth) were filled with ca. 3 L of soil. Two-year-old seedlings originating from a private nursery (Agrofor Nursery, St-Apollinaire, QC) of each species were planted in these pots (for each species, 12 individuals per soil origin). Seedlings were previously grown in containers with a standard nursery mix (peat moss, perlite, vermiculite and Osmocote©). Seedlings were not fertilized during the pot experiment, and their roots were gently washed prior to potting to remove soil particles. Prior to being assigned to a soil origin treatment, seedling height and fresh mass were measured to select homogeneous individuals, thereby avoiding initial bias. Pots were arranged in a completely randomized layout. To expose all seedlings to similar greenhouse conditions, pots were randomly relocated twice during the experiment. The soil was watered to field capacity every 3 days. Weeds were removed manually as they appeared. During the experiment, leaf chlorophyll concentration was estimated using a SPAD (502Plus, Konica Minolta, Mississauga, ON)

chlorophyll meter (three measurements per leaf/three leaves per plant). Prior to leaf senescence, the seedling in each pot was harvested. Root dry mass, stem dry mass, leaf dry mass, stem height and branching length (ramification number and length) were measured. Height growth rate was calculated for the whole experiment.

Statistical analyses

All statistical analyses were performed using R software (version 4.0.2.). We tested the effect of management type and time since harvesting relative to unmanaged forest reference sites, on CWD and soil properties using linear mixed-effects models (*lme4* package, function *lmer*) with site (that accounted for paired site) and plots as random effects. Treatment means were compared to the unmanaged reference using post-hoc multiple means comparisons (Tukey contrasts, *multcomp* package). For each variable, we also analyzed whether means were significantly different among treatments. Modification of CWD volume in each of the 4 decay classes per site following management was analyzed using a linear mixed-effects model (*lme4* package, function *lmer*), with site as a random effect; a log (X+1) transformation was applied to the raw data. Effects of soil origin treatments on variables related to tree growth that was measured in the greenhouse experiment were analyzed using one-way ANOVA. Responses of three tree species were evaluated independently. Significantly different means among soil origin treatments were separated using post-hoc Tukey's tests (*stats* package). Homogeneity of variance was verified using Levene's test and normality was tested using Shapiro-Wilk tests and the Durbin-Watson test for the distribution and auto-correlation of residuals. A significance level of $\alpha = 0.05$ was applied to all analyses. Permutational multivariate analysis of variance (PERMANOVA), with 999 permutations (*vegan* package, function *adonis2*), was

used to partition the amount of variation in soil properties according to treatments and sites. Principal component analysis (*FactoMineR* package, function *PCA*) was performed to synthesize the variation of soil properties among treatments. PCA results were presented for soil variables in the forest floor and the mineral horizon for both EA and UA managed forests.

Results

Effects of even-aged and uneven-aged forest management on soil properties along a harvest chronosequence

According to the multivariate variance partitioning test (function *adonis 2*) the treatments (management type and time-since-harvesting) explained a considerable proportion of the variation in soil properties ($R^2 = 0.15$, $P < 0.001$). The sites have a smaller but significant effect on the variation of soil properties ($R^2 = 0.02$, $P = 0.017$). The first component of PCA (Dimension 1; Figure 2) explained 36 and 42% of the variation of soil properties in the forest floor layers and 42 and 46 in the mineral soil horizon, respectively, for UA and EA managed forests. In the forest floor, Dimension 1 was positively correlated with C, Mg, exchangeable bases, Ca, K, P and negatively correlated with Al, while Dimension 2 was correlated with pH and C/N ratio (Figure 2a and c). In the mineral horizon, Dimension 1 was positively correlated with pH, exchangeable bases cations, Ca and Mg and negatively corelated with Al, and Dimension 2 was correlated with C and percentage of organic matter (Figure 2b and d). For both managed forest types and forest soil layers, the quality of representation for the first two dimensions was highest for exchangeable bases, together with concentrations of C, Ca and Mg (Cos 2 analysis, data not shown). In both soil layer, the first dimension clearly segregated soil of unmanaged forest from soil of EA managed

forest. In the forest floor, UA managed forest are separated from the unmanaged forest along both the first and second dimensions. Both PERMANOVA and PCA results revealed differences between the treatments (different combinations of management type with time-since-harvesting) and the unmanaged reference. These effects are described more specifically in Table 3.

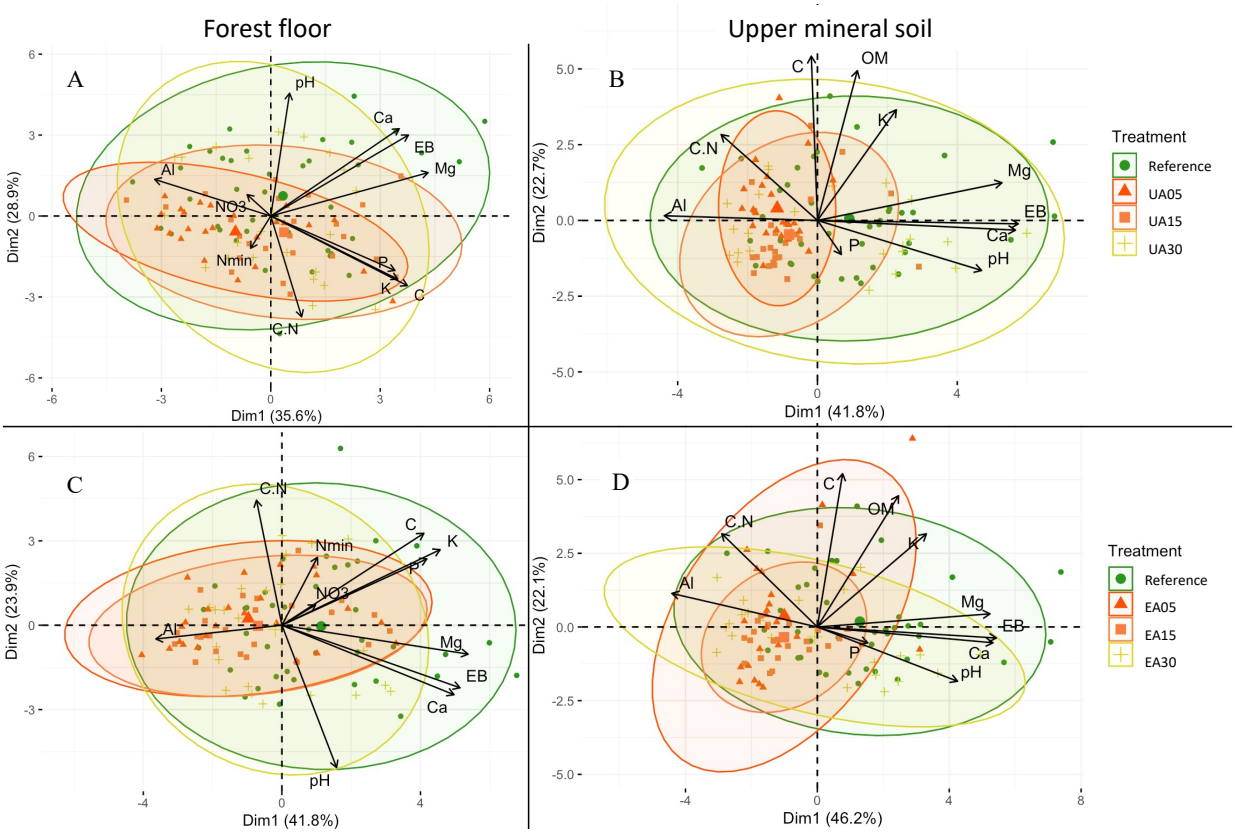

Figure 2. Principal component analysis of soil properties in the forest floor after uneven-aged (i.e., UA) (A) and even-aged (i.e.,EA) (C) management, and in the upper mineral soil after uneven-aged (B) and even-aged (D) management. Ellipses show the influence zone of each treatment. The larger circles, squares, triangles and crosses represent the position of each treatment along those two dimensions. The number after the management type (i.e., EA or UA) represents time-since-harvesting, 5, 15 or 30 years. Reference, Unmanaged forest, C.N, ratio C/N, EB, Exchangeable base cations, OM, organic matter, NO3, potential net nitrification rate, Nmin, total mineralizable N.

Both EA and UA management affected organic matter inputs, especially 5 and 15 years after forest harvesting. Litter mass in EA5 and UA5 forests was lower than that in

unmanaged forests ($P < 0.01$ and $P < 0.01$, respectively; Table 3). However, these significant differences were no longer observed 15 and 30 years after forest harvesting in both UA and EA management types. American beech litter mass was quite variable along the chronosequence, reaching mean values in excess of 109 $g \cdot m^2$, 15 years after EA and 30 years after UA management, compared to mean values that were lower than 68 $g\ m^2$, 5 years after harvesting and in the reference (Table 3). Branch mass on the forest floor experienced a decrease 5 and 15 years after UA management, but this significant decrease was no longer observed at year 30.

There was a strong decrease in CWD volume (means < 29 $m^3 \cdot ha^{-1}$) in EA managed forests compared to unmanaged forests (mean of 72.2 $m^3 \cdot ha^{-1}$), with no recovery pattern observed (Table 3). Following UA management, a significant decrease in CWD volume was only observed 5 years after harvesting (mean of 18.5 $m^3 \cdot ha^{-1}$; $P < 0.01$). CWD volume in UA15 and UA30 sites (mean of 51 $m^3 \cdot ha^{-1}$) was lower than unmanaged forests**.** In terms of CWD decomposition, the mean volume of CWD decay class 4 (very decayed to completely soft) was 40.0 $m^3 \cdot ha^{-1}$ in the unmanaged forest, compared to 19.0 and 19.2 $m^3 \cdot ha^{-1}$ 15 and 30 years after UA management, respectively (Table 1). For EA management, the mean volume of CWD decay class 4 was significantly lower than the unmanaged level **(***P* < 0.001) all along the chronosequence (means of 1.1, 6.5 and 4.9 $m^3 \cdot ha^{-1}$, 5, 15 and 30 years after harvesting, respectively). Thirty years following EA management, the volume of wood of decay class 1 **(**not decayed, completely hard), as well as decay classes 2, 3 and 4 were significantly lower than the unmanaged reference (Table 3).

In forest stands that have experienced UA management, the values of most soil chemical properties that were affected in the short-term by harvesting were approaching those in the

unmanaged reference as time-since-harvesting increased (Table 3). In contrast, forest stands experiencing EA management exhibited generally stronger and longer effects of harvesting on soil chemical properties than forest stands subjected to UA management. In fact, following EA management, the significant differences with unmanaged forest that were observed shortly after harvesting were still present for most (14/16) soil variables 15 years after harvesting, and were still significant for about half of them 30 years after harvesting (Table 3). Soil pH values in EA5 (mineral soil), EA15 (mineral soil), UA5 (forest floor and mineral) and UA15 (forest floor) stands were lower than those in unmanaged forest stands. In the upper mineral soil, available K in all EA treatments was lower than in unmanaged forests. EA5, EA15, EA30 (both soil layers), UA5 and UA15 (mineral soil only) sites were associated with significant reductions in soil available Ca and Mg, compared to unmanaged forest sites. EA5 sites had higher levels of available Al in the forest floor ($P < 0.001$) and upper mineral soil ($P < 0.05$), relative to UA30 and unmanaged forests sites. Conversely, EA5 sites had lower base saturation in the forest floor ($P < 0.001$) and upper mineral soil ($P < 0.05$), compared to UA30 and unmanaged forests sites. In the short-term (*i.e.*, 5 years after harvesting), EA management increased the potential net nitrification rate ($P < 0.05$) and decreased ammonification rate ($P \simeq 0.05$) compared to the unmanaged forest (Table 3). Total C and N, available P, texture and aggregate stability were weakly variable among treatments. However, EA15 sites had lower percentages of organic matter ($P < 0.05$) and dry aggregate stability ($P < 0.05$). At this point along the chronosequence, a tendency towards lower C and N concentrations in both soil layers was observed (Table 3).

Table 3. Soil properties in forest floor and upper mineral soil (2-20 cm) as influenced by even-aged and uneven-aged forest management along a chronosequence of forest harvesting.

		Even-aged management			Uneven-aged management			Reference
		5 years	15 years	30 years	5 years	15 years	30 years	
Forest floor								
CWD volume	$m^3 \cdot ha^{-1}$	27.0 * (7.2) b	17.3 ** (6.4) b	7.9 ** (2.6) b	18.5 ** (5.6) b	52.2 (9.4) ab	51.1 (14.8) ab	72.2 (14.6) a
Decay class 1	$m^3 \cdot ha^{-1}$	13.6 (4.5)	0.8 · (0.4)	0.0 * (0)	3.3 (0.5)	5.9 (0.8)	4.8 (1.7)	4.6 (2.6)
Decay class 2	$m^3 \cdot ha^{-1}$	5.8 (2.2) ab	3.3 * (0.4) ab	1.0 *** (0.1) b	4.6 (1.8) ab	12.5 (5.3) a	9.5 (1.4) ab	13.5 (2.7) a
Decay class 3	$m^3 \cdot ha^{-1}$	6.5 * (0.7) ab	6.7 (1.1) ab	2.0 ** (1.1) b	2.9 * (1.4) ab	14.8 (2.7) a	17.6 (4.8) a	14.1 (3.9) a
Decay class 4	$m^3 \cdot ha^{-1}$	1.1 *** (0.3) c	6.5 *** (3.9) bc	4.9 *** (1.1) c	7.7 *** (1.7) bc	19.0 (3.7) ab	19.2 (5.3) ab	40.0 (3.3) a
Litter mass	$g \cdot m^{-2}$	623.0 ** (96.0) b	803.2 · (51.3) ab	1007.5 (93.2) ab	624.0 ** (43.9) b	956.8 (60.0) ab	1036.2 (82.1) ab	1108.3 (66.4) a
American beech litter mass	$g \cdot m^{-2}$	61.8 (20.4)	109.5 (18.3)	85.6 (20.8)	58.2 (14.3)	88.4 (17.3)	119.8 (23.4)	67.9 (12.7)
Branch mass	$g \cdot m^{-2}$	187.9 (52.9)	123.6 (18.4)	152.4 (23.1)	47.5 ** (6.1)	103.1 * (10.8)	163.6 (23.9)	163.0 (16.0)
Forest floor (FH)								
pH		5.15 (0.08) ab	5.06 (0.09) ab	5.17 (0.16) ab	4.79 * (0.08) b	4.81 · (0.09) b	5.04 (0.15) ab	5.30 (0.11) a
C	$g \cdot kg^{-1}$	25.0 (2.8)	24.2· (2.6)	26.4 (2.5)	31.7 (2.2)	37.4 (1.8)	32.9 (2.7)	31.9 (2.3)
N	$g \cdot kg^{-1}$	1.48 (0.17)	1.46 (0.15)	1.56 (0.13)	1.81 (0.11)	2.04 (0.08)	1.84 (0.13)	1.81 (0.12)
C/N		17.2 (0.4)	16.6 (0.4)	16.7 (0.5)	17.4 (0.4)	18.3 (0.4)	17.5 (0.5)	17.4 (0.5)
P	$mg \cdot kg^{-1}$	90.5 (13.9)	95.2 (12.6)	96.4 (10.6)	113.3 (16.8)	165.4 · (19.1)	137.2 (16.5)	122.5 (11.7)
K	$mg \cdot kg^{-1}$	282.3 · (36.6)	286.3 · (31.1)	315.1 (33.2)	395.0 (51.8)	499.3 (35.2)	428.4 (56.5)	398.4 (27.2)
Ca	$mg \cdot kg^{-1}$	2117 ** (377) b	2522 ** (334) b	3452 · (533) ab	2333 ** (272) b	3802 (423) ab	4022 (524) ab	5140 (517) a
Mg	$mg \cdot kg^{-1}$	233.6 ** (40.9) b	297.0 * (40.8) b	315.7 · (36.0) ab	255.0 ** (29.7) b	378.3 (29.8) ab	356.6 (34.4) ab	450.0 (39.2) a
Al	$mg \cdot kg^{-1}$	1677.9 *** (204.4) a	1335.2 · (184.9) ab	1167.8 (140.8) ab	848.6 (109.3) b	935.7 (178.1) b	770.1 (87.1) b	946.7 (102.8) b
Base saturation	%	40.5 *** (5.0) c	51.7 ** (5.2) bc	57.8 · (4.4) abc	59.8 · (4.4) ab	69.5 (4.5) ab	71.6 (3.3) a	70.8 (3.1) a
Exchangeable base cations	$cmol \cdot kg^{-1}$	13.2 ** (2.3) b	15.8 ** (2.0) b	20.7 · (2.9) ab	14.8 ** (1.7) b	23.4 (2.4) ab	24.2 (2.8) ab	30.4 (2.9) a
Mineralized N	$mg \cdot kg^{-1} \cdot d^{-1}$	1.19 (0.14)	0.85 (0.11)	0.91 (0.19)	1.45 (0.11)	0.92 (0.18)	0.96 (0.13)	1.07 (0.26)
Net nitrification rate	$mg \cdot kg^{-1} \cdot d^{-1}$	1.19 * (0.14) a	0.61 (0.08) bc	0.58 (0.07) bc	1.02 (0.13) ab	0.52 (0.10) c	0.50 (0.07) c	0.75 (0.12) bc
Ammonification rate	$mg \cdot kg^{-1} \cdot d^{-1}$	0.0· (0.04)	0.24 (0.08)	0.33 (0.14)	0.43 (0.09)	0.40 (0.12)	0.46 (0.12)	0.32 (0.23)
Upper mineral soil (2-20 cm)								
pH		4.68 ** (0.07) cd	4.84 * (0.06) bcd	5.09 (0.12) abc	4.61 ** (0.07) d	4.93 (0.07) abcd	5.18 (0.12) ab	5.22 (0.10) a
Organic matter	%	2.04 (0.23) bc	1.63 * (0.16) c	1.95 (0.12) bc	2.42 (0.12) ab	1.87 (0.14) bc	2.31 (0.23) ab	2.34 (0.18) ab

C	g·kg^{-1}	8.16 (1.15)	6.15 (0.50)	6.14 (0.50)	8.62 (0.73)	6.80 (0.82)	7.91 (0.78)	7.67 (0.50)
N	g·kg^{-1}	0.51 (0.07)	0.39 (0.03)	0.39 (0.03)	0.53 (0.04)	0.46 (0.07)	0.53 (0.04)	0.51 (0.03)
C/N		16.2 (0.6)	16.1 (0.5)	16.1 (0.9)	16.1 (0.6)	15.5 (0.6)	15.2 (0.8)	15.0 (0.6)
P	mg·kg^{-1}	5.58 (1.14)	4.16 (0.68)	6.05 (1.83)	4.97 (0.81)	3.75 (0.71)	3.10 (0.35)	6.32 (1.09)
K	mg·kg^{-1}	73.8 * (10.0) b	65.2 ** (4.5) b	65.9 * (6.6) b	89.9 (4.4) ab	79.4 (6.2) ab	82.2 (6.7) ab	99.8 (7.1) a
Ca	mg·kg^{-1}	481.0 ** (88.8) c	424.3 ** (63.2) c	856.0 * (190.0)bcd	453.2 ** (42.2) c	552.0 * (118.9) bc	1185.3 (222.2) ab	1334.0 (175.3) a
Mg	mg·kg^{-1}	47.0 ** (8.1) c	52.2 ** (7.5) c	79.7 $^{\cdot}$ (12.8) bcd	55.2 ** (4.3) c	59.9 ** (8.5) bc	99.4 (14.5) ab	115.5 (9.4) a
Al	mg·kg^{-1}	1808.8 * (81.5) a	1696.0 $^{\cdot}$ (66.1) ab	1635.7 (123.4) ab	1651.6 (64.7) ab	1578.6 (81.6) ab	1435.9 (96.5) b	1334.0 (60.0) b
Base saturation	%	13.3 ** (2.5) b	12.9 ** (1.9) ab	22.5 (4.0) ab	14.2 ** (1.2) ab	15.9 * (2.5) ab	29.5 (4.6) a	31.0 (2.8) a
Exchangeable base cations	cmol·kg^{-1}	2.98 ** (0.52) c	2.72 ** (0.38) c	5.11 (1.05) abc	2.95 ** (0.23) c	3.46 * (0.66) bc	6.96 (1.21) ab	7.88 (0.94) a
Soil texture								
Sand	%	52.2 (13.4)	49.6 (4.9)	53.3 (7.7)	50.6 (5.8)	47.6 (10.7)	48.2 (7.8)	43.7 (10.4)
Silt	%	36.7 * (11.4) b	41.1 (3.9) ab	41.1 (7.0) ab	44.3 (5.0) ab	45.1 (7.6) ab	42.4 (6.8) ab	47.8 (7.0) a
Clay	%	11.1 (2.5)	9.2 (2.0)	5.6 (1.3)	5.0 (2.1)	7.3 (4.7)	9.4 (1.4)	8.5 (5.8)
Aggregate stability		2.10 (1.49)	2.03 (1.59)	1.87 (2.19)	2.72 (1.54)	3.72 (1.91)	3.45 (1.72)	3.45 (2.95)
Dry		1.31 (0.36)	1.00* (0.25)	1.31 (0.30)	1.25 (0.18)	1.29 (0.26)	1.37 (0.24)	1.37 (0.25)
Wet		1.02 (0.30)	0.75 $^{\cdot}$ (0.14)	1.06 (0.32)	0.96 (0.13)	0.96 (0.17)	1.08 (0.25)	1.04 (0.28)

Values in parentheses are standard errors of the mean. One or several asterisks indicate a significant difference between the treatment and the unmanaged forest (reference) according to the linear mixed models, * P < 0.05; ** P < 0.01; *** P < 0.001; · P < 0.1. Within a line, means with different letters indicate a significant difference (p ≤ 0.05; Tukey's tests). Log (X+1) transformation was applied for statistical analysis of mean volume of CWD in different decay class, calculated for each site.

Seedling growth responses to soil origin treatments in the greenhouse experiment

The soil originating from one (*i.e.*, medium-high fertility; yellow birch and trembling aspen; $P < 0.05$), two (*i.e.,* medium-low fertility**;** $P < 0.01$, for the three species), and three harvesting impacts (*i.e.,* low soil fertility; $P < 0.001$, for the three species) resulted in lower height growth and total dry biomass, relative to the soil from the unmanaged forest reference (*i.e.,* high soil fertility) (Table 4, Figure 3). A significant treatment effect on leaf chlorophyll concentration was measured for each species ($P < 0.05$); lower mean chlorophyll values were measured in seedlings growing in the soil originating from three

harvesting impact (*i.e.,* low soil fertility). The soil originating from three harvesting impacts resulted in higher root/shoot ratios of birch species ($P < 0.001$ for white birch; $P \sim 0.05$ for yellow birch), and in lower root/shoot ratios for trembling aspen ($P < 0.01$). A significant treatment effect on branching pattern was observed for yellow birch only ($P < 0.01$); yellow birch seedlings growing in the soil with the lowest fertility had greater number of small branches per unit of length.

Table 4. Height growth rate, branching pattern, biomass allocation and leaf chlorophyll concentration of seedling growing in a pot experiment in soils from different forest management histories, including an unmanaged forest reference and forests with characteristics of one, two or three clear-cutting impacts forming a gradient of decreasing soil fertility.

		Height growth rate ($cm \cdot day^{-1}$)	Branching /length ($nb \cdot cm^{-1}$)	Total biomass (g)	Ratio root/shoot	Ratio npt/pt	Leaf chlorophyll (SPAD value)
Yellow birch	Reference	0.19 a (0.05)	0.14 b (0.06)	7.31 a (1.54)	0.72 ab (0.08)	1.91 (0.21)	35.37 a (3.01)
	1 impact	0.18 a (0.06)	0.16 b (0.04)	5.19 b (1.32)	0.63 b (0.08)	1.63 (0.22)	31.75 ab (4.28)
	2 impacts	0.14 ab (0.04)	0.16 ab (0.11)	4.51 b (1.05)	0.69 b (0.12)	1.82 (0.43)	32.71 a (2.89)
	3 impacts	0.07 b (0.03)	0.30 a (0.17)	2.07 c (0.60)	1.00 a (0.19)	2.47 (0.35)	23.90 b (1.55)
White birch	Reference	0.29 a (0.07)	0.11 (0.08)	6.29 a (1.46)	0.62 b (0.18)	1.96 (0.63)	39.67 a (3.18)
	1 impact	0.23 ab (0.07)	0.10 (0.05)	4.50 ab (1.22)	0.55 b (0.09)	1.72 (0.40)	38.04 ab (6.26)
	2 impacts	0.16 bc (0.08)	0.22 (0.14)	3.85 bc (1.12)	0.79 ab (0.21)	2.10 (0.37)	44.65 a (4.82)
	3 impacts	0.11 c (0.05)	0.08 (0.08)	2.05 c (0.65)	0.99 a (0.26)	2.77 (0.81)	32.23 b (6.86)
Trembling aspen	Reference	0.21 a (0.07)	0.02 (0.02)	7.68 a (2.42)	1.17 a (0.30)	3.52 (0.95)	49.03 a (6.56)
	1 impact	0.11 b (0.06)	0.04 (0.04)	4.23 b (1.78)	1.18 a (0.18)	3.95 (2.42)	43.55 ab (4.87)
	2 impacts	0.09 b (0.06)	0.02 (0.02)	2.68 bc (1.25)	1.02 ab (0.32)	3.59 (1.38)	37.18 bc (11.02)
	3 impacts	0.09 b (0.04)	0.02 (0.02)	2.18 c (1.03)	0.80 b (0.24)	2.98 (0.97)	30.26 c (6.78)

Values in parentheses are standard errors of the mean. For each species, within a column, means with different letters indicate a significant difference ($p \leq 0.05$; Tukey's tests). npt/pt, non-photosynthetic tissues/photosynthetic tissues.

Figure 3. Photograph(s) of yellow birch seedlings taken from the greenhouse experiment demonstrating the decrease in tree seedling growth that was observed in soil experiencing different forest management histories, including an unmanaged forest reference and forests with characteristics of one (1), two (2) or three (3) clear-cutting impacts forming a gradient of decreasing soil fertility.

Discussion

Different patterns in which forest harvesting alters soil physico-chemical attributes

Harvesting of hardwood forests in eastern North America has been conducted for centuries (Brisson & Bouchard, 2003). However, the long-lasting effects of different silvicultural systems on soil properties in these forests have been poorly studied. As predicted, our results demonstrate that key soil properties were modified by forest harvesting with a greater magnitude over the shorter-term and in EA managed forest. The magnitude of soil response to forest harvesting was similarly important in the forest floor and mineral layer (Figure 2). In order to facilitate the interpretation of our results, we synthesized the temporal dynamics of soil properties following EA and UA management into three different general patterns (Figure 4). The three patterns are, 1) a constant increase or decrease with time, which allows soil attributes to converge on unmanaged forest levels

after a major short-term impact; 2) a constant increase or decrease with time, which diverges from the unmanaged forest levels; and 3) a major, but ephemeral increase or decrease once along the chronosequence (*i.e.*, at 5 or 15 years after harvesting).

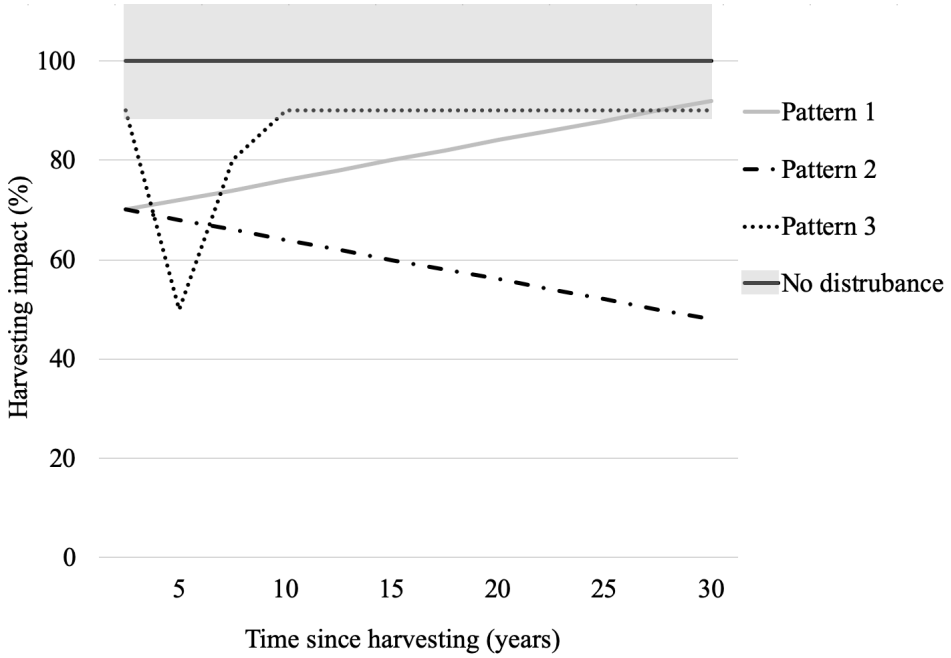

Figure 4. Temporal dynamics of soil properties following forest harvesting relative to unmanaged forests (no disturbance), comparing three contrasting patterns. Pattern 1, a constant increase or decrease with time, which allows them to converge on unmanaged forest levels after a major short-term impact. A constant increase is illustrated here. Pattern 2, a constant increase or decrease with time, that diverges from the unmanaged forest levels. A constant decrease is illustrated here. Pattern 3, a major, but ephemeral increase or decrease once along the chronosequence (i.e., at 5 or 15 years after harvesting). An ephemeral decrease 5 years after harvesting is illustrated here.

In the present study, the temporal variation of many soil properties could be associated with the first pattern, such as available Ca, Mg and Al for forest stands involving EA management, and available Ca, Mg, exchangeable base cations, percentage of base saturation, pH (mineral horizon), total litter mass and CWD volume for forest stand experiencing UA management. Many of those variables may have implications for long-term soil fertility (Dyck *et al*., 2012). The present study allows us to observe the dynamics of soil resources that are known to decrease in deciduous forest of North America following

forest harvesting or biomass removal (Federer *et al*., 1989; Siemion *et al*., 2011; Royer-Tardif *et al*., 2017). This pattern of returning to the unmanaged levels with time is essential, with the objective of recovering natural soil fertility after harvesting. Despite this recovery pattern, some soil properties, such as Ca concentrations and percentage of base saturation, were still significantly lower than that in the unmanaged forest reference 30 years after application of EA management. Indeed, the mean deviation of Ca concentration from unmanaged level was still about 33 % and 20 % less, 30 years after EA and UA management, respectively (Table 3). Since repeated harvesting has been observed to decrease soil Ca (Federer *et al*., 1989), our results underscore the importance of waiting for full recovery before planning another harvesting impact to avoid further declines in soil properties. In a temperate sugar maple-dominated forest simulation, decreasing tree nutrient pools following whole-tree forest harvesting (UA management with a rotation length of 30 years) suggested a potential soil depletion especially for Ca and P (Royer-Tardif *et al*., 2017). Watmough & Dillon (2003) argued that hardwood forest productivity in eastern North America may be altered within just a few decades if Ca continues to deplete at high rates due to acid deposition and harvesting. Generally, 30 years after UA management, means of many observed variables were still lower than those of the unmanaged forests, but not to a significant level. These results suggest that harvesting using UA management will need at least this period of time to allow soil resources to recover, while EA management will need a much longer period for its soil fertility to recuperate. To our knowledge, this is the first instance that this temporal validation of soil fertility recovery has been reported over a large operational forest management experiment. Similarly, total litter mass and CWD volume in UA stands followed the first pattern by re-

increasing and converging towards the unmanaged forest levels 15 and 30 years after harvesting (Table 3). The mean CWD volume that was obtained in our unmanaged forests (*i.e.*, 72.2 $m^3 \cdot ha^{-1}$) was similar to that estimated in other similar unmanaged deciduous forests (Leduc & Bergeron, 1998; Angers *et al*., 2009). In terms of CWD decomposition, the volume of CWD of decay Class 4 (very decayed to completely soft) following UA management did not reach half of the mean volume found in unmanaged forest (40.0 $m^3 \cdot ha^{-1}$). Angers *et al*. (2009) also reported few effects of harvesting using UA management on total amounts of CWD, but a significant modification of dead wood decomposition stage did occur, partially due to the loss of progressive inputs of dead wood to the forest floor. Forest litter is another important source of organic matter in soils (Kalbitz *et al*., 2000) that could influence soil C sequestration (Lal *et al*., 2005), which was observed to be low immediately after harvesting (Table 3). Five years after harvesting, we did not observe a more substantial decrease in litter following clearcutting (EA management) compared to partial cutting (UA management), which is contrary to results that were obtained by Lindo & Visser (2003). This difference between EA and UA management is likely due to the high mass of small branches in the forest floor litter that was observed following EA management in the present study.

The second pattern was observed in UA managed forest stands with the increase of American beech litter mass with time, together with the constant diminution of available P in the mineral soil (Table 3). UA management has been reported to increase abundance of American beech in forest stands compared to reference sites (Roy & Nolet, 2018). In the present study, we observed that mean beech litter mass doubled along the UA chronosequence, reaching 120 $g \cdot m^{-2}$. Mean American beech litter mass that was associated

with unmanaged forest was much lower (68 $g \cdot m^{-2}$). As American beech produces an acidic litter that decomposes very slowly (Neirynck *et al*., 2000; Aubert *et al*., 2004), an increase in beech litter abundance could be associated with a decrease in the quantity of soil cations (Guckland *et al*., 2009). Phosphorus also could be an important growth-limiting factor in northern hardwood forests (Grawdowski & Thomas, 2006). The rapid increase in forest tree and shrub density 15 years following UA management (Table 1), with an increased need for assimilable P, could explain this constant decrease in P in the mineral soil at this time. The second pattern was also reflected in the decrease of CWD volume with time in EA forest stands. The loss in volume of CWD decay Class 4 in EA managed forests was important and reached only one-eighth of that in the unmanaged forests 30 years after harvesting. CWD volume is essential for maintaining forest soil fertility. For example, in forests dominated by sugar maple, woody material removal has been associated with significant long-term decreases in available Ca and alterations to nutrient cycling (Federer *et al*., 1989; Hagan & Grove, 1999). The importance and positive ecological value of dead wood in forest ecosystems, including CWD, no longer needs to be demonstrated. For example, the quantity, size and heterogeneity of CWD decomposition classes contribute to the persistence of fungal and plant diversity, and provide habitat for thousands of saproxylic species (Sandström *et al*., 2019).

The third pattern was exemplified through the significant increase in potential net nitrification rates and the decrease in potential ammonification rates that were observed only five years after harvesting in EA forests. Several studies have also observed an increase in available nitrate after harvesting (mostly following clearcutting), highlighting the sensitivity of this soil resource to soil perturbation in the short-term (Barton *et al*., 1999;

Jerabkova *et al*., 2011; Devine *et al*., 2012; Clarke *et al*., 2015). Even if it did not last long, higher nitrate concentrations in soils or drainage water following harvesting is mentioned as a cause of productivity decreases and pollution (Vitousek *et al*., 1979; Jerabkova *et al*., 2011). Variation in soil microclimatic conditions (*e.g.*, increases in soil temperature and moisture) that have been observed shortly after harvesting, especially clearcutting, is one of the causes of short-term increases in nitrification rates and leaching (Sørensen *et al*., 2009; Sundqvist *et al*., 2014; Clarke *et al*., 2015). As was observed in the present study, partial cutting (UA management) is known to have a smaller negative impact than total cutting (EA management) on soil nitrate fluxes (Lindo & Visser, 2003).

The third pattern was amplified in EA forest stands through changes in other soil properties such as total C and N, organic matter concentration and aggregate stability (wet and dry), which were associated with ephemeral depletion 15 years after harvesting. A decrease in aggregate stability has also been observed 15 years after high-intensity harvesting (Zhou *et al*., 2015) and could be associated with basic-cation imbalance and soil acidification (Augusto *et al*., 2015). Total C concentration in the forest floor decreased by 24%, 15 years after harvesting in EA forests compared to the unmanaged forests. Similarly, Saint-Laurent *et al*. (2000) measured that total cutting in a balsam fir–yellow birch forest of eastern Quebec resulted in an average 13.5% decrease in organic C concentrations, between 7 and 22 years after harvesting. The long-term effect of forest harvesting on C in the forest floor can be quite variable (Hume *et al*., 2018), with either persistent decreases (Lal *et al*., 2005; Nave *et al*., 2010) or neutral C responses (Johnson & Curtis, 2001).

If the third pattern was observed in forest stands under UA management, it was not statistically significant, again suggesting less severe impacts of this management practice on soil properties. Interestingly, in UA managed forest stands, we observed that total N and C and available P in the forest floor tended to peak 15 years after harvesting, while these same soil properties and organic matter concentration in the upper mineral soil tended to reach a low (Table 3). Several studies have associated the loss of C and soil nutrients with a decrease in organic matter content in the different soil layers (Powers *et al*., 2005; Nave *et al*., 2010; Muscolo *et al*., 2014). In general, soil C and nutrients were altered in a lesser extent in UA than in EA forest stands.

Constant decrease in seedling growth with a gradient of decreasing soil fertility

Tree growth, biomass allocation to roots versus shoots, and concentrations of leaf nitrogen are variables that are sensitive to variation of soil fertility (Canham *et al*., 1996; Kubiske *et al*., 1998; Achat *et al*., 2015). Based on our greenhouse experiment and consistent with expectation, we found a constant decrease in seedling height growth rate (> 42%) and total biomass accumulation (> 47 %) for three pioneer species that had been grown in soil corresponding to the two lowest soil fertility sites (*i.e.,* simulated effects of two and three clearcut harvesting impacts, without recovery) (Table 4). Changes in soil fertility following forest harvesting could have negative effects on forest productivity over both the short- (Powers *et al*., 2005) and long-term (Nave *et al*., 2010). If forest stands respond in the same manner as the experimental stands in the present study at the individual seedling scale, then the recovery of soil fertility following management appears crucial for sustaining forest productivity. Imbalances or decreases in soil nutrients, which may be accentuated by soil acidification, can lead to general nutrient deficiency and impair tree growth (Larcher,

1995). The meta-analysis of Achat *et al*. (2015) also suggested that diminution in tree growth rates increased with increasing harvesting intensity (*i.e*., removing residues on forest soils). Moreover, modification of yellow birch branching rate, which could be inferred as an expression of plant stress (Rasheed & Delagrange, 2016), was observed within soil simulating three impacts of EA management (*i.e.,* low soil fertility).

Changes in root/shoot ratio and decreases in concentrations of leaf chlorophyll were mostly observed in the lowest soil fertility sites. We noted a decrease in allocation of biomass to roots in trembling aspen, while we observed an increase in allocation to roots in the birch species. It is known that different tree species used opposite patterns of root biomass allocation following nutrient stresses (Canham *et al*., 1996). Basic cation deficiency, especially Ca, could have impaired root growth (Larcher, 1995). Yet, symptoms of N deficiency in broadleaved forest trees include a decrease in shoot/root ratio and in leaf nitrogen concentrations. As was observed with birch species, plants could allocate relatively less biomass to leaves and more to their roots under limiting nutrient supplies in the soil (*e.g.,* N and P) (Lambers, Chapin & Pons, 2008). In terms of C allocation, fine roots are more sensitive to changes in soil chemistry, particularly following a disturbance (Vogt *et al*., 1995). Those shifts in resource allocation would generally reduce plant growth (Lambers, Chapin & Pons, 2008).

Conclusions

In hardwood forest, we determined the effects of EA and UA forest management on coarse woody debris (CWD), litter mass and key soil physico-chemical properties 5, 15 and 30 years after harvesting, relative to old-growth forest reference sites. Relative to old-growth

forests, sites that were subject to forest harvesting were characterized by soils with significantly lower values of key soil attributes, including pH, available K, Ca and Mg and base saturation. Both the forest floor and mineral soil layers experienced a major modification of soil properties. After UA management, most soil attributes returned to the unmanaged levels with time-since-harvesting. Generally, EA management leads to greater deviation from the unmanaged forest in the study chronosequence, like a marked decrease in CWD volume in the forest floor of EA managed forests. With a lack of recovery of important soil attributes, the decrease in tree biomass is expected to increase following management rotation. This hypothesis was tested in the greenhouse pot experiment, where the soil with a gradient of decreasing fertility resulted in lower height growth rates and total dry biomass for the three tree species (trembling aspen, white birch and yellow birch), relative to the soil from the unmanaged forest reference (high soil fertility). This study demonstrated that forest harvesting can alter on soil fertility over both the short- and long-term, which may increase with harvest intensity. Caution must be exercised when interpreting these effects and using soil nutrient capital as a metric of forest management sustainability. The biological significance of changes in soil nutrients observed following forest management should be assessed considering other forest dynamics such as productivity, nutrition (*e.g.,* Ponder *et al*., 2012; Kranabetter *et al.*, 2017), abiotic (*e.g.,* light availability) and biotic conditions (*e.g.*, recruitment), as well as time since harvesting (Vadeboncoeur *et al.*, 2014).

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CHAPITRE III. Long-term effects of different harvesting intensities on soil microbial communities in a hardwood temperate forest

Abstract

Soil microbial communities regulate the fate of soil organic matter and allow plants to adjust to external conditions, tolerate stresses and modulate their nutrition in forest ecosystems. Yet, the long-lasting effects of different harvesting intensities on soil microbial communities remain poorly understood. We assessed even-aged (EA, clear-cuts) and uneven-aged (UA, partial harvests; 30% by single-tree selection) management effects on soil bacterial and fungal abundance and fungal community composition 5, 15 and 30 years after harvesting, relative to unmanaged old-growth controls, in a tolerant hardwood forest in southern Quebec, Canada. In total, 189 plots were sampled in 63 randomly selected sites. EA and UA managed forests generally made the soil environment more favorable for bacterial communities over both the short- and long-term. Five years after harvesting, EA and UA had lower fungal species richness than in unmanaged forests. Five years after harvesting, EA managed forests had higher bacteria abundance than unmanaged forests. At the same time, fungal community dissimilarity and the proportion of fungal pathogens and parasites in EA managed forests were higher than in unmanaged forests. No significant effect of forest harvesting treatments was observed for the proportion of saprotrophic fungi or fungal phylogenetic diversity. UA managed forests and unmanaged forests were associated with higher concentrations of P and C in the FH layer, higher forest density and diversity, and higher proportions of symbiotic fungi.

Key words, Forest harvesting intensity, Chronosequence, Fungi, Bacteria, Fungi guild, Northern hardwood forest

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Introduction

Plants exhibit a diverse array of interactions with microbe communities. They latter have the ability to adjust to external conditions, can confer tolerance to biotic and abiotic stresses on their hosts, and modulate plant mineral nutrition and moisture acquisition (Berendsen *et al*., 2012; Jacoby *et al.,* 2017). Soil fungal and bacterial also regulate the fate of soil organic matter (carbon mineralization and stabilization) and nutrient cycling, which is crucial for forest ecosystem functioning (Malik *et al.,* 2016; Uroz *et al*., 2016). Specifically, symbiotic fungi (*e.g.,* mycorrhizae), with their large mycelia biomass in forest soil, transfer large quantity of P and N to trees, and may produce most of the soil dissolved organic carbon (Baldrian, 2017). Many studies have assessed the effects of forest perturbations, such as forest harvesting, on soil microbial communities (*e.g*., Holden and Treseder, 2013; Parlade *et al*., 2019). Yet, our empirical understanding remains limited regarding how strongly the effects of different harvesting intensities influence soil microbial communities over the short- and long-term, especially in hardwood forests.

Hardwood forests in Northern America are generally managed as low-intensity silvicultural systems that use partial harvesting and uneven-aged (UA) management (Nolet *et al*., 2017). Yet, high-intensity sylvicultural systems that implement total harvesting and even-aged (EA) management are also used. Both EA and UA forest management may alter several interrelated abiotic and biotic components of forest ecosystems. Forest harvesting can alter the soil microbiome through changes in soil physical and chemical properties, forest composition and structure, and dead wood accumulation (Uroz *et al*., 2016). Both edaphic and forest conditions could modulate microbiome habitat and resources, and microbial dispersal and colonization (*e.g.,* Lemanceau *et al*., 2017). Clear-cutting generally

influences the dynamics of microbial communities more strongly than does partial cutting or unmanaged forest (Wu *et al*., 2011; Holden & Treseder, 2013). For example, Bailey *et al*., (2002) showed that more intensive land management practices result in a lower fungal/bacterial biomass ratio. Indeed, soil fungal communities have been reported to be more sensitive to forest harvesting disturbances than soil bacterial communities, which are highly variable among samples (Hartmann *et al*., 2009, 2012a,b).

Soil fungi can be divided into three important trophic groups based on their carbon acquisition strategies in the soil, i.e., symbiotic, saprophytic and parasitic (Nguyen *et al*., 2016a). These trophic modes, which include different guilds, are related to different ecosystem functions, such as nutrient cycling and forest productivity. Furthermore, soil fungi may switch from one trophic mode to another during their lifespans (Nguyen *et al*., 2016a). By altering the quantity and quality of dead wood and litter inputs, forest harvesting modifies the abundance of saprotrophic fungi (Hiiesalu *et al.,* 2017; Lewandowski *et al*., 2019). Forest harvesting can also reduce the abundance of symbiotic fungi (Marshall, 2000; Durall *et al*., 2006). The detrimental effects of harvesting on abundances within the symbiotic ECM fungi guild are expected to increase with increasing harvesting intensity (Dahlberg *et al*., 2001; Parlade *et al*., 2019). One possible mechanism that could lead to the modification of fungi guilds after harvesting is the reduction of photosynthesis products that are released into the soil as root exudates, *i.e.,* non-structural carbohydrates (NSCs), inorganic ions and water (Bertin *et al*., 2003), due to decreases in forest density (Parlade *et al*., 2019). The decrease in nutrients and energy sources is expected to have a lesser effect on fungi that are less dependent on root exudates, such as parasitic, pathogenic or saprophytic fungi.

Forest harvesting can modify abiotic soil factors (*e.g.*, changes in soil organic matter and pH, and variation in soil moisture and temperature) that could influence the biomass, structure and diversity of soil fungi and bacteria (Hartmann *et al*., 2009; Zhang *et al*., 2010; Strukelj *et al*., 2015; Lewandowski *et al*., 2019; Maillard *et al*., 2019). Numerous studies have highlighted soil pH as an important variable influencing bacteria communities (*e.g.*, Lauber *et al*., 2009). Recent studies also highlighted that tree species identity largely determined soil bacteria community composition (Dukunde *et al.,* 2019) or soil fungi community (Baldrian, 2017). Moreover, biotic factors that are related to dead plant material (*e.g.*, forest litter, woody debris) and living plants (*e.g*., forest composition or structural diversity) could be modified by forest harvesting and could influence communities of fungi (Nguyen *et al*., 2016b; Hiiesalu *et al.*, 2017; Sun *et al*., 2017) and bacteria (Purahong *et al*., 2015; Lewandowski *et al*., 2019). With time, the modification of forest canopy, root exudates or biomass and soil porosity or microclimatic conditions (*e.g.,* temperature and moisture) being targeted to affect soil microbial communities (Uroz *et al*., 2016; Dunkunde *et al*., 2019). Clearly, further work is required to assess the long-lasting effects of forest harvesting on soil microbial communities in hardwood forests. In northern coniferous forests, diversity and structure of soil bacterial and fungal communities remained significantly altered by logging disturbances more than a decade after harvesting, with different responses to varied levels of harvesting disturbances (Hartmann *et al*., 2009, 2012a,b).

The first objective of this study was to assess the effects of EA and UA forest management on bacterial and fungal communities in the forest floor, 5, 15 and 30 years after harvesting in a hardwood forest. Larger changes in soil microbiome variables are expected following

more intensive forest management, due to more drastic modifications to both biotic and abiotic factors. Based on this mechanism, we tested two hypotheses, 1) soil microbial communities would be more responsive to forest harvesting under EA managed forests compared to UA managed forests; 2) the magnitude of soil microbial responses to forest harvesting would be greater over the short-term for both management intensities. A second objective was to explore the relationships between soil microbial communities and abiotic (*i.e.*, chemical properties in the forest floor) and biotic (*i.e.*, vegetation properties) conditions.

Methodology

Study sites, experimental design and data collection

Soil microbial communities were assessed in unmanaged forest controls, and even-aged (EA, 25 sites) and uneven-aged (UA, 25 sites) managed stands that were along a harvest chronosequence. The controls were 12 sites in old-growth forest that were > 100-years-old. Dominant and co-dominant trees were over 200-years-old, with no obvious signs of past harvesting. Managed stands were sampled < 5 years, 15 years and 30 years after harvesting; hereafter, these are referred to as EA5, EA15, EA30, UA5, UA15 and UA30. The sites were selected based upon random stratification (following latitude and longitude) of a hardwood forest in the sugar maple (*Acer saccharum* Marshall) -- basswood (*Tilia americana* L.) bioclimatic domain (Saucier *et al*., 2009). The sites were located within a 26 500 ha private forest (Kenauk Nature site network; 45.71° N to 45.84° N, -74.95° W to 74.77° W). Soils in the study area were Dystric Brunisols (USDA, Typic Dystrocrepts), with moder-type humus, which had developed on glacial till deposits that are composed

mainly of gneiss, quartzite and granite (Lajoie, 1967; Soil Classification Working Group, 1998).

Over the past 40 years, harvesting in the Kenauk Nature forest has consisted mainly of strip cutting, which included 50-meter-wide strips of high-intensity harvesting (*i.e.,* clear-cutting or EA management), alternating with 50-meter-wide strips of low-intensity harvesting (30% basal area removed) through single tree selection (UA management). This resulted in paired EA and UA sites that were concurrently harvested and matched in terms of soil type (exposure, slope, drainage, texture). The selected sites were restricted to minimal slopes and stand areas > 0.52 ha. In each site, three circular plots (400 m^2) were randomly selected (Chapter I). Soil samples were collected in 2017, between June and July. In 2017, annual precipitation in the study area was 1191 mm and mean summer temperature was 16.4 °C (Environment et Changement climatique Canada, 2020). Forest soils had mean pH ranging from 4.2 to 6.1. Average (± SD) percentages of sand, silt, and clay in the different treatments were, EA, 51 (± 1.9), 40 (± 1.6) and 9 (± 0.6), respectively; UA, 49 (± 1.7), 44 (± 1.3) and 7 (± 0.7), respectively; and unmanaged forest control, 44 (± 2.9), 47 (± 1.9) and 9 (± 1.6), respectively (Chapter II).

Given that forest floor microbial communities are deemed to be more susceptible to forest harvesting than those in the mineral soil (Hartmann et al., 2009), we focused soil sampling on the FH-layer (0-2 cm). In each plot, eight soil cores were carefully collected (tools rinsed with 70% ethanol between plot sampling) and bulked into a composite sample. Bulked soil samples were transported on ice and stored within 12 h at either 4ºC (chemical properties) or -80 °C (fungi and bacteria).

Sampling, analyses and calculations of different forest variables related to overstory and understory vegetation, coarse woody debris, forest litter, and soil chemical properties are detailed in Chapters I and II. For the herb layer, abundance and taxonomic identity of all 212 plant species that were inventoried were used to calculate phylogenetic diversity using Faith's phylogenetic diversity index, including abundance of species (Scheiner et al., 2017; Faith, 2018) (*i.e.,* Plant Diversity). In each site, forest structural diversity was calculated using the Shannon Index for 5 different DBH classes (1.1-4 cm, 4-9.1 cm, 9.1-20 cm, 20-35 cm, >35 cm) (*i.e.,* Forest structural diversity). Forest diversity in composition was also calculated using the Shannon Index for 20 different tree species (*i.e.,* Forest compositional diversity). We combined those two variables to characterize forest diversity in composition and structure using the Shannon Index for 89 combinations of species and DBH class (*i.e.,* Forest Diversity). Forest basal area in each site was calculated as the total cross-sectional area at 1.3 m for all stems of shrubs and trees having a DBH > 1.1 cm (*i.e.,* Forest Density). Mean litter weight and CWD volumes were calculated for each site (*i.e.,* CWDL). Chemical soil quality of the selected organic F-H horizon was determined by routine analyzes. The mean pH (*i.e.,* pH) and the mean concentration of total C (*i.e.,* C), exchangeable bases (*i.e.,* Base_exchangeable), P (*i.e.,* P) and Al3+ (*i.e.,* Al) were calculated for each site.

DNA extraction

Soil DNA was extracted using Power Soil Kits (Qiagen Inc. Canada, Montreal, QC) following the manufacturer's instructions. The soil that had been stored at -80 °C was homogenized by beating, where 0.25 g of soil was placed in PowerBead tubes and processed according to the manufacturer's protocol. We added a 10 min heating step (65

°C) prior to homogenization (1800 RPM, 60 sec; MM400 Mixer Mill, Retsch GmbH, Haan, Germany).

PCR, sequencing and bioinformatics

To measure soil fungi diversity, 10 µL of DNA (concentration 10 ng/µL) was amplified by PCR. Fungal Internal Transcribed Spacer 1 was amplified using the forward primer ITS1F (5′- CTTGGTCATTTAGAGGAAGTAA -3′), paired with the reverse primer ITS2 (5′-GCTGCGTTCTTCATCGATGC--3′) (Fierer *et al.,* 2005). The amplified products were sent to the McGill Genome Centre (McGill University, Montreal, QC) for sequencing on an Illumina MiSeq platform using a PE300 kit (volume 0.005 µL). DNA sequences were run with QIIME (Caporaso *et al.,* 2010).

Illumina sequences for each sample were provided with paired-end fastq files demultiplexed (*i.e.,* split into individual per-sample fastq files) and removal of barcodes/adapters. The DADA2 pipeline (Callahan *et al*., 2016) was used for fungi sequences analysis. A OTU summary table was provided with the number of OTU in each sample after filtered, denoised, merged and chimera steps performed with dada2 package (Callahan, 2021). With this package, a quality profile was performed for each read (forward and reverse read separately), using heat map frequency that give quality score of each base position. Raw reads were quality trimmed, filtered, denoised, merged (fusion of Paired End reads) and chimera were removed. For filter, standard filtering parameters in DADA2 were used (maximum number of expected errors allow in a read). Forward- and reverse-read trimming was applied up to positions 246 and 233, respectively. For filter and trimming parameters, amplicon length ranged between 295 and 302 bp. In the following steps, DADA2 algorithm were used to denoised sequence variant and the forward and reverse

reads were merged if the reads overlap by at least 12 bases. An amplicon sequence variant table was constructed, and chimeric sequences were identified and removed using DADA2 package. Taxonomy where assign to those sequence variants with the function assignTaxonomy using Bayesian classifier method (http,//benjjneb.github.io/dada2/). OTU clustering using similar sequences (alignment positions with a gap content > 97% were excluded) and annotation was performed using the SILVA reference database (Chong *et al.,* 2020). The barcode library VAL12501024-LIB-E07 was used.

Quality control (QC) and standard data treatment on raw ITS data was performed by the Canadian Centre for Computational Genomics (C3G, Montreal Node) using *dada2 Microbiome Analyst* (Chong *et al*., 2020). To reduce low-abundance and spurious OTUs, only OTUs containing at least 4 reads in at least 2 samples were retained (Coleman-Derr *et al*., 2016). The selected cut-off taxon that was used for fungi phylogenetic and functional analysis based on sequences from the SILVA database was "Order," since fungi from the same "Family" could be assigned to a contrasting fungal guild (Nguyen *et al*., 2016a).

Quantitative PCR analysis

Relative abundances of fungi and bacteria in each soil sample were quantified using a modification of the technique that was described by Fierer *et al*., (2005). Quantitative PCR (qPCR) analysis was conducted using a Thermal cycler C1000 Touch BioRad CFX96 Real-Time System. The experiment was designed based upon recommendations of Taylor *et al*., (2014, 2019). First, we used a SPUD assay (Nolan *et al*., 2006) to test for the presence of PCR inhibitors in the soil DNA extracts. For this assay, each qPCR reaction mixture consisted of 20 µL in total, 10 µl of *Power* SYBR™ Green Master Mix (Bio-Rad), 0.25 µl

of each primer Spud-forward and Spud-reverse at concentration of 10 µM, 4 µL of soil DNA extracts, 1 µL of *Solanum tuberosum* DNA at concentration of 1.9 ng/µL, and 4.5 µL of ddH_2O. Each sample was run in triplicate and a No Template Control (NTC, ddH_2O instead of DNA) was included on each plate. We constructed a standard curve using 10^8 to 10^2 copies/µL (10-fold dilutions) of purified PCR product that had been amplified from *Solanum tuberosum* DNA using the Spud primer. The PCR reactions were run for 40 cycles (2 min at 95 °C for activation, 5 s at 95 °C for denaturation, and 20 s at 60 °C for annealing and extension), followed by a melt-curve analysis (65 °C to 95 °C, in 0.5 °C increments). The presence of inhibitors in the soil DNA extracts was determined by comparing the observed *Solanum tuberosum* DNA quantity from the Cq value to the known quantity that was added to the reaction.

Second, we ran two separate qPCRs to estimate bacterial and fungal DNA concentrations in the samples. For bacteria, we amplified a fragment of the 16S rRNA gene using primers Eub338 (forward, ACTCCTACGGGAGGCAGCAG) and Eub 518 (reverse, ATTACCGCGGCTGCTGG); for fungi, a fragment of the ITS1 region was amplified using primers ITS1 (forward, TCCGTAGGTGAACCTGCGG), and 5.8s (reverse, CGCTGCGTTCTTCATCG) (Fierer *et al*., 2005). To calculate starting DNA concentrations, we constructed a standard curve using 10^8 to 10^2 copies/µL (10-fold dilutions) of purified PCR product that had been amplified using the same primers from *Escherichia coli* DNA (bacteria) or *Saccharomyces cerevisiae* DNA (fungi). The reaction mixture contained 10 µL of *Power* SYBR™ Green Master Mix (Bio-Rad), 0.5 µL of each primer at a concentration of 10 µM, 4 µL of DNA extract, and 5 µL of ddH_2O. Each sample was run in triplicate; to detect possible contamination, a No Template Control (NTC,

ddH_2O instead of DNA, run in triplicate) was included on each plate. For the amplification, we ran a two-step PCR program for bacteria or fungi with 2 min at 98 °C for activation, 40 cycles (15 s at 98 °C for denaturation, and 30 s at 70 °C for annealing and extension), followed by a melt-curve analysis (65 °C to 95 °C, in 0.5 °C increments). The qPCR data analysis was performed with CFX Maestro Version 3.1.1517.0823. The starting DNA quantity (SQ) for each sample and the relative abundance of fungi versus bacteria was calculated using the triplicate mean that was determined by qPCR (Gamper *et al*., 2008; McGuire *et al*., 2010). Low inhibition was detected; Potato DNA values in the samples ranged from 78 to 100 percent of to the initial concentration. The ratio of the mean SQ concentration of foreign Potato DNA measure in the samples divided by the initial Potato DNA concentration incorporated in the sample was used to correct for potential inhibition. Soil fungi DNA extraction and qPCR methodology, following by qPCR data analysis, was performed with Bio-Rad CFX Maestro software Version 3.1 (Bio-Rad).

Microbiome description

To describe the effect of different intensities of forest harvesting on fungal communities, we measured a range of variables and diversity indices (Table 1). Fungi and bacteria abundance, together with the fungi/bacteria ratio, was calculated from the qPCR data (Edgar, 2017; Taylor *et al*., 2019). Based upon available data from the metagenomics, species accumulation curves using OTUs were selected to represent total fungi species richness after different treatments and time-since-harvesting.

Table 1. Methods used to measure selected microbiome variables.

Variables	Methods
Bacteria abundance Fungi abundance Fungi/bacteria ratio	Bacteria and fungi DNA concentration measured with qPCR
Fungi species accumulation curves Bray-Curtis dissimilarity in fungi community Fungi specific species abundances	Total fungi OTU obtained following amplicon sequencing
Fungi phylogenetic diversity Proportion of fungi guild	Assigned or proportion of assigned fungi OTU at least to order level, obtained following amplicon sequencing

Recent studies have reported multiple biases that are incurred in using OTU read numbers as estimators of species abundance (*e.g*., Edgar, 2017; Baksay *et al*., 2020). In the present study, a linear mixed model showed a strong positive correlation ($R^2 = 0.84$) between the number of reads and the fungi DNA concentration measured by qPCR (Supplementary information; Figure S1). Based on this analysis, the number of OTU read counts was weighted by the total fungi abundance that was measured by qPCR in the exact same sample. This abundance estimate was used for fungal phylogenetic diversity (PD) and fungi guild (or trophic mode) analysis. In each plot, fungi PD was calculated based on Faith's PD (Scheiner *et al.,* 2017; Faith, 2018), which is an index varying from 0 to 1, with 1 representing the highest diversity. Fungi guild and trophic mode were assessed using the FUNGuild database (Nguyen *et al*., 2016a), using only confidence scores of "Probable" and "Highly Probable." The FUNGuild dataset was used to impute missing data.

Identification of each fungal species that increases or decreases following harvesting, and dissimilarity between fungi communities using *Bray-Curtis dissimilarity* were assessed with abundances of the 625 OTU reads, using *Microbiome Analyst* platform (Chong *et al*., 2020).

Statistical analysis

Statistical analyses were performed using R (version 4.0.2). Effects of EA5, EA15, EA30, UA5, UA15, UA30 and Control on fungal and bacterial abundance, and the fungi/bacteria ratio were analyzed (at the plot level) using linear mixed-effects models (*lme4* package, function *lmer*), with site as a random effect (Bate *et al*., 2015). A square-root transformation was applied to fungal and bacterial abundance to improve the distribution of the residuals. Treatment means were compared using post hoc, multiple means comparisons (Tukey contrasts, *multcomp* package). Two pre-analyses were used to select best explanatory models for 1) bacterial abundance and 2) proportions of ECM fungi using a model comparison approach with the Kullback-Leibler information divergence, as presented by Anderson *et al*., (2000) (*AICcmodavg package*, Mazerolle, 2015). Among the models that were tested, the two best explanatory models for bacteria abundance were 1) soil pH, and 2) forest density as single variables. Based upon this pre-analysis, linear mixed models, with site as a random effect, were used to analyze the effect of those two variables on bacteria abundance (square-root transformed). Among the tested models, forest structural diversity as a single variable was the best model for explaining the proportion of ECM fungi. Two other models that included forest composition diversity and soil C concentration variables obtained an AICc weight > 1%. Linear mixed models with sites as a random effect were performed for these three explanatory variables.

Mean fungi PD and proportions of fungi trophic modes were compared along the chronosequence for EA, UA and unmanaged forest (at the site level) using one-way ANOVA. For fungi trophic mode, a square-root transformation on fungi OTU proportions was applied improve the normality of the residuals. Mean abundances of specific fungi

OTU were compared among the different treatments (filtered and log- transformed counts in Microbiome Analyst) using one-way ANOVA. Significantly different means among treatments were determined using post hoc Tukey's tests (*stats* package). Statistical significance was declared at $\alpha = 0.05$. Homogeneity of variance was verified using Levene's test and normality was tested using Shapiro-Wilk tests and the Durbin-Watson test for the distribution and auto-correlation of residuals.

Analyses of group similarities (*vegan* package, function *ANOSIM*) with 999 permutations were applied to fungal community comparisons using Bray-Curtis index of dissimilarity in Microbiome Analyst (Chong *et al.,* 2020). Non-metric multidimensional scaling (NMDS) illustrates those communities. Permutational multivariate analysis of variance (PERMANOVA), with 999 permutations (*vegan* package, function *adonis2*), was used 1) to compare fungi communities between managed forest plots and unmanaged forest plots, and 2) to analyze the partitioning of variability (considering the matrix of microbiome variables that were measured) that was explained by the treatments and the sites. Means dissimilarity between treatments was evaluated using pairwise comparisons (*vegan* package, function *pairwise.adonis*), with adjusted *P*-values (Holm's stepdown method). Finally, a principal component analysis (*FactoMineR* package, function *PCA*) was performed to reveal the structure of dependence and correlation among 1) microbial community variables, and 2) a selection of biotic and abiotic variables, *i.e.*, plant diversity in the herb layer, forest diversity, forest density, litter and coarse woody debris volume, pH, soil concentration of P, Al and C and concentration of exchangeable base cations. Changes that were induced by different management treatments were also demonstrated on A) bacteria abundance, soil pH and forest density, and B) proportions of ECM fungi,

forest structure diversity, forest composition diversity and soil C concentration, using separate principal component analyses (*FactoMineR* package, function *PCA*).

Results

PCR and q-PCR data

Seventy percent of fungi sequences were conserved after filtering for the final analysis and a total of 876 different fungi OTUs were identified. Exclusion of low-abundance and spurious OTUs reduced that number to 625. Of these 625 OTUs, 248 were assigned to kingdom level, 377 to phylum level, 303 to class level, and 289 to order level or lower. Based upon available data that were obtained from the metagenomics (*i.e.,* 4 596 763 reads for 625 different OTUs), only the 289 OTUs that were assigned at least to Order were used for analysis of PD and proportions of functional guilds. Percentage of assigned fungi OTUs at least to Order, compared to total OTUs, was 36.9%, 27.3% and 37.9% along the chronosequence for EA management, 46.6%, 28.1% and 21.4% along the chronosequence for UA management, and 33.8 % in unmanaged forest control. With respect to this variability, relative abundance was used for comparisons of different fungi guilds and fungi orders following treatment.

For q-PCR analysis, no wells failed quality control rules; the R^2 of the standard curve was always > 0.98. Quantification cycle (Cq) standard deviation was always < 0.2. Standard errors for the three methodological replicates varied from 0.2% to 17% for bacteria (mean = 4% for the 185 samples) and from 1% to 19% for fungi (mean = 6% for 185 samples).

Effect of forest harvesting treatments on abundance of bacteria and fungi

The three linear mixed models were highly significant ($P < 0.001$) for mean bacteria abundance, mean fungi abundance and the F/B ratio (dependent variables), relative to the treatments, *i.e.,* the combination of management type and years-since-cutting (independent variables), with sites as a random factor.

Mean bacteria abundance in unmanaged forests was significantly lower ($P = 0.0014$) than that in managed forests (except UA30) (Figure 1a). For UA management, 30 years post-harvest, bacteria abundance in forest stands was significantly lower than 5 or 15 years after harvesting ($P = 0.049$). Regardless of time-since-harvesting in the EA managed forests, bacteria abundance was more than 34% higher (*i.e.,* > 671,700 copies/μL) than the mean that was estimated for unmanaged forests (*i.e.*, 441,988 copies/μL). No significant differences were observed for total fungi abundance between unmanaged forest control and the other treatments (Figure 1b). Yet, the chronosequence demonstrates a non-significant trend of increasing fungi abundance 15 years following harvesting for both EA and UA management (Figure 1b). Mean F/B ratio in unmanaged forests was significantly higher ($P = 0.005$) than that in managed forests (except UA15) (Figure 1c). F/B ratio in EA managed forests (0.0182) was 32% lower than in unmanaged forests (0,0267).

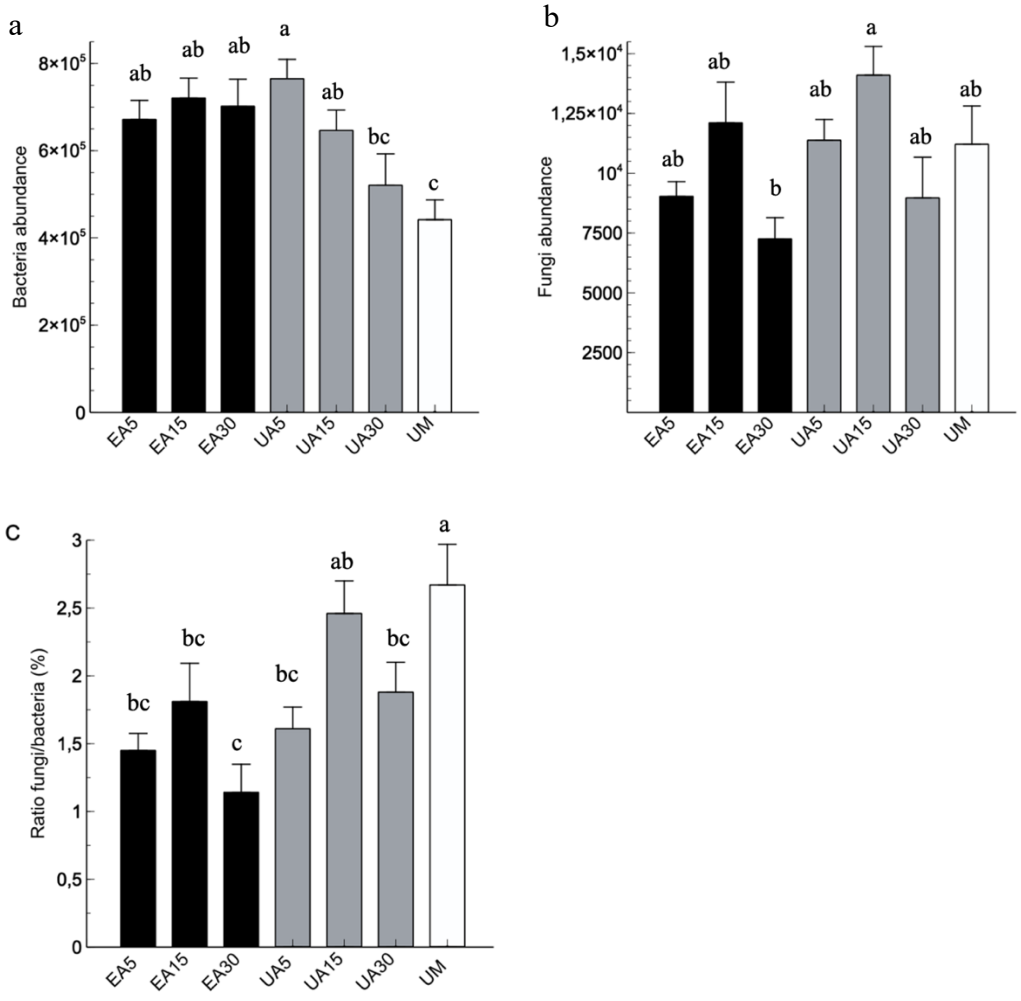

Figure 1. Mean bacterial (a) and (b) fungal abundance (DNA concentrations in mol/μL), and (c) mean F/B ratios in unmanaged forest controls (UM) and in even-aged (EA) and uneven-aged (UA) managed forests 5, 15, 30 years after harvesting. Means with different letters indicate significant differences ($P \leq 0.05$). Error bars are standard errors. For EA5, N = 24 (plots); EA15, N = 24; EA30, N = 27; UA5, N = 24; UA15, N = 24; UA30, N = 27; UM, N = 39.

Effect of forest harvesting treatments on fungal diversity and composition

The species accumulation curve (for 22 plots per treatment) showed that total fungal species richness was the highest in unmanaged plots (380 OTU) and lowest in UA5 (323 OTU) and EA5 (331 OTU) (Figure 2). Indeed, the rankings of the seven treatments were reasonably consistent across accumulation curves (Kendall's W =0.726; $\chi^2 = 91.47$, df = 6, $P < 0.001$), which can be ordered as, UM > UA15 = UA30 > EA30 = EA15 = EA5 = UA5.

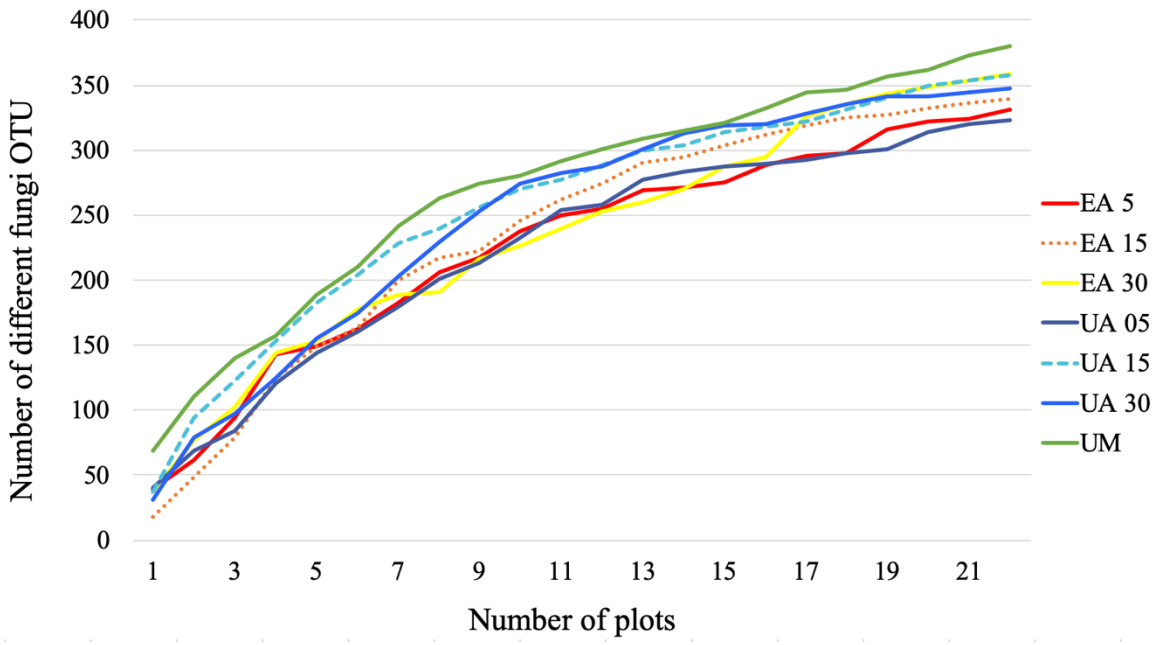

Figure 2. Species accumulation curves for soil fungi in unmanaged forest stands (UM) and stands following even-aged (EA) and uneven-aged (UA) management along a chronosequence (5, 15, 30 years after harvesting) calculated with the presence of UTO reads that were obtained from PCR next-generation sequencing.

A small number of abundant fungal species and a large number of less abundant species were measured. In fact, 35 OTUS with more than 20,000 reads each account for around 75% of total OTU abundance. Moreover, a large proportion of assigned fungi sequences (*i.e.,* 77% of different OTUs, 478 of 625) constituted less than 5% of total OTU abundance.

Six different fungi species were significantly affected by forest harvesting treatments ($P < 0.001$). Three of these species were abundant (> 20,000 reads). Moreover, three species, including species from the phylum Ascomycota, were more abundant shortly after harvesting and could be referred to early-stage species (Table 2). One of these, an animal pathogen in the family Herpotrichiellaceae, was significantly more abundant in EA5 managed forests. Another fungal species, which lacked phylogenetic resolution, was significantly lower following EA forest management. Two other species were significantly

more abundant in EA15 and UA15 managed forest and could be referred to as mid-stage species.

Table 2. Mean fungi abundance per sites (± standard errors) for even-aged and uneven-aged forest management along a 30-year chronosequence of forest harvesting and unmanaged forest. Means within the same row followed by the same letter do not significantly differ at $P < 0.05$.

OTU	Description	*P*-values	Even-aged management			Uneven-aged management			Unmanaged
			5 years	15 years	30 years	5 years	15 years	30 years	
FJ553943	Ascomycota	> 0.0001	134 ±82 a	52 ±33 ab	19 ±15 b	90 ±55 a	9 ±5 b	0.6 ±0.6 c	8 ±3 b
FM999494	Agaricomycetes	0.0016	277 ±204 c	7111 ±4058 a	530 ±350 c	604 ±315 c	808 ±549 bc	1129 ±557 bc	1868 ± 985 b
GU174289	NA	> 0.0001	1938 ± 785 b	1800 ± 642 b	1036 ± 258 bc	1747 ± 619 b	7292 ± 2681 a	184 ± 76 c	1660 ± 465 b
HM030587	NA	> 0.0001	1946 ±1221 bc	1220 ±647 c	3346 ±2004 abc	3629 ±1386 ab	3289 ±1176 ab	10642 ±6482 a	4469 ±2650 ab
HM069355	NA	> 0.0001	226 ±65 a	57 ±27 bc	32 ±17 c	338 ±139 a	66 ±16 b	28 ±23 c	69 ±37 b
HQ124509	Herpotrichiellaceae Animal pathogen and fungal parasite	> 0.0001	233 ±81 a	5 ±3 c	27 ±18 d	76 ±28 b	11 ±6 cd	6 ±6 cd	2 ±2 d

NA, not available.

According to multivariate variation partitioning, the forest harvesting treatments explained a large portion of variation in fungal communities ($R^2 = 0.14$, $P < 0.001$) and the sites had a smaller, but significant effect on variation in these communities ($R^2 = 0.07$, $P < 0.001$). Fungal communities in EA5 managed forest were more dissimilar than in unmanaged forests (adjusted $P = 0.021$), compared to the other managed forests along the chronosequence (Figure 3). No significant difference ($P = 0.521$) in mean fungi PD was observed among the different treatments. Proportions of assigned fungi orders among mean fungi PD in each treatment are shown in Figure 4.

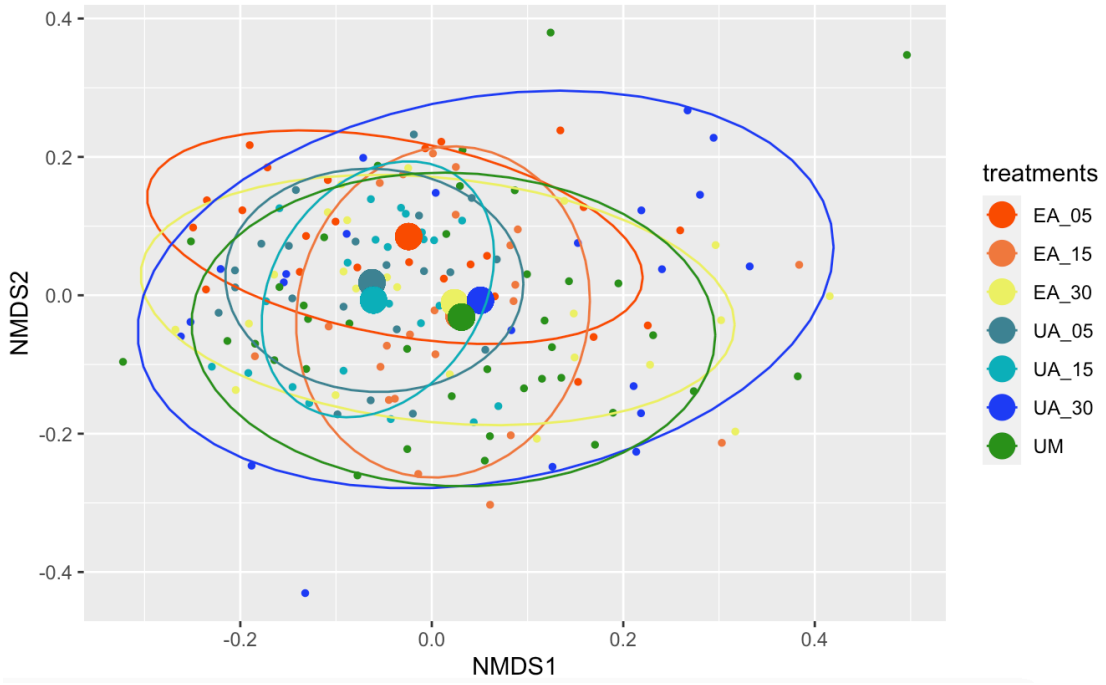

Figure 3. Representation with NMDS of soil fungi community dissimilarity that was calculated with Bray-Curtis indices (BC_{ij}), based on 625 fungi OTUs and their abundances, in unmanaged forest controls (UM), and even-aged (EA) and uneven-aged (UA) managed forests 5, 15 and 30 years after harvesting (Total of 189 plots). *P*-values and adjusted *P*-values (Holm's stepdown method) to detect significant differences among fungi communities compared to unmanaged forest control, EA05 (*P*-value, 0.001; adjusted *P*-value, 0.021) *, EA15 (0.474; 0.948), EA30 (0.054; 0.432), UA05 (0.014; 0.196), UA15 (0.017; 0.221) and UA30 (0.479; 0.948). Means that are significantly different from unmanaged forest controls are represented by *** ($P < 0.001$), ** ($P < 0.01$), * ($P < 0.05$).

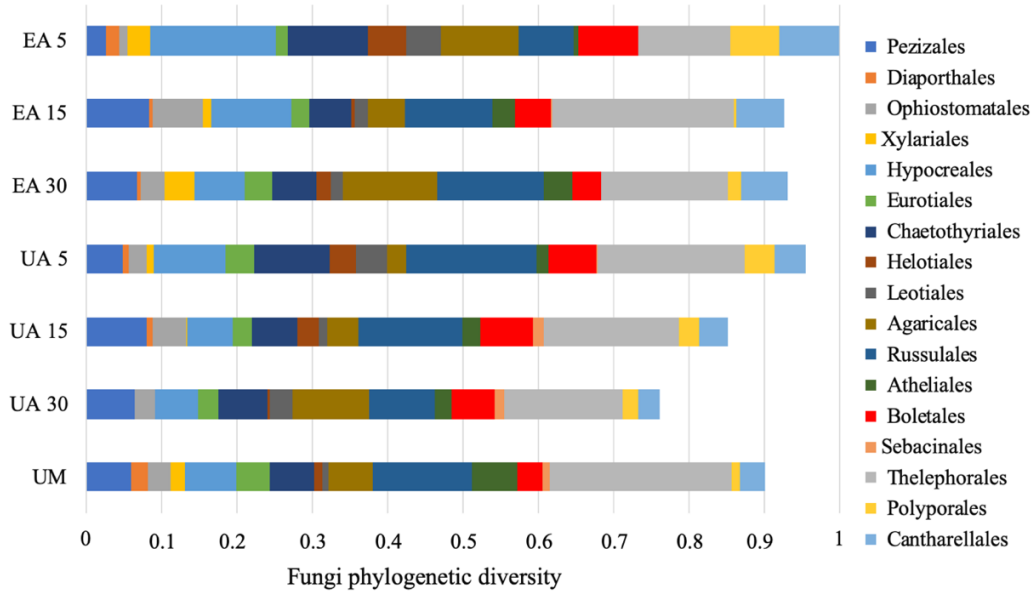

Figure 4. Proportion of assigned fungi orders among mean fungi phylogenetic diversity that was measured in unmanaged forest controls (Unmanaged), and even-aged (EA) and uneven-aged (UA) managed forests 5, 15 and 30 years after harvesting. Total of 63 sites.

The mean proportion of pathogenic and parasite fungi in EA5 was higher than that in the other treatments, (P = 0.003; Figure 5). There was no significant effect of forest harvesting treatments on the proportion of symbiotic (P = 0.106) and saprotrophic (P = 0.345) fungi. Furthermore, statistical analysis revealed no significant effect of forest harvesting treatments on the proportion of fungi guilds **(**P = 0.12**)**. Overall, fungal guilds were dominated by ectomycorrhizal species (> 75% of relative abundance) (Figure 6). Higher proportions of wood saprotrophs (mean = 9.7%), plant pathogenic (3.0 %) and animal pathogenic (0.7 %) fungi were measured in the EA5 treatment compared to other treatments (all means < 0.7, 1.8 and 0.2, respectively) (Figure 6). A high proportion of undefined and soil saprotrophs (means = 18.1%) were also observed in UA30 compared to other treatments (all means < 11.2%) (Figure 6).

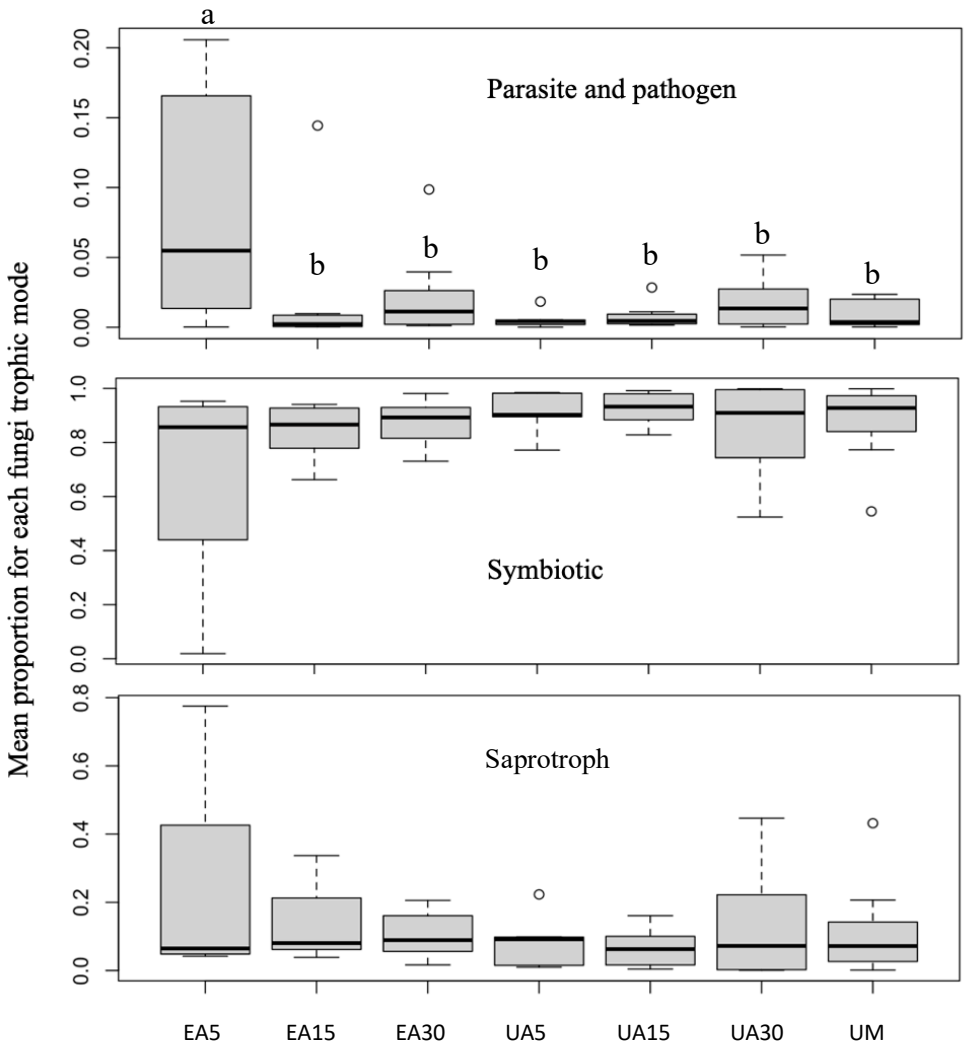

Figure 5. Box-and-whisker plots representing mean proportions of parasitic and pathogenic, symbiotic and saprotrophic fungi trophic modes (raw data) in unmanaged forest controls (Unmanaged), and even-aged (EA) and uneven-aged (UA) managed forests 5, 15, 30 y after harvesting. Total equal 1. Means with the same letters do not significantly differ ($P < 0.05$; Tukey's test).

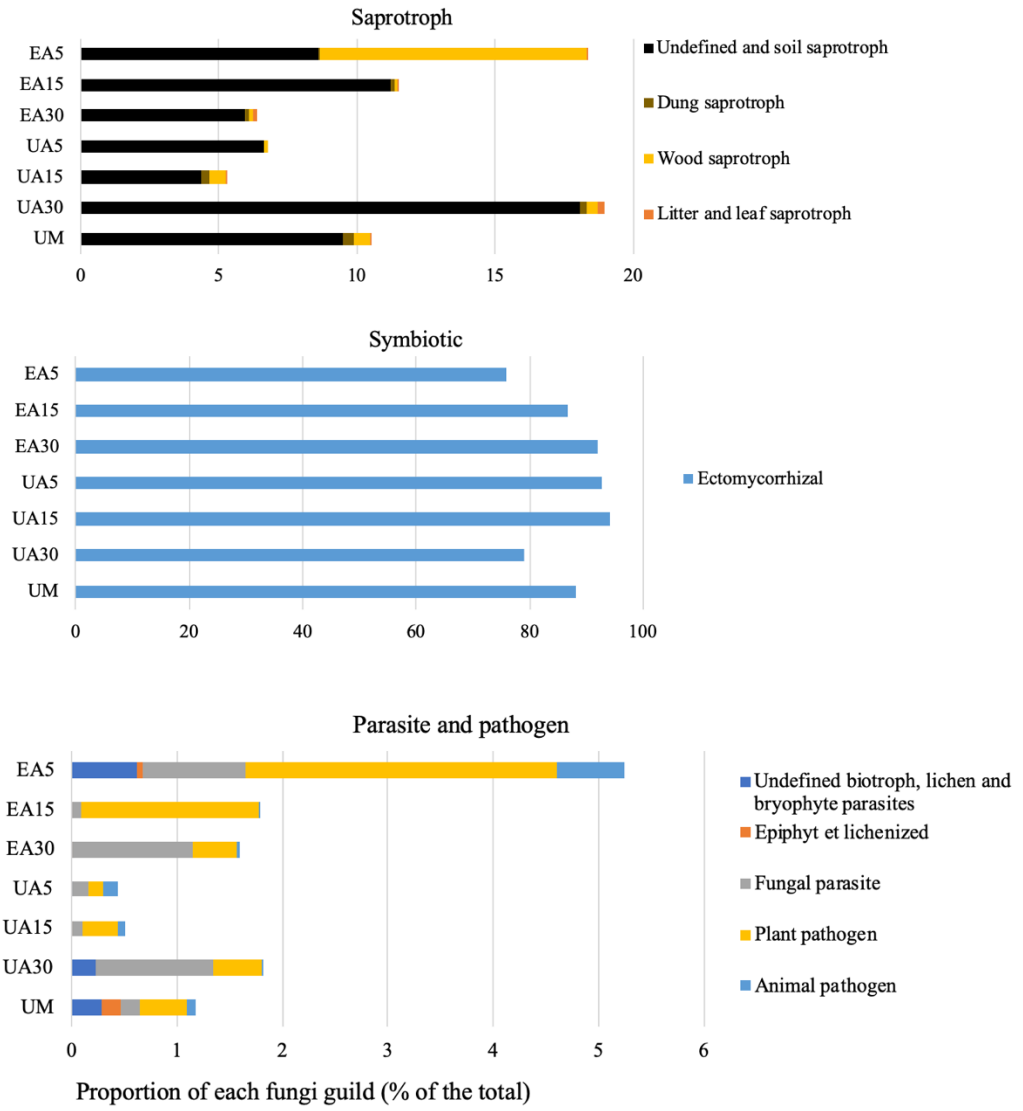

Figure 6. Proportions of fungal guilds for each trophic mode (saprotrophic, symbiotic and parasitic and pathogenic) in unmanaged forest controls (Unmanaged), and even-aged (EA) and uneven-aged (UA) managed forests 5, 15 and 30 years after harvesting. The total for all fungi guild in each treatment is 100% (Total of 63 sites). For the symbiotic fungal guild, only ectomycorrhiza are represented due to low proportions of endophytic and arbuscular mycorrhizal fungi in our sample.

Relationships between soil microbial communities and abiotic and biotic forest conditions

The first and second components of PCA (Dimensions 1 and 2; Figure 7) explained respectively 33.5% and 19.4% of variance in the selected forest variables. Dimension 1 was correlated with proportions of saprotrophic, symbiotic and parasitic fungi, forest

diversity, forest density, available soil-P, and C concentrations (Table 3; Figure 7a). Dimension 2 was correlated with plant diversity and bacteria abundance, CDW volume, soil pH, and exchangeable base concentrations (Table 3; Figure 7a). Ordination of treatments on the two first principal components showed a clear differentiation between unmanaged forests (higher CWD volume, forest density and diversity, plant diversity, pH, exchangeable bases and F/B ratio) and other managed forests along the chronosequence, especially EA managed forests (higher proportion of parasitic and pathogenic fungi trophic modes, bacteria abundance and soil Al concentrations), based on centroid locations of each treatment (Figure 7a). UA managed forests were converging on unmanaged forests with increasing time-since-harvesting (Figure 7a).

Among the variables that were tested, bacteria abundance was significantly and negatively correlated with forest density ($P < 0.001$) and soil pH ($P = 0.011$). The association between bacteria abundance, forest density and soil pH and the treatments is illustrated in Figure 7b.

The proportion of ECM fungi was significantly and positively correlated to forest structure diversity ($P = 0.0003$), soil C concentration ($P = 0.0004$) and forest compositional diversity ($P = 0.003$). Interestingly, neither the linear mixed model for forest density nor soil pH was significantly correlated with the proportion of ECM fungi (both $P > 0.05$). The association between proportions of ECM fungi, forest structure diversity, forest composition diversity and soil concentration of C with the treatments is illustrated in Figure 7c.

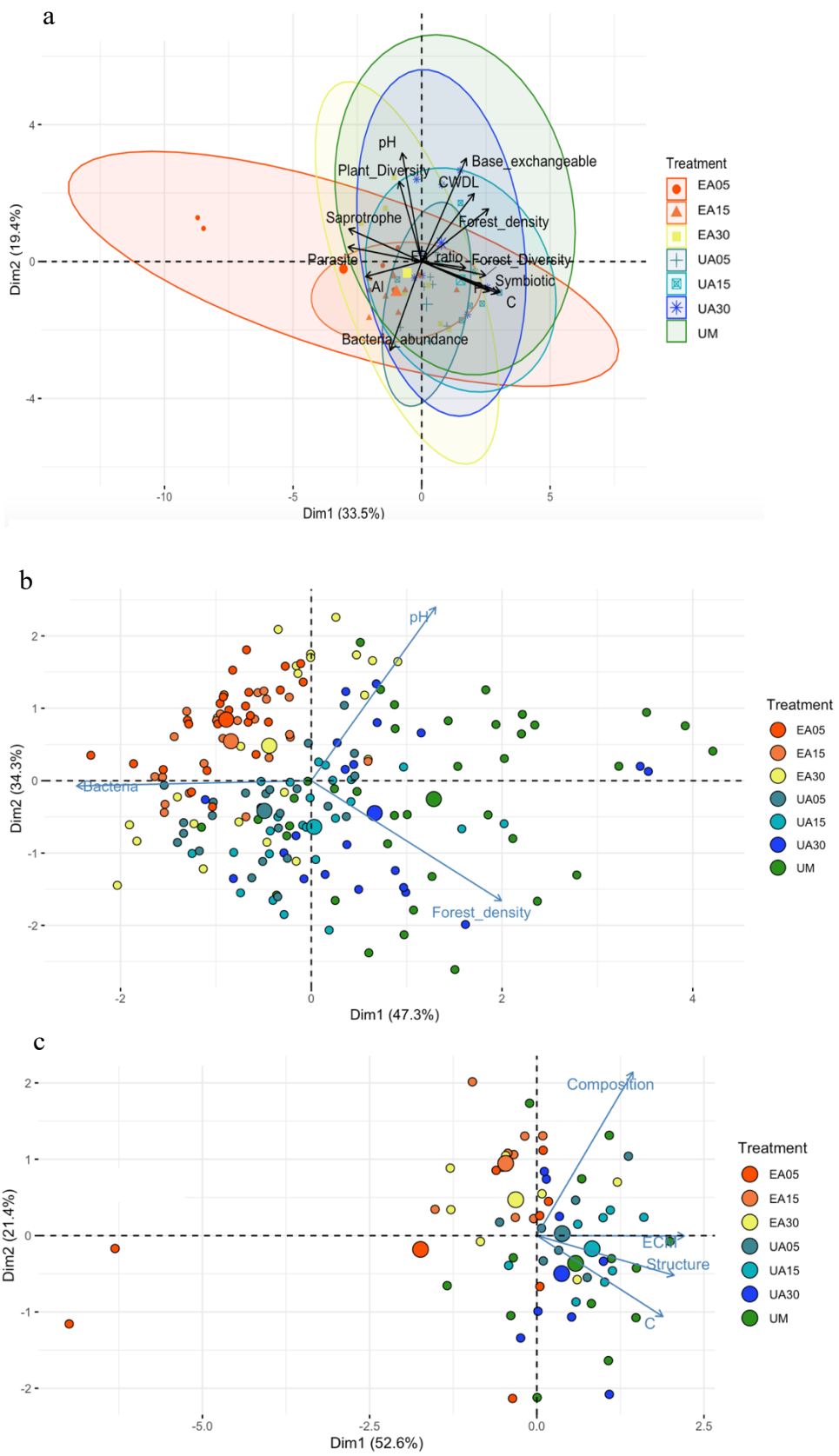
a
pH
Plant_Diversity
Base_exchangeable
CWDL
Saprotrophe
Forest_density
Parasite
ratio
Forest_Diversity
Symbiotic
Al
C
Bacteria_abundance
Dim1 (33.5%)
Dim2 (19.4%)
Treatment
EA05
EA15
EA30
UA05
UA15
UA30
UM
b
pH
Bacteria
Forest_density
Dim1 (47.3%)
Dim2 (34.3%)
Treatment
EA05
EA15
EA30
UA05
UA15
UA30
UM
c
Composition
ECM
Structure
C
Dim1 (52.6%)
Dim2 (21.4%)
Treatment
EA05
EA15
EA30
UA05
UA15
UA30
UM

Figure 7. Principal component analysis for a) abiotic and biotic forest properties after uneven-aged (UA) and even-aged (EA) management in 63 sites (ellipses show the influence zone of each treatment), b) bacteria abundance, pH and forest density, and c) proportion of ECM fungi, forest structure diversity, forest composition diversity and concentration of soil C after UA and EA management, and unmanaged forest control (UM). Larger symbols (*e.g.,* circle, triangle) represent the positions of each treatment along PCA1 and PCA2. For (b), PCA used 189 plots. Dimension 1 Contribution (%), Bacteria - 51.62, pH, 14.51; Forest density, 33.87. Dimension 2 Contribution (%), Bacteria, -0.06; pH, 67.58; Forest density, - 32.35. For (c), PCA used 63 sites. Dimension 1 Contribution (%), ECM, 33.10; Structure, 28.67; Composition, 14.05; soil C, 24.17. Dimension 2 Contribution (%), ECM, 0.00; Structure, - 4.53; Composition, 76.69; soil C, - 18.72. The number after the management type (i.e., EA or UA) represents time-since-harvesting, 5, 15 or 30 years. UM, Unmanaged forest; Saprotrophic, Proportion of saprotrophic fungi; Symbiotic, proportion of symbiotic fungi; Parasitic, proportion of parasitic and pathogenic fungi; FB ratio, Fungi/Bacteria ratio; CWDL, Coarse woody debris and litter volume; C, concentration of carbon, P, concentration of phosphorus; Al, concentration of aluminum; Exchangeable bases, concentrations of exchangeable bases; Bacteria, mean bacteria abundance; ECM, proportion of ectomycorrhizal fungi; Structure, forest structural diversity; Composition, forest compositional diversity.

Table 3. Contribution of abiotic and biotic forest variables to the first two dimensions of the principal component analysis ordination.

Variables		Dimension 1 Contribution (%)	Dimension 2 Contribution (%)
Biotic	Saprotroph	**11.19 (-)**	2.18
	Symbiotic	**12.99 (+)**	1.92
	Parasite and Pathogen	**11.37 (-)**	0.43
	Plant_Diversity	1.07	**13.15 (+)**
	Forest_Diversity	**8.66 (+)**	0.39
	Bacteria_abundance	2.09	**16.31 (-)**
	FB_ratio	4.06	0.08
	CWDL	5.81	**9.48 (+)**
	Forest_density	**9.44 (+)**	5.67
Abiotic	pH	0.80	**24.20 (+)**
	P	**9.51 (+)**	1.99
	Al	6.57	0.44
	C	**11.76 (+)**	2.36
	Exchangeable bases	4.34	**21.97 (+)**

Values represent the contributions of selected variables for a given axis (%). The variables with strong correlations with the principal component ($P > 0.05$) are represented in bold; positive correlations have (+) signs and negative correlations have (-) signs. The quality of representation for the first 2 dimensions was highest for exchangeable bases, pH, abundance of symbiotic fungi as well as concentration of C (Cos 2 analysis). Information is presented for 63 sites.

Discussion

There is increasing evidence that forest harvesting may substantially alter soil microbial communities (*e.g.*, Hartmann *et al.*, 2009, 2012a,b; Lewandowski *et al.*, 2019). In the

present study, using a large operational forest management setting that compared different harvesting intensities along a chronosequence, we have provided new and more precise information regarding modifications to the microbiome brought about through harvesting in temperate hardwood forests.

Forest harvesting promote bacteria abundance

Forest harvesting led to substantial diminution of the F/B ratio, relative to that observed for the unmanaged forest. This decrease was strongest under high intensity management (*i.e.,* all means were at least 32% lower), compared to lower intensity management. Similar results have been observed by Bailey *et al*., (2002), who found higher F/B ratios under conditions of less intensive management. The significant decrease in F/B ratio in the upper soil layer with management in hardwood forest is consistent with studies by Chatterjee *et al*., (2008) in coniferous forests (*Pinus contorta* ssp. *latifolia* (Engelmann) Critchfield; *P. ponderosa* Douglas ex C. Lawson). Our results are also consistent with Wu *et al*., (2011) and the multi-biome meta-analysis of Holden and Treseder (2013), who observed more important changes in microbial variables (*e.g.,* fungi and bacteria abundance) following clear-cutting compared to partial cutting or to unmanaged forests. Fungi are known to be more efficient than bacteria for C and N stabilization and storage in the soil (Malik *et al*., 2016). In this respect, a higher F/B ratio could be associated with important ecosystem functions such as greater soil C storage (Cardenas *et al*., 2015). The lower F/B ratio that was observed following harvesting in EA and UA managed forests was associated with an increase in bacteria abundance. Similarly, Lewandowski *et al*., (2019) observed higher abundances of soil bacteria, especially gram-negative species, in partially harvested forests compared to unharvested forest controls. They explain their results in terms of greater

resource availability from easily decomposing organic matter for bacteria, following the harvest treatment.

The present PCA analysis segregated unmanaged forests from the other treatments based on the high plant diversity, high pH and concentrations of exchangeable base cations, as well as high volume of CWD in the former, together with low abundances of bacteria (Figure 7a). Plant diversity and soil pH have been identified as factors shaping the soil bacteria community of hardwood forests (*e.g.,* Ren *et al*., 2018). Also, these results have highlighted the well-known importance of unmanaged hardwood forest soils in conserving high quantities of CWD (McGee *et al*., 2007; Vanderwel *et al*., 2008), plant diversity (Graae & Heskjaer, 1997; Bell *et al*., 2016), soil pH and concentrations of base cations (Federer *et al*., 1989; Cleavitt *et al*., 2018).

Based upon our analyses, assessment of the role of forest management on bacteria abundance might be indirectly related to how management affects soil pH and forest density (Figure 7b). In the present study, where soil pH is relatively high, bacteria abundance significantly increases with soil acidification that is observed following forest management harvesting. In contrast, in forests with soils that are already acidic (*e.g.,* large-scale experiment designs, such as EMEND, in the boreal forest of northern Alberta; Spence and Volney, 1999), bacterial abundance decreases following harvesting (Hannam *et al*., 2006). Both results agree with the large-scale meta-analysis of Holden and Treseder (2013), where the general decrease in bacteria abundance that was reported following harvesting in numerous biomes was not observed in hardwood forest. Moreover, using

another methodology, Taylor *et al.,* (1999) also found a negative correlation between pH and active bacterial densities in the forest floor of northern hardwood forest.

Among the variables that were tested, forest density was identified as being negatively correlated with bacteria abundance. The marked decrease in forest density due to overstory tree removal likely led to modification of microclimatic soil conditions that was observed shortly after harvesting, especially clear-cutting (*e.g.*, increase in soil temperature and more direct precipitation, among others; Clarke *et al*., 2015; Zhou *et al*., 2015; Siebers & Kruse, 2019). It is still unclear how these complex interrelated modifications affect bacteria abondance. Yet, it is clear that the increase in bacteria abundance (> 34% increase after high intensity management along the chronosequence compared to unmanaged forest control) could lead to an increase in soil bacteria respiration and an increase in the flux of CO_2 to the atmosphere (Lewandowski *et al.,* 2019).

Compared to bacteria, no clear pattern of modifications to fungal abundance following harvesting could be observed in the present experiment. This inconsistent pattern could be due to the lack of synergy along the chronosequence among important variables that are likely influence fungi abundance, such as soil variables (*e.g.*, C concentrations, soil moisture content), biotic forest variables (*e.g.*, forest structural and compositional diversity), and within the microbiome (Taylor *et al*., 1999; Zhang *et al*., 2010; Simard *et al*., 2012).

Modification of fungal communities along a chronosequence of forest harvesting

For high intensity harvesting, fungi species richness increases along the chronosequence (Figure 2). This result concurs with other studies that have been conducted in coniferous

stands, where ECM fungal richness in the organic horizon increases with stand age (*e.g.,* Visser, 1995; Johnson *et al*., 2005). In these studies, ECM fungal richness increased in relation to the presence of early to mid- or late-stage fungal species and modifications to root exudates with tree ontogeny.

In disturbed communities, some fungi species are known to dominate, possibly due to their ability to re-establish a network of interconnected hyphae, to sporulate rapidly, to adapt to new plant hosts or due to availability of new soil resources (Feddermann *et al*., 2010; Willis *et al*., 2013; van der Heyde *et al.,* 2017). This pattern was observed in the present study, where the 5% most abundant fungi species accounted for around 75% of total abundance. We identified three fungi species, including an ascomycete and an opportunistic animal pathogen in the family Herpotrichiellaceae, which clearly increased shortly after high-intensity harvesting (Table 2). Furthermore, the first 5 years following high-intensity management was targeted to modify more strongly total fungi community composition (Figure 3). Other long-term studies also have detected strong modification of soil microbial communities immediately after harvesting, even if fewer obvious impacts persisted for up to 50 years (Kyaschenko *et al*., 2017; Chen *et al*., 2019). The changes that were detected in fungal communities may indicate both modifications in plant host or resource availability, and a new environmental selection pressure that could result from recent high-intensity management (Kohout *et al*., 2018; Liu *et al*., 2019).

Contrary to expectation, we did not detect significant differences in fungi PD among treatments. We could not associate increased fungi PD diversity with an increase in plant diversity or plant attributes, as has been suggested in a recent study (Nguyen *et al*., 2016b).

However, we observed that a high proportion of fungi from the orders Thelophorales and Russulales (generally, ECM fungi) were found in unmanaged forest, while a high proportion of fungi from the Hypocreales (principally, parasitic fungi) were found recently after high-intensity harvesting (Figure 4).

Parasitic or pathogenic trophic modes significantly increased in recent high-intensity harvested forest (Figure 5). In coniferous forests, Parlade *et al*., (2019) also found more pathogens and parasitic fungi in the short-term after clear-cutting compared to partial cutting and unmanaged forest. The fact that both studies in different forest types, lead to the same conclusion highlights a possible role for recent high-intensity harvesting in increasing pathogenic and parasite fungi. This increase in proportion of fungal parasites and pathogens shortly after high-intensity harvesting could be related to the biotic filter (*e.g*., competitive relationships between other fungi species and bacteria) that greatly and rapidly influenced fungi colonization (Bâ *et al*., 2011). The importance of interactions within the microbiome is less obvious several years after colonization, where modifications to soil chemical properties (*e.g*., soil C, N and P concentrations), and to forest composition and structure start to become increasingly important with respect to patterns of fungal succession (Bâ *et al*., 2011).

Two important processes are known to control overall fungi trophic mode, 1) a decrease in the amount of photosynthate transfer from living trees, and 2) alteration in the decomposition process in the soil microbiome habitat (Kohout *et al*., 2018). In coniferous forests, a substantial reduction in symbiotic fungi abundance was observed after intensive forest management (Dahlberg *et al*., 2001; Durall *et al*., 2006), notably symbiotic ECM

fungi (Parlade *et al*., 2019). As mentioned by Parlade *et al*., (2019), the important decrease in sources of C from living tree photosynthate, therefore, could be a plausible explanation from the ECM fungal guild decrease that was observed immediately after high-intensity harvesting. In the present study, forest density was closely, but not significantly correlated with the proportion of ECM fungi ($P = 0.06$). Interestingly, our results demonstrate that forest structural diversity (*i.e.*, high richness and evenness of tree sizes) was a better explanatory variable, which was strongly correlated with the proportion of ECM fungi ($P = 0.0003$). Forest structural diversity was even more strongly correlated with the proportion of ECM fungi than was forest compositional diversity or soil C concentrations. This result highlights the importance of ontogeny or diversity in host plant age to attain an increasingly higher proportion of the ECM fungal guild in forest stands. Many mechanisms could explain this result, including 1) the importance of differences in host carbon supply that occur as plant age (Bertin *et al*., 2003), or 2) heterogeneity in growing conditions in forests with high structural diversity, allowing early, multi- and late-stage ECM fungi to proliferate. According to Johnson *et al*., (2005), understanding the response of symbiotic fungi communities to plant aging should be a primary concern in forestry.

Overall, PCA results revealed an overall stronger negative association between more intensive forest harvesting (EA) and symbiotic fungal abundance, forest diversity and density, together with concentrations of soil P and C, compared to less intensive forest harvesting (UA) (Figure 7a). These results agree with the more important effect that is generally detected after clear-cutting compared to partial cutting (or unmanaged forest) with respect to 1) the decrease in nutrient and soil C concentrations (*e.g.,* Hume *et al.*,

2018), 2) the decrease in symbiotic fungi (*e.g.,* Parlade *et al*., 2019), and 3) stronger modifications of forest density and structure (*e.g.,* Moola & Vasseur, 2008). With their PCA analysis of coniferous forest, Parlade *et al*., (2019), also observed opposite path along the first PCA dimension between symbiotic ECM fungi and parasite and pathogen one. This opposite path might represent a modification of ecological niches in favors to parasite and pathogen fungi recently after high-intensity forest harvesting. The absence of microbiome analysis in the mineral horizon was an important limitation in the present study. In fact, based upon a general hypothesis regarding vertical segregation among symbiotic fungi, we have likely missed the arbuscular mycorrhizal (AM) fungi that principally occupy the mineral horizon, compared to ECM that are known to dominate the organic horizon (Carteron *et al*., 2020).

Saprophytic fungi, which degrade lignin and are less dependent on C that is supplied by living trees, appear to be less vulnerable than symbiotic fungi to clear-cutting (Parlade *et al*., 2019). In the present study, the proportion of the saprotrophic fungal trophic mode did not differ significantly among treatments, compared to the proportion of symbiotic fungi that tended to be lower shortly after clear-cutting (EA5) (Figure 6; Figure 7b). Better phylogenetic resolution would be required for further analysis of relationships between fungi communities and harvesting intensity in the present study.

Conclusion

Numerous mechanisms involving interactions with vegetation and soil variables could lead to modification of the microbiome following forest harvesting. Moreover, long-term modification of microbiome communities following forest harvesting could indicate

important modifications to soil nutrients, or C pool sizes (Liu *et al*., 2019). This study has tried to disentangle these complex interactions in deciduous forest, by measuring modifications to the microbiome and forest variables after harvesting. Results that were obtained from this experiment demonstrated significant modifications of the microbiome (*e.g.,* increase in bacteria abundance, decrease in F/B ratio) that occurred 5 and 15 years after harvesting, for both harvesting intensities relative to the unmanaged forest controls. Among harvesting intensities, the difference from unmanaged forest control was generally higher for high-intensity management. Soil bacteria abundance was negatively correlated with soil pH and forest density, while the proportion of ECM fungi was positively correlated with forest structure diversity. For the fungi community, the strongest modifications and the increase in proportion of pathogenic and parasite fungi were observed shortly after high-intensity harvesting. Alterations to the soil microbiome can be considered among the longest-lasting impacts that high-intensity harvesting can exert on forest variables. In fact, PCA results suggested a positive association between lower intensity (UA) management or unmanaged forest conditions, with higher concentrations of P and C in the FH layer, higher forest density and diversity, and a higher proportion of symbiotic fungi (compared to high-intensity (EA) management). The significant effects of forest harvesting on the soil microbiome should be taken into consideration when estimating or simulating the effect of forest management in hardwood temperate forest.

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Supplementary information

Comparison of two methods for abundance estimation

Next-generation amplicon sequencing is widely used to assess bacterial or fungal communities. Abundance data are required in many alpha and beta diversity metrics that are used to assess alteration of microbe communities following disturbance. The quantification of species abundances, which are used for diversity calculations, are often made with OTU read frequencies. For example, next-generation sequencing has been used to assess abundance in microbial communities in soils (*e.g.,* Hartmann *et al*., 2012a,b; Hartmann *et al*., 2014). Some studies, for example of pollen abundance, found positive relationships between DNA quantities and the frequencies of OTU reads (Baksay *et al*., 2020). However, OTU read frequencies are often assumed to be approximations of species abundances, but this assumption has not been tested with soil fungi communities. Moreover, as explained in the literature, there are multiple biases in using OTU read frequencies as estimators of species abundance. Many factors could lead to large differences between OTU read frequency and real species abundance (see Table S1).

Table S1. Biases in estimating abundance with OTU read frequencies.

Bias in estimation of abundance with OTU read frequency data	**References**
Genomes contain varying numbers of copies of the ribosomal genes; strains with more copies tend to be more common in the reads	Kembel *et al*., 2012 from Edgar, 2017
PCR amplification efficiency is strongly degraded if a template has mismatches with the primers	Pawluczyk, 2015; Sipos *et al*., 2007 from Edgar, 2017
G+C content; GC content affects polymerase efficiency	Polz & Cavanaugh, 1998 in Pawluczyk, 2015; Baksay *et al*., 2020
Shorter sequences amplify more efficiently	Dabney & Meyer, 2012 from Edgar, 2017; Baksay *et al*., 2020
All genes are not amplified at equal efficiency by the primer set used and could be influenced by the PCR conditions or cycle number	Smith, 2005
Presence of inhibitory substances contained in the sample	Racki *et al*., 2014
Accumulation of spurious sequences, chimeras and Taq polymerase inhibitors, during PCR and sequencing processes	Baksay *et al*., 2020
DNA extraction efficiency; DNA recovery yield	Zemb *et al*., 2020

The objective here was to validate whether we could use OTU read frequencies from next-generation amplicon sequencing as abundance information for fungal metrics. However, the lack of tested methodologies to perform qPCR on specific soil fungal species makes validation a challenge. The methodology that we used compared total fungal abundance with OTU read frequencies and qPCR DNA abundance from the same exact soil samples from 169 different plots. The relationship between OTU read frequencies and DNA abundances (qPCR) that were obtained from the exact same samples were analyzed using a linear mixed-effect model that was fitted using REstricted Maximum Likelihood

(REML), with sites as a random effect. Square-root transformation was applied to improve residual distribution. The linear mixed model showed a positive correlation (R^2 = 0.84) between soil fungal OTU reads and qPCR DNA abundances. The correlation between OTU read abundances (raw data) and qPCR DNA abundances (raw data) are shown in Figure S1. This correlation could be seen as a good correlation or not, depending upon the precision expected with the results. One of the differences observed between the two methods is a lower relative fungi abundance in the unmanaged control vs. other treatments, with OTU reads compared to DNA abundance (data not shown).

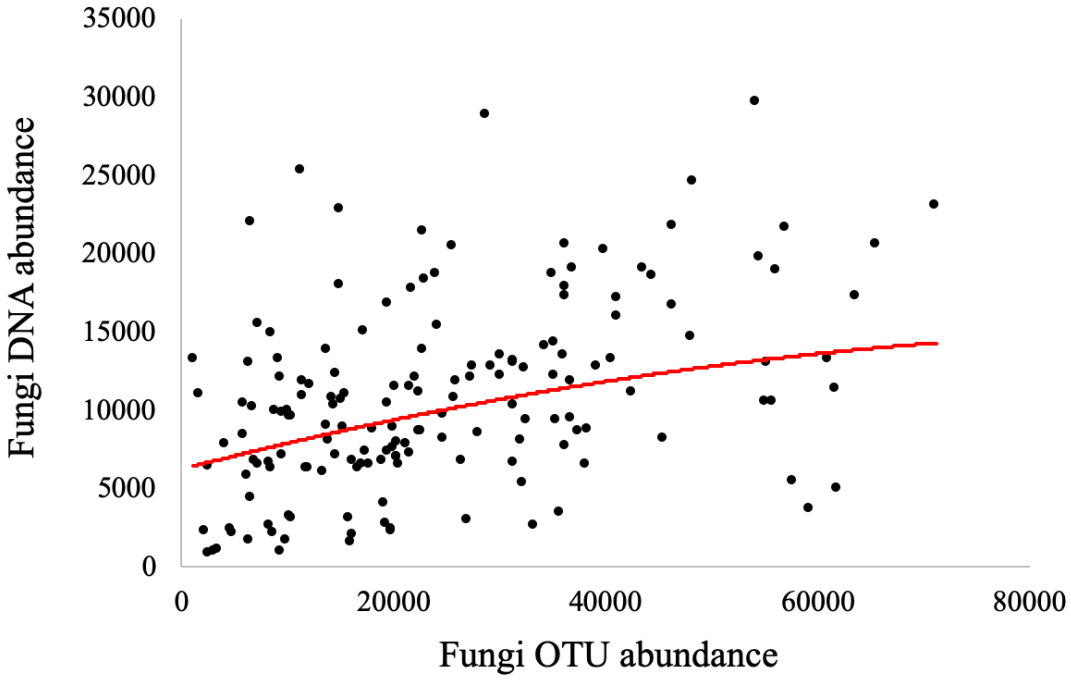

Figure S1. Relationship between fungi DNA abundance (raw data) measurements with qPCR and total fungi OTU read abundances (raw data) for each plot. Linear relationship with square-root transformation, (√DNA) = 0.19 x (√OTU) + 70.53. The regression (predicted DNA) is represented in red in the figure.

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CHAPITRE IV. Applied biodiversity metrics, concepts to choose them well

Abstract

The evaluation of biodiversity is an important tool for conservation, management of natural resources and assessments of ecosystem functioning. Choosing an appropriate and understandable diversity metric should lead to better decisions and more sustainable resource management. Simple biodiversity metrics, like richness, can be used in conservation studies, for example, in the attempt to make a list of species, with a description of their conservation status. Nevertheless, it is clear now that such a metric is simply not sufficient to assess diversity, which also includes Evenness and Disparity components. Alpha diversity metrics are used to measure the entropy or disorder of the community, which is a simplification of the Evenness assessment. Yet, care must be taken when averaging or comparing alpha metrics between landscapes or treatments, since bias can appear due to heterogeneity of the environment. Using beta metrics in addition to alpha ones can improve the assessment of Evenness but are generally more complex to choose and use. Also, using species-dependent information to calculate these metrics informs about Disparity and clearly helps in improving the accuracy of diversity assessment. This paper aims to explore and demonstrate, in a simple manner, the importance in understanding and choosing appropriate diversity metrics to reach accurate conclusions. We simulated two theoretical situations in which calculations of different biodiversity metrics were performed on subsamples of these communities. Tested diversity metrics explored Richness, Evenness or Disparity components of biodiversity and two scales of diversity partitioning, better known as alpha and beta diversity. We concluded that when using alpha diversity metrics to compare treatments, there is a need to better reflect Evenness by developing and including a term that takes into account the contribution of a site to a treatment. We suggest, for many biodiversity questions with functional or conservation concerns, to select species-dependent metrics since they reflect Disparity. To do so, there is a need to increase knowledge and data availability on species traits or phylogeny to be able to analyze the complete community.

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Ce chapitre sera soumis pour publication

Introduction

Evaluation of biodiversity is an important tool for conservation purposes, natural resource management, or assessments of ecosystem functioning. In these fields, practitioners frequently must calculate, compare, and give an appreciation on the diversity of one or more groups, *i.e.*, microbial, fungal, plant or animal species. Either approach is a mathematical challenge or a tough choice among countless options for estimating an appropriate metric that is representative of diversity (Yan *et al*., 2007; Miller *et al*., 2016; Daly, Baetens & Baets, 2018; Marshall *et al*., 2020). In a great effort to provide fundamental bases regarding what biodiversity indices actually consist of, Daly, Baetens and Baets (2018) stated that Richness (*i.e.,* the number of species), Evenness (their relative abundances or apportioning), and Disparity (contrasting importance of each species on a genetic, phylogenetic or functional basis) are understood to be the three critical components of biological diversity estimates.

Disparity is a component that is generally neglected in assessments of biodiversity, except by some theoretical ecologists. On the one hand, the use of species-independent metrics (*i.e.,* no reference is made to Disparity; all species are assumed to have similar importance in the landscape) is simple, but it has been more and more frequently criticized because it misses an important element of biodiversity (*e.g.*, Scheiner *et al.*, 2017a; Daly, Baetens & Baets, 2018; Minelli, 2019). On the other hand, the inclusion of disparity seems to have generally led to more valuable conclusions, but uses complex or non-dimensional estimators (Faith, 1992; Daly, Baetens & Baets, 2018). Pending the formulation of a simpler and "perfect" index, which would take into account disparity, users of species-independent metrics should express their conclusions with some restraint.

The meaning that is given to "diversity" or "biodiversity" varies greatly, depending upon the field of activity. The misinterpretation of these terms can go as far as compromising the objectives of conservation or management and their completion (Limoges *et al*., 2013). For example, in the meta-analysis of Verheyen *et al*., (2017), five surveys reported that *increased forest management intensity* has a positive effect on ground-layer species richness in temperate forest (*e.g.,* Hédl *et al*., 2010), while two other surveys reported a negative effect (*e.g.,* Økland *et al.,* 2003). One can conclude that this environmental driver is beneficial to the preservation of biodiversity, yet when the metrics that are used in these studies are explored more thoroughly, conclusions may differ markedly.

Indeed, attempts to evaluate diversity without a clear understanding of its metrics eventually can lead to misleading or even erroneous inferences (Daly, Baetens & Baets, 2018; Willis, 2019; Marshall *et al*., 2020). For instance, several field studies were conducted at small- and medium-scales that assessed disturbance effects on diversity, and which based their evaluations on species-independent diversity metrics only (*e.g.,* Shannon index or Richness). Many of those studies were not able to detect a significant difference in diversity (*e.g.,* Gilliam *et al*., 1995; Fredericksen *et al.*, 1999; Elliott & Knoepp, 2005; James, 2012; Duguid & Ashton, 2013). Yet, the literature most generally reflects diversity losses in disturbed landscapes over broad, even global scales (Pellens & Grandcolas, 2016). Preserving “biodiversity,” in the manner that this term has been delimited by the United Nations, requires the maintenance of all life on Earth, together with the natural characteristics that they exhibit (Convention on Biological Diversity, 2008). At smaller scales (*e.g.,* the scale of a bioclimatic domain), this translates into the need to conserve

local and specific biodiversity. Thus, the measurement of this diversity should not only be concerned with the absolute number and relative abundance of species, but rather by their identity, the occurrence of their characteristics and even their degree of naturalness in the ecosystem (as defined by Limoges *et al*., 2013).

Choosing an appropriate and comprehensible diversity metric is critically important for final users, such as forest managers and practitioners, given that it would serve habitually as a decision-making tool. One possible solution to such an issue lies in closing the gap between the biodiversity assessment that is used in theoretical ecology and the one that is used for practical management and conservation purposes. To do so, a better explanation of the metrics and the development of simpler, but accurate ones are appropriate options. Indeed, the adequate measurement and understanding of biodiversity is critical, especially when it deals with the management of a fragile or non-renewable biological component of an ecosystem.

On what basis should diversity metrics be selected?

Alpha species-dependent or independent diversity metrics?

Alpha-diversity metrics generally refer to the diversity of subsamples within a landscape. These could be based upon a species-independent measure (*i.e.*, no reference to Disparity; assumes all species have a similar importance in the landscape) or based upon a species-dependent measure (*i.e.,* references Disparity and, thus, defines contrasting relative specificities of species). A classical, species-independent, alpha-diversity metric that is widely used is the Shannon index (*H*), which is based upon the number of species that are encountered. In their review, Daly, Baetens and Baets (2018) clearly detailed the interest

that continues to be shown in using such an index, but also highlighted its limitations in terms of failing to address the Disparity component of diversity. This can be remedied by using phylogenetic or functional information on species (Scheiner *et al.*, 2017a), since differences between species are acknowledged in terms of their identity or traits, respectively (Scheiner *et al*., 2017b). The substantial advantage of these species-dependent metrics is that they recognize that in any ecosystem, many species can be functionally redundant or phylogenetically closely related. The use of species-dependent metrics would thus take into consideration species that are similar to some degree *versus* those species that are functionally or phylogenetically unique (Faith, 1992; Hillebrand *et al.*, 2009; Cadotte, 2011). The use of phylogenetic diversity may also identify taxa that tend to be disadvantaged (but which do not necessarily disappear) following a disturbance (Turcati, 2011; Flynn *et al.*, 2011). Both metrics can be very informative, yet phylogenetic and functional diversity metrics both require the user to possess a sufficient amount of information on phylogenetic histories or trait values (Cornelissen *et al.*, 2003) that are related to the species being identified in the study. Recently, phylogenetic diversity has been used for practical decisions regarding biodiversity conservation (Scheiner *et al.*, 2017a; Tucker *et al.*, 2017). Nevertheless, even if the importance of using species-dependent metrics is being more and more frequently demonstrated in the production of accurate biodiversity assessments (Minelli, 2019), species-independent metrics (such as richness and the Shannon index) remain the most frequently implemented diversity metrics, given their greater simplicity (Daly, Baetens & Baets, 2018). This leads us to conclude that there is a need for either simple species-dependent metrics or add-ons to species-independent metrics to improve their accuracy.

Additional importance of sampling scale and beta diversity metrics

Depending upon the scale of sampling, Richness alone or the use of an alpha species-independent diversity metric like the Shannon index alone could provide appropriate estimates of diversity. If the sampling scale approaches the size of the landscape under study, Richness very closely approximates gamma diversity (*i.e.*, total number of species in the landscape). However, this implies exhaustive (and typically, unfeasible or unreasonable) field measurements.

Yet, Beta diversity metrics alone can inform us about the relative dissimilarity between communities. When assessed within a community, it can refer to the evolution of community homogeneity through time or differences encountered in a before-after study (*e.g.,* site dissimilarity within a treatment). Furthermore, beta diversity can be informative if the interest is in viewing the dissimilarity of communities between different treatments (*e.g.*, site dissimilarity between treatments). Among various metrics, Bray Curtis dissimilarity or the Sorensen index is commonly used to calculate (within- or between-) beta diversity (Verhoef & Morin, 2010). As is the case of for alpha metrics, these beta-diversity metrics could be performed on species-independent information (*e.g.,* with a matrix of species abundances) or on species-dependent information (*e.g.,* with an abundance matrix containing different trait values), with the latter taking into account the disparity component of biodiversity.

Improving the metrics for adequate applied uses

An important point regarding alpha-diversity metrics is that if the experimental design includes different sub-communities or different scales (*e.g.,* plot, sites), as is often the case,

the classical alpha diversity metric will not reflect the compositional dissimilarity between sub-communities, plot or sites. This is known as the replication principle (Daly, Baetens & Baets, 2018). Indeed, these metrics would not be able to discriminate between homogenous landscapes, where each of the plots or sites is similar to the next, and heterogenous landscapes, where each of the plots or sites is highly dissimilar to the next. Thus, the problem is not the diversity metric itself; rather, it is the extrapolation of conclusions that are based upon means of these classical alpha-diversity metrics at a treatment or landscape scale.

Several approaches may offer a workaround for this weaker aspect of alpha metrics. First, complex mathematical add-ins (*e.g.*, Hill numbers; Chao, Chiu & Jost, 2016) or statistical parameters (Willis, 2019) can enhance adherence to this replication principle, yet they can be quite difficult for practitioners to interpret. Second, with accurate cross-interpretation, the use of combinations of alpha- and beta-metrics can be very informative, particularly where species-dependent metrics are used, since they offer a better approach to estimating the Evenness component of diversity. This option is usually selected, although the analyst needs to make numerous calculations and interpretations. Finally, a third option would be to add a simple term to alpha metrics, which would reflect the contribution of each plot in the whole subsampled plot area that is affected by the same treatment or conditions. This last option has the potential for remaining simple and being less time-consuming than the first option. Most of the time, it may yield enough information to conclude or decide whether there is a need to proceed to the second option.

To illustrate further the purpose that has been described so far, we designed two simple theoretical situations to explore and demonstrate the importance in understanding and choosing appropriate diversity metrics in an applied context. With the help of simulated landscape communities experiencing contrasting hypothetical situations, we aimed,

i) to establish how the use of the simplest and widely used biodiversity metrics may actually offer very contrasting levels of confidence in responding to such a simple question as "Does this disturbance influence diversity?" and

ii) to provide information based upon simple add-in or combinations of diversity metrics, which would clearly improve our level of confidence in diversity assessments without necessarily exploring all available metrics.

Methodology

Theoretical communities

We responded to the simple and frequently asked question "Does this disturbance influence diversity?" by performing two theoretical experiments (*i.e.,* I and II). In each of these experiments, two theoretical communities (*i.e.,* referred as "landscapes") were used for calculation and comparison of plant diversity metrics (Figure 1; Figure S1). These are consistent of one experiencing a disturbance (*i.e.,* Disturbed) *versus* the other, which is not disturbed (*i.e.,* Control). Plant density was set to be equal in each treatment and area, *i.e.,* 100/ha. For both communities, three sampling scales were used, *viz*., landscape, site and plot, which corresponded respectively to 2.4 ha, 0.1 ha and 0.0167 ha. The first experiment (*i.e.,* theoretical experiment I) is fully explored in the main text, while the second experiment (*i.e.,* theoretical experiment II) is presented in the Supplemental Information

(SI); the latter has additional information and comparisons to explore more deeply the results that were obtained with the calculation of diversity metrics.

In experiment I, the two theoretical communities were generated using simulations. Those simulations were performed on a plant community that was composed of 28 species with different light requirements (Table S1) that were accessed from Humbert *et al.* (2007) and Ellenberg light indicator data. In this experiment, the number of replicates (*i.e.,* subsamples) in each landscape was six sites that were randomly selected (Figure 1). Based on species ecology, abundance status was assessed for each species in each landscape. Furthermore, we included, but only in control sites, two species with secure conservation status, i.e., showy orchis (*Galearis spectabilis* [L.] Raf.) and downy rattlesnake plantain (*Goodyera pubescens* [Willd.] R.Br.), and one endangered species, butternut (*Juglans cinerea* L.); we also included an apparently secure species, Canadian maidenhair (*Adiantum pedatum* L.), which is vulnerable to harvesting. We attributed to disturbed landscape only one particular species, dandelion (*Taraxacum officinale* L.). In the control landscape, we set the simulation to generate a community containing more than 50% and around 20% shade-tolerant and mid-tolerant species, respectively. Based on the estimated effects of clear-cutting on plant communities (*e.g.,* Bergstedt & Milberg, 2001; Jalonen & Vanha-Majamaa, 2001; Tonteri *et al*., 2016), we set the Disturbed community to have an abundance of shade-tolerant species that had been reduced by 70% compared to the control, and which was compensated by an equivalent increase in the abundance of intolerant species. No clear modification of abundance of mid-tolerant species was set for either community. Indeed, as mentioned by Tonteri *et al*. (2016), mid-tolerant species have not been observed to respond as strongly as shade-tolerant or intolerant species to clear-cutting.

In theoretical experiment II (Figure S1), we simplified the communities, but increased their differences in order to simulate a moderate, but significant effect of the disturbance. Here differences were larger than in Experiment I, but still not obvious at first sight. In the second experiment, the number of replicates (*i.e.,* subsamples) that were used for calculations in each landscape was three sites, which were still randomly selected.

Diversity metrics

Classical alpha and beta metrics

Theoretical diversity was calculated with a selection of alpha and beta biodiversity metrics that explored Richness, Evenness or Disparity components (Table 3-10), for both treatments (Disturbed *vs*. Control) at the site scale. The landscape scale was considered the reference for the "true" diversity (Jost, 2006, 2019). A species accumulation curve was produced for each scale of interest; landscape, site and plot (*i.e.*, three plots per site). For this curve, a 95% confidence bound around the mean was constructed at the site scale using all possible combinations obtained from the six selected sites.

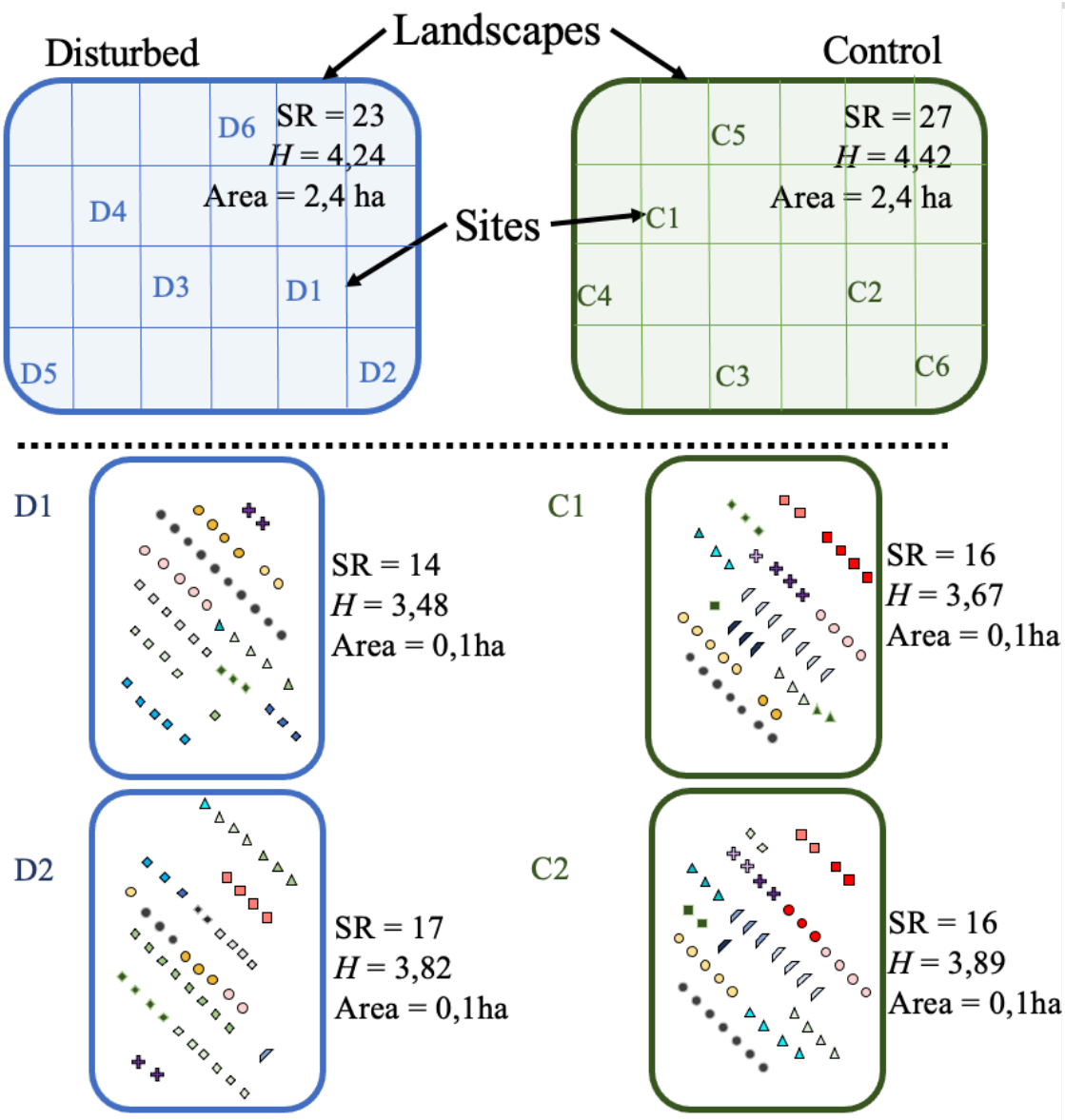

Figure 1. Representation of sampling scales (landscape and site scales) used in the theoretical experimental design I with communities (one experiencing disturbance and not the other) used for calculation and comparison of plant diversity metrics. Six sites (D1 to D6, for Disturbed; and C1 to C6, for Control) are sampled for each landscape (plant community in D1, D2 and C1, C2 could be visualized). Associations between each symbol and the name of the plant species are listed in SI Table 1.

Total species richness (number of species that were recorded) and mean species richness per site was calculated. Alpha diversity that was selected was the mean Shannon index *H* and the mean Faith's phylogenetic diversity using abundance of species (PD) (Scheiner *et al.*, 2017a; Faith, 2018). PD was set from 0 to 1, with 1 representing the highest diversity.

Beta diversity was measured to quantify the compositional dissimilarity, using the Bray-Curtis index of dissimilarity (BC_{ij}) (Legendre *et al*., 2005; Anderson *et al*., 2011).

Dissimilarity was calculated within-treatment (within) using every paired site that had the same treatment, and between-treatment (between) for each paired site that had different treatment. Beta diversity was applied to both species-independent (species abundance matrix) and species-dependent (matrix of functional trait information) data. The type of data, special requirements to acquire them, and the time needed to perform them was evaluated for each metric (Table 1). A suggestion of simple, but complementary information was proposed (Table 1) to enhance the scope and accuracy of the diversity assessment. We also tested the significance of a simple add-in to the mathematical term of some metrics that would reflect the contribution of a site to a treatment. These new metrics were identified as *H″* and PD" (Table 1).

For the species-dependent metrics, the four selected traits that were used were seed dispersal, seed weight, root depth and vegetative propagation, given that they are the traits frequently most available, which are related to perturbation effects (de Bello *et al*., 2010, Roy *et al*., in press). For quantitative data, the mean values for each species were calculated using multiple studies that are available in the TOPIQ database on functional traits (Aubin *et al*., 2012). Trait values were grouped into meaningful categories to cope with trait values that were both qualitative and quantitative. When a species had multiple associations to a qualitative value, it was represented by the matrix of proportion of trait values for this species (total of all values for a species = 1). For species with missing information, we used a replacement approach (Table S1), which collects information that is available from the TOPIQ database or the Angiosperm Phylogeny Group III 2009 for phylogenetically or

physiologically similar species. Similarly, for PD, to cope with the lack of phylogenetic resolution for some genera or families, we also extrapolated results that were obtained for phylogenetically related species (Kumar *et al*., 2017) (Table S1; Figure S2).

A new add-in for the alpha metrics

For the new metrics, which were identified as *H″* and PD", a *R'i* term reflecting the relative importance of a site for a species within the same treatment was included. The mathematical development of the term is not the purpose of this article; the focus was to test its potential contribution to biodiversity metrics. In this context, the *R'i* term is simply the abundance of the i^{th} species in the site compared to the mean abundance of the i^{th} species per sites within the same treatment (*e.g*., Figure S3). If the i^{th} species in a site is less abundant than the mean abundance for this species (within a treatment), *R'i* is less than 1. If the i^{th} species in a site is equally abundant than the mean abundance for this species (within a treatment), *R'i* is 1. If for all species *R'i* equal 1, then *H″* and PD" would equal *H* and PD, respectively.

Table 1. Equations, field data that are needed, requirements and time that are needed to measure different biodiversity metrics at the site scale. A suggestion of complementary information is listed for each biodiversity metric.

Biodiversity metrics	**Assessed component of biodiversity**	**Equations**	**Field data needed**	**Evaluation**		**Complementary information**
				Requirement	**Time consuming**	
Richesse SR	Richness	S	Species		Very low	Species accumulation curves
Shannon index *H*	Richness Evenness	$-\sum_{i=1}^{s} pi \ln pi$	Species Abundance		Low	Shannon index *H''* $-\sum_{i=1}^{s} (pi \ln pi * R'i)$
Phylogenetic diversity Faith's PD	Richness Evenness Disparity	$\sum_{i=1}^{s} \sum_{j \in b(Si)} L'ij$	Species Abundance	Assigned each species to a complete phylogenetic tree Replacement of phylogenetically unknown species Reconstitution of phylogenetic tree	High	Phylogenetic diversity PD" $\sum_{i}^{s} ((\sum_{j \in b(Si)} L'ij) * R'i)$ Important changes in species phylogeny
Bray-Curtis index of dissimilarity BC_{ij} for paired community	Richness Evenness	$1 - (2\text{Cij}/(\text{si} + \text{sj}))$	Species Abundance		Medium	Distinction of between- and within-dissimilarity Important changes in specific species taxons
Functional trait dissimilarity using Bray-Curtis index	Richness Evenness Disparity	BC_{ij} for paired trait community instead of species community	Species Abundance	Assigned each species to a complete matrix of functional trait values Replacement of unknown species for each trait value	Very high	Distinction of between- and within-dissimilarity Important changes in functional trait

S = Total number of species in a community;
pi=ni/Nj;
ni = Number of individuals of the i^{th} species;
Nj= Total number of individuals;
$L'ij$ = niLj/Nj′ is the proportional share of the *j*th branch segment of the *i*th species; weighted by its relative abundance for each branch *j* that belongs to *b*(*Si*);
Lj= Length of the j^{th} branch segment of a cladogram of *S* species;
Sj= Number of species that share the *j*th branch;
Nj'= Total number of individuals that share the j^{th} branch;
b(*Si*)= Set of branches in the path from the root to the tip of the *i*th species;
$R'i$ = Relative importance of a site for a species, compared to all sites within the same treatment. In this theoretical experiment, $R'i$ = Abundance of the i^{th} species in the site compared to the means abundance of the i^{th} species per sites within the same treatment. i.e. $R'i$=1 if the abundance of the i^{th} species in the site was equal to the mean abundance of the i^{th} species per sites within the same treatment.
C_{ij} = Sum of the lesser abundance values for only those species that are common between sites
si+sj = Sum of the total abundance counted at both sites
BC_{ij} is bounded between 0 and 1, where 1 means the two sites are more dissimilar
PD was set from 0 to 1, with 1 representing the highest diversity

Statistical analysis

All statistical analyses were performed in R software (version 4.0.2.). Effects of disturbance on species richness, Shannon index, Shannon index", phylogenetic diversity, and phylogenetic diversity" were analyzed using one-way ANOVA. Significantly different means between disturbed and control sites were separated using *post hoc* Tukey's tests found in the *stats* package in R. Statistical significance was declared at $\alpha = 0.05$. Analyses of group similarities (ANOSIM) were performed with 999 permutations using Bray-Curtis index of dissimilarity (BC_{ij}); these were used to illustrate the mean dissimilarity within-treatment and the importance of mean dissimilarity between-treatment. Means dissimilarity between treatments (between-treatment) was evaluated using pairwise comparisons (*vegan* package, function *pairwise.adonis*) with adjusted *P*-values (Holm stepdown method). Non-metric multidimensional scaling (NMDS) illustrates those communities. PERMANOVA (permutational multivariate analysis of variance) with 999 permutations (*vegan* package, function *adonis2*) was used to analyze the partitioning of variability (considering the matrix of plant traits), which is explained by the treatments and sites. Principal component analysis (*FactoMineR* package, function *PCA*) was computed to reveal the structure of dependence and correlation among plant traits (Laliberté & Legendre, 2010). To summarize changes that were induced by different treatments, PCA results have been illustrated.

Results

All diversity metrics are similar in terms of field data that are needed to compute them, but are quite different in terms of the time required for their calculation (Table 1). Once the biodiversity metrics are calculated, it is simple and not time-consuming to add the complementary information (Table 1). Functional trait dissimilarity is the most time-

consuming diversity metric to compute, followed by phylogenetic diversity (Table 1). Species richness and Shannon index are the metrics that can be most rapidly performed. The increase in time requirement for functional trait dissimilarity is largely attributed to compiling of a complete matrix of functional traits (with adequate replacements of unknown trait data). For phylogenetic diversity, the increase in time requirement is associated with both compilation of a complete phylogenetic tree (with replacements of unknown species) and the calculation of phylogenetic diversity.

Does this disturbance influence diversity? Species richness

The expected answer, using known theoretical data (*i.e.*, references values) for experiment I, is that total species richness is about 15% lower in the disturbed landscape compared to the control landscape. In fact, at the landscape scale ("true diversity" reference values), total species richness (SR) was 23 for the disturbed landscape and 27 for the control landscape (Table 2, Figure 2). A similar lack of detection for SR differences is obtained in experiment II (Table S2). As known theoretical data at the landscape scale are not available in a real-life experiment, it is mean SR at the site sampling scale that is often used to answer that question. Here, mean SR of both theoretical experiments (I and II) failed to detect differences between treatments (P = 0.57 and 1.00, Table 2; SI Table 2). The use of complementary information (*i.e.,* species accumulation curves) usually solves such a problem, but here, it did not allow detection of the difference in the richness set between treatments, because the number of sampled sites in the control treatment (*i.e.,* 6 sites) was not large enough to reach the plateau of the species accumulation curves (Figure 2).

Table 2. Known theoretical reference values (at the landscape scale) and means that were calculated for alpha- and beta-diversity metrics in disturbed compared to control sites for theoretical experiment I. Associated *P*-values are listed. R-statistic refers to dissimilarity *between* compared to *within* and Significance refers to the statistically significance of within-dissimilarity following ANOSIM.

Metrics	Reference values		Mean calculated		*P*-value
	Disturbed	Control	Disturbed	Control	
Richness	23	27	15.83 ±0.47	16.17 ±0.31	0.57
Shannon index	4.24	4.42	3.63 ±0.05 b	3.81 ±0.05 a	0.03 *
Shannon index *H″*			5.98 ±0.34	6.18 ±0.34	> 0.05
Phylogenetic diversity	0.80	0.92	0.70 ±0.02 b	0.84 ±0.01 a	< 0.001 ***
Phylogenetic diversity PD"			0.84 ±0.10	0.83 ±0.04	> 0.05
Dissimilarity in species community based upon identity (all pairs)			Statistic R= 0.813, Significance = 0.002 Between > Within (SI Figure 4A)		
(within-treatment)			0.51 ±0.03 a	0.38 ±0.03 b	0.02 *
(between-treatment)			0.59 ±0.02		0.005** Treatment R^2= 0.38
Dissimilarity in species community based upon functional traits (all pairs)			Statistic R = 0.931, Significance= 0.002 Between > Within (SI Figure 4B)		
(between-treatment)					0.004** Treatment R^2= 0.49

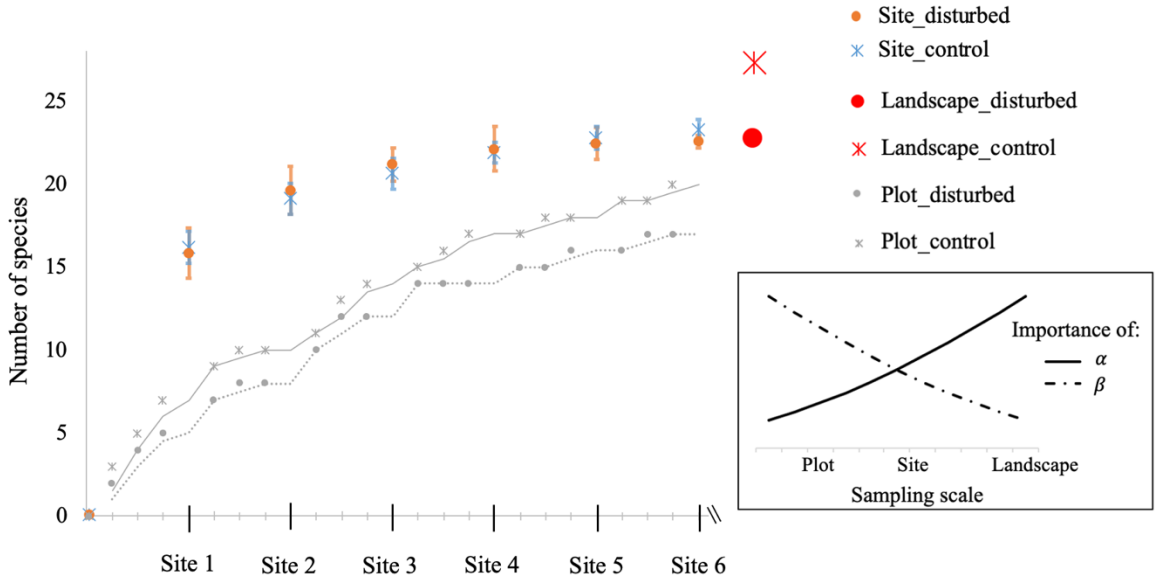

Figure 2. Species accumulation curves for different sampling scales (landscape, site and plot scales) and the two treatments (disturbed and control). Error bars represent the 95% confidence bounds calculated around the mean at the site scale (all possible combinations from the six selected sites).

Species accumulation information at the plot scale (with only one combination) was added in order to illustrate the importance of sampling scale. The inset illustrates the importance of adding a beta component to diversity metrics.

Does this disturbance influence diversity? Alpha metrics

In experiment I, alpha diversity that was calculated with Shannon index (*H*) and with Phylogenetic diversity (PD) at the landscape scale (*i.e.,* reference values) were lower in Disturbed compared to Control conditions (*i.e., H* = 4.24 compared to 4.42 and PD = 0.80 compared to 0.92, respectively). When calculated at the site subsampling scale, mean *H* and PD did detect a difference between treatments ($P = 0.03$ and $P < 0.001$, respectively). The control site had a significantly higher alpha plant diversity compared to disturbed sites (Table 2). When adding the $R'i$ term (Relative importance of a site for a species; combination of alpha and beta information), both Shannon index" (H'') and Phylogenetic diversity" (PD") metrics failed to detect a significant difference ($P > 0.05$) between communities (Table 2). However, in the theoretical experiment II, at the site sampling scale, mean *H* and PD did not detect a difference between treatments ($P = 0.463$ and $P = 0.115$, respectively), while both H'' and PD" metrics detected a significant difference ($P < 0.05$) between disturbed and control sites (Table S2).

Does this disturbance influence diversity? Beta metrics

Two different types of information can be drawn from the analysis of beta metrics. First, the mean within-treatment dissimilarity that was based upon species-identity or species-traits was significantly different (statistical significance of within-dissimilarity = 0.02) (Table 2, Figure 3). The use of this beta metric demonstrated that heterogeneity of the plant community based upon species-identity or species-traits is greater in the disturbed

treatment. Mean plant community dissimilarity within communities that experienced the same treatment (within-treatment) is significantly lower for the control treatment (mean BC_{ij} = 0.38; *i.e.,* more homogenous communities), compared to disturbed communities (BC_{ij} = 0.51) in experiment I (Table 2). In contrast, in experiment II, similar heterogeneity of within-treatment communities was observed for disturbed and control communities (*P* = 0.256; Table S2).

Second, plant communities that were based upon species-identity or species-traits are significantly different between treatments (*P* = 0.005 and *P* = 0.004, respectively). In fact, this beta metric was clearly able to detect differences in plant community composition between treatments (between-treatment) (Table 2, Figure 3). As we had set important differences in simulated communities between treatments, the dissimilarity in plant community between the two treatments was expected to be high. Calculated at the site sampling scale, the mean between-treatment dissimilarity was indeed moderately high (BC_{ij} > 0.59) (Table 2; Figure 3). Moreover, mean dissimilarity was significantly higher between sites that had been assigned to different treatments (between-treatment), compared to sites that had been assigned to the same treatment (within-treatment) (R Statistic = 0.81 and 0.93, respectively). Similar results regarding plant community composition between treatments were obtained in experiment II.

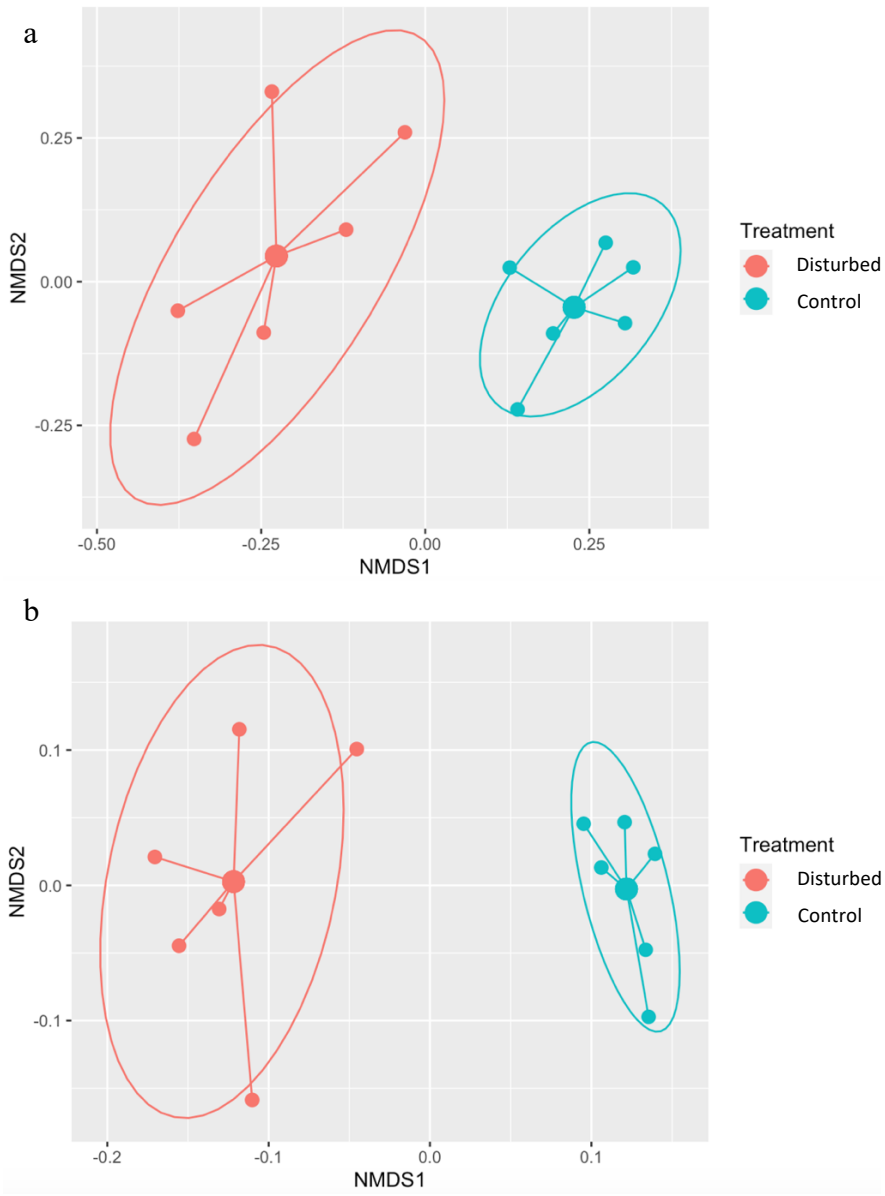

Figure 3. NMDS results of species community comparisons based upon a) plant identity and b) plant traits, between Disturbed and Control sites. The larger circles represent the positions of the treatment centroids along these dimensions.

Does this disturbance influence diversity? Species-dependent metrics

Comprehensive differences in community composition can be revealed from species-dependent metrics. Importantly, for species-dependent metrics that are based upon either identity or traits, the differences in associations that were observed between treatments are

similar at the site and landscape (*i.e.,* reference values) scales (Figures 4 and 5). For instance, the use of phylogenetic diversity can demonstrate a decrease in species with a long phylogenetic history following disturbance (Figure 4). From our examples, one can also conclude that more abundant species from Orders with a longer phylogenetic history, such as the Lycopodiales, Polypodiales, Pinales, Liliales and Asparagales, were positively associated with Control sites, while species from Orders with a shorter phylogenetic history, such as the Ericales and Asterales, were positively associated with Disturbed sites (Figure 4).

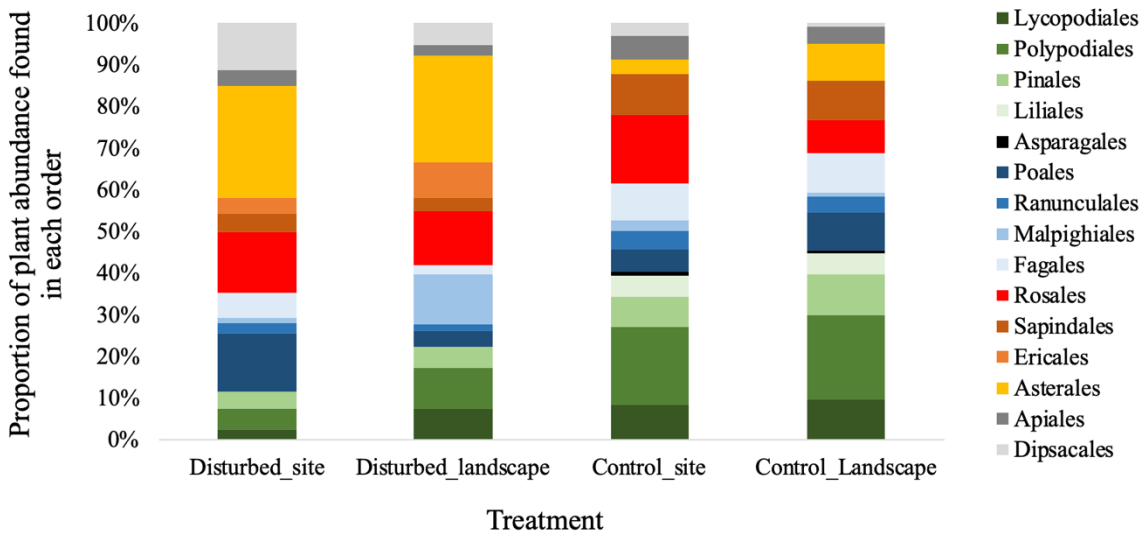

Figure 4. Proportion of plant abundances found in each order for disturbed and control communities at the site (6 sites) or landscape (24 sites) scale.

Similarly, other results could be targeted only by using species-dependent diversity metrics (*i.e.*, plant traits). For instance, based upon the species that we chose to add or remove in both communities, one can conclude that very small seeds (< 0.02 mg), seed dispersal by animals and insects or explosive dispersal, and roots of intermediate depth or > 6 m depth were positively associated with Control sites (Figure 5). On the other hand, small seeds

(between 0.5 and 5 mg), superficial root depth, and seed unassisted dispersal were positively associated with Disturbed sites (Figure 5). Similar results were obtained in experiment II (data not shown).

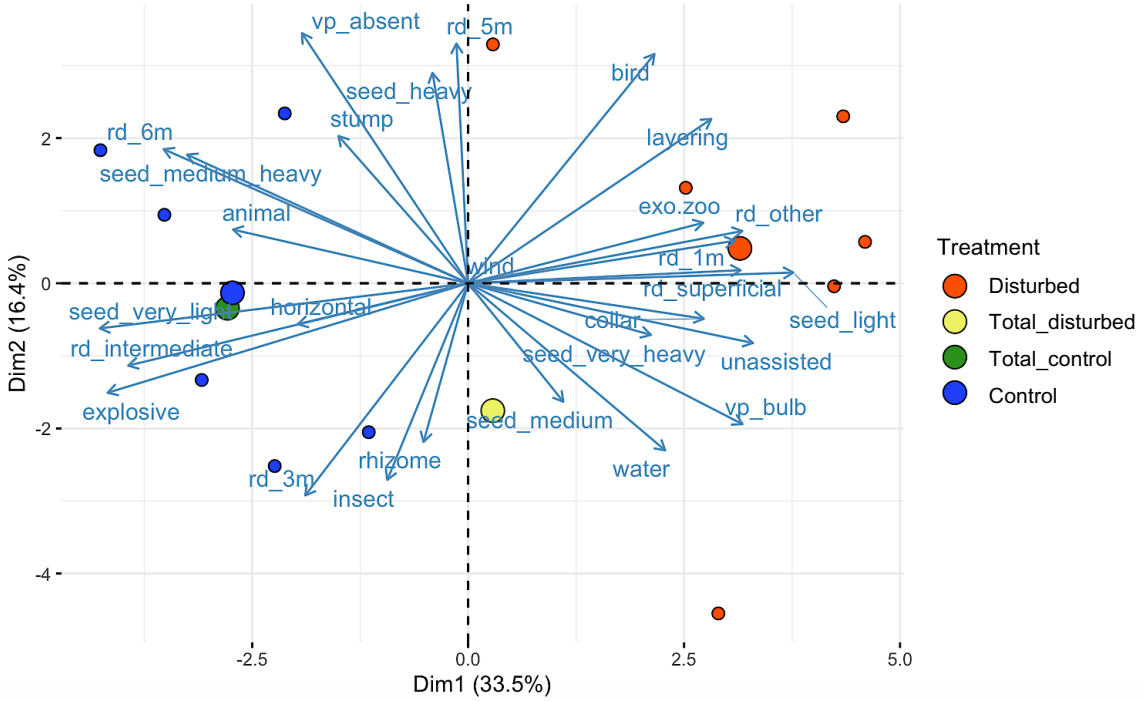

Figure 5. Principal component ordination (PCA) of plant traits after managed or unmanaged treatment at the site (Disturbed or Control) or landscape scale (Total_disturbed or Total_control). Large circles represent the position of each treatment along the first two dimensions. The biplot (blue vectors) indicates the magnitude and direction of the correlations among selected variables (plant traits), which are described as follows. Seed mass, *seed_very_light*, < 0.02 mg; *seed_light*, between 0.02 and 4 mg; *seed_medium*, between 4 and 20 mg; seed_*medium_heavy*, between 20 and 50 mg; *seed_heavy,* between 50 and 100 mg; *seed_very_heavy*; > 100 mg. Seed dispersal mode, *insect* (mostly ants, myrmecochorous); *bird* (ingestion, endo-zoochorous); *water* (hydrochorous), *explosive* (explosive discharged, ballistichorous), *animal* (endo-zoochorous), *unassisted* (autochorous), *wind* (anemochorous) and *exo_zoo* (Animal carried externally, exo-zoochorous). Rooting depth, *rd_superficial* (10-30 cm); *rd_intermediate* (30-100 cm); *rd_1m* (100-200 cm); *rd_3m* (200-400 cm), *rd_5m* (400-600 cm)*; rd_6m* (> 600 cm). Vegetative propagation, *absent; bulb*; *stump; layering; horizontal* (horizontal stem rooting); *rhizome* (rhizome, suckering root and stolon); *collar* (collar and sprout).

Discussion

Regarding the question "Does this disturbance influence diversity?" that was asked in our theoretical exercises, we demonstrated that computation of simple to more complex metrics leads to complementary answers (*e.g.,* Table 3). For example, in our first theoretical experiment, the inclusion of representativeness, through the simple add-in, showed that despite alpha metrics differing between communities, differences in biodiversity were not so clear due to inverse patterns of alpha and beta diversity between both communities (Tables 2 and 3). Similarly, conclusions changed in our second theoretical experiment when using the simple add-in. In this second case, despite alpha diversity being equivalent, the inclusion of the representativeness detected a significant difference in the biodiversity between both communities. With such results, the simple add-in again called attention to heterogeneity issues between both communities, highlighting the need to explore diversity further than simply reporting alpha diversity (Table S2).

In parallel, the use of species-dependent metrics helped in identifying the species, or group of species that were involved in the differences detected by the alpha, beta or add-in metrics. Such precision is critical since it allows the practitioner to "judge" the actual and functional relative importance of these changes.

Table 3. Answers that were obtained for the question "Does this disturbance influence diversity?" using different diversity metrics or additional explanation that was obtained with the addition of complementary information with the experimental design I. Suggestions about "When to use this metrics alone to answer the question' are also listed.

Biodiversity metrics	**Answer to the question, « Does this disturbance influence diversity ? »**	**When to use this metric alone?**	**Additional explanation that was obtained from complementary information**
Richness SR	No modification in mean richness	At the landscape scale, comparison of richness	Species accumulation curves, Not enough sites to reach the plateau
Shannon index *H*	Decrease in mean alpha diversity	At the landscape scale, comparison of richness/ evenness	Shannon index *H''*, Need to explore beta diversity; no modification of diversity based upon this alpha-beta diversity index
Phylogenetic diversity Faith's PD	Decrease in mean alpha diversity	At the landscape scale, comparison of richness/ evenness/disparity	Phylogenetic diversity PD", Need to explore beta diversity; no modification of diversity based on this alpha-beta diversity index Lower abundance of Lycopodiales, Polypodiales, Pinales, Liliales and Asparagales Higher abundance of Ericales and Asterales
Bray-Curtis index of dissimilarity BC_{ij} for paired community	Significant modification of plant species communities (between-treatment)	At the site scales, to access modifications in richness/evenness of the communities	More heterogenous plant communities after disturbance (increase in beta diversity within-treatment)
Functional trait dissimilarity using Bray-Curtis index	Significant modification of plant traits communities (between-treatment)	At the site scales, to access modifications in richness/evenness/disparity of the communities	More heterogenous plant trait communities after disturbance (increase in beta diversity within-treatment) Decrease in proportion of plant traits, very small seed (< 0.02 mg), seed dispersal by animal, insects or ballistochory and root of intermediate depth or > 6 m depth Increase in proportion of plant traits, small seed (between 0.5 and 5 mg), superficial root depth and seed propagation unassisted

Precision in the diversity questions

Modifications in diversity could refer to i) modification in mean species richness, ii) species evenness, or iii) representativeness of ecological functions in the communities. Thus, the actual intension behind the question "Does this disturbance influence diversity?" is crucial in the choice of appropriate diversity metrics. If the goal is to detect the effect of a particular disturbance on the integrity of plant communities, one could ask more precise questions, such as i) "Is the plant community more heterogeneous after disturbance?" ii)

"Are some plant species or plant orders lost after disturbance?" or iii) "Which plant traits or functions are altered by the disturbance?" With these more precise questions, the identification of which metrics should be used to answer them is being raised. In these cases, the use of i) beta diversity, ii) phylogenetic and iii) functional-species dependent metrics is indicated.

In our theoretical exercises, the erroneous use of alpha diversity solely (no matter whether it is with species dependent or independent metrics) would have led us to conclude "slightly yes" in the first case and "no" in the second, while the response was "yes, clearly" in both cases, thanks to the use of the add-in. To deal with the meaning of these differences, the use of species-dependent metrics is essential and would focus upon plant or function losses.

Interpretation of species richness

In our theoretical exercises, we demonstrated that computation of the simplest metrics (SR) leads to the answer, "No." This metric is not designed to detect changes in plant communities, especially when differences in diversity are not obvious. At our "true diversity" scale (*i.e.,* landscape), lower total species richness was set in both experiments. Differences in landscape diversity are rarely assessed in practical situations because its measurement is not humanly possible at such large scales. Of course, an approximation of it can be obtained by combining the total number of species found across all units that have been sampled to describe a landscape (*i.e.,* the plateau of the species saturation curve). Experimental studies have already recognized species accumulation curves as a simple, but efficient indicator for modifying species richness (*e.g.,* Gotelli & Colwell, 2001; Moreno & Halffter, 2001). Furthermore, this approximation is also used in attempts to determine

whether the number of replicates (*i.e.,* the sampling effort) is appropriate for a biodiversity analysis. In our theoretical cases, the species accumulation curves did not completely reach the plateau with the sampling effort that we simulated (6 and 3 in experiments I and II, respectively), suggesting that more sampling is required to obtain accurate conclusions.

Alpha, beta or both metrics?

Species relative abundance (i.e., a simplification of Evenness) is obviously important to adequately describe diversity, making alpha diversity metrics, such as *H,* widely used. In numerous forestry or ecology studies, both SR and *H* metrics are calculated to inform on mean richness and relative abundance of species. In doing that, only an appropriate sampling scale and sampling effort would guarantee the detection of modified alpha diversity, especially in a broader context like the effects of a disturbance. Given that sampling effort is generally limited in real life, the use of beta diversity can assure that the heterogeneity component of biodiversity that is hidden behind the sampling scale effect can be captured (Figure 2).

Consequently, with respect to sampling and inference scales, the addition of a heterogeneity term to an alpha metric generally allows us to assess better quantitative diversity measures by including the heterogeneity component. This is what was done with *H″* and PD" metrics. In our first theoretical experiment, the add-in term mitigates the difference that is reported by alpha metrics between communities, suggesting that diversity differences were more complex than first expected. In our second theoretical experiment, use of the add-in completely reversed the conclusion by reporting contrasting diversity, which in this case was due to contrasting heterogeneity within both communities.

When are species-dependent metrics advantageous?

H metrics can indicate (experiment I) or fail to detect (experiment II) a decrease in diversity in a disturbed community. Such a result may question the conclusions reached by studies that only used this metric to detect differences in plant diversity (*e.g.,* Gilliam *et al*., 1995; Fredericksen *et al.*, 1999; Elliott & Knoepp, 2005; James, 2012; Duguid & Ashton, 2013), Faith (2018) also pointed out that these classical metrics could have failed in indicating a potential concern about biodiversity conservation. In real-life experiments, calculation of PD enhances the capacity to detect significant differences between treatments, as observed in studies on plant or microbiome communities (*e.g.*, Dinnage, 2009; Hartmann *et al*., 2014, Faith, 2018). In our theoretical simulations, computing these species-dependent metrics (*i.e.*, mean PD at the site scale) never missed in helping to capture the differences. The time and effort that is required to calculate PD or plant trait community metrics is particularly high. So, one can ask if species-dependent metrics is actually worth it? The answer resides in another question, "Am I interested in species particularity or are they all the same to me?"

Species-dependent measures lead to a better understanding of disturbance effects on the ecology of communities compared to species-independent measures (Minelli, 2019). In our simulations, they were capable of demonstrating that species with a longer phylogenetic history or species with very small seed (< 0.02 mg) were clearly disadvantaged by disturbance, compared to species with a shorter phylogenetic history or species with seed masses between 0.5 and 5 mg. Thus, such results could be compared to other studies (*e.g*., Aubin *et al.*, 2007, 2009) and add to the comprehensive eco-physiological explanation of community changes.

For beta diversity metrics (BC_{ij}), NMDS helps to visualize general dissimilarity between communities (Figure 3), but provides no tangible information regarding why these communities are actually dissimilar. For practitioners or managers, these concerns are present in the question "Does this disturbance influence diversity?" since it represents the need for knowing whether a management practice affected a particular species or induced dissimilarly. For example, forest managers generally want to know whether a treatment increased commercial tree abundance or non-commercial or shrub species are increased. Similarly, for conservation purposes, practitioners might want to learn about how a disturbance may affect the ecological functions or the phylogenetic tree of an ecosystem. This implies visualization of associate species or trait dissimilarity with treatments (*e.g.,* Figure 4). One important point is that with species-dependent metrics, once the species phylogenetic or trait information is collected, it is not time-consuming to perform these associations (complementary information listed in Table 1). And yet, the need to better understand the relationship between phylogeny and ecosystem functioning has been identified in many studies (*e.g.,* Srivastava *et al*., 2012).

From our results, it is clear that if there is a concern about ecosystem functioning, or conservation of biodiversity, species-dependent metrics are preferred. Both PD and functional diversity (FD) calculations are more complex and time-consuming than the classical alpha species-independent diversity metric. Yet, they always lead to more adequate conclusions. Nevertheless, care must be taken regarding these analyses since studies are frequently encountered where only part of the community (the part where we know species-specific information) has been analyzed with respect to FD or PD. When only part of the community is analyzed, discussions and recommendations should

acknowledge its limitations. In our theoretical experiments, we obtained a complete traits matrix by selecting species with known information or for which replacement values from similar species were possible (see replacement of unknown species, Table S1). When studying a limited number of well-known species (*e.g.*, 12 tree species), these steps might not be too long. However, when a community is composed of more than 50 species for which functional or phylogenetic data are scattered or non-existent, this will require laborious data research, and compiling. To help in making such important metrics more attainable, increasing data collection on species traits or phylogenies are a priority, together with making them available.

Conclusion

In summary, we argue that any particular diversity metric should not be seen as a magic number expressing *the diversity*, but should be constrained to form part of the explanation. Moreover, care must be taken in interpreting averaged alpha diversity metrics. Several similar theoretical approaches (Daly, Baetens & Baets, 2018; Willis 2019) were recently used with the aim of i) identifying erroneous uses of diversity metrics, ii) clarifying their meaningfulness, and iii) modifying or adjusting them for more accurate inferences. This clearly highlights the growing concern of scientists in the face of more and more broadly usage of "diversity assessments" in environmental studies. For alpha diversity metrics, we highlighted the need to develop and include a term that reflects the contribution of a site for a treatment, but other statistical solutions (Willis, 2018) or mathematical approaches can surely be developed. Finally, we demonstrated that for biodiversity questions dealing with functional or conservation concerns, species-dependent metrics should be preferred. However, we acknowledge that this metric would require that significant work should be

done to increase our knowledge and data availability on species traits or phylogeny. Here, we hope to help ecologists and foresters in their choices and interpretations of biodiversity metrics.

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Supplementary information

Table S1. Latin bionomial, visual code and light requirement (that refers to shade-tolerant (S), mid-tolerant (M) or intolerant (I) species) for each species. Replacement species that are used when data on phylogeny or functional traits were not available are listed.

Name	Code	Light requirement	Phylogenetic data Replacement	Functional trait data Replacement
Lycopodium obscurum		S		*Dryopteris marginalis*
Lycopodium annotinum		S		*Dryopteris marginalis*
Adiantum pedatum		S		*Dryopteris marginalis*
Dryopteris marginalis		S		
Dryopteris carthusiana		S		*Dryopteris marginalis*
Abies balsamea		S		
Pinus strobus		M		
Medeola virginiana		S		
Galearis spectabilis		S		*Cypripedium acaule*
Goodyera pubescens		S		*Cypripedium acaule*
Carex arctata		M		*Carex albursina*
Carex brunnescens		I		
Carex intumescens		M		
Actaea rubra		M	*Actaea asiatica*	
Viola canadensis		M	*Viola arvensis*	
Juglans cinerea		I		
Ostrya virginiana		S		
Rubus idaeus		I		
Ulmus americana		M	*Ulmus glabra*	
Acer saccharum		S		
Vaccinium myrtilloides		I	*Vaccinium corymbosum*	
Taraxacum officinale		I		
Lactua canadensis		I		
Achillea millefolium		I		
Solidago rugosa		I	*Solidago canadensis*	
Symphyotrichum cordifolium		I		
Aralia nudicaulis		M	*Aralia spinosa*	
Viburnum lantanoides		I		

Table S2. Known theoretical reference values (at the landscape scale) and means calculated for alpha and beta diversity metrics in disturbed compared to control sites for the theoretical experiment II. Associated *P*-values are listed. R statistics refer to dissimilarity *between* compare to *within* and Significance refers to the statistically significance of within dissimilarity following ANOSIM.

Metrics	Reference values		Mean calculated		*P*-value
	Disturbed	Control	Disturbed	Control	
Richness	19	24	12 ±0.58	12 ±0.58	1
Shannon index	2.15	2.97	2.22 ±0.14	2.35 ±0.08	0.463
Shannon index *H″*			2.10 ±0.16 a	2.70 ±0.12 b	0.043 *
Phylogenetic diversity	0.78	0.90	0.55 ±0.03	0.62 ±0.02	0.115
Phylogenetic diversity PD"			0.45 ±0.03	0.55 ±0.02	0.049 *
Dissimilarity in species community based on identity (all pairs)			Statistic R= 0.91, Significance= 0.10 Between > Within		
(within-treatment)			0.41 ±0.05	0.51 ±0.06	0.256
(between-treatment)	0.66		0.77 ±0.04		
Dissimilarity in species community based on functional traits (all pairs)			Statistic R= 1.0, Significance= 0.1 Between > Within		

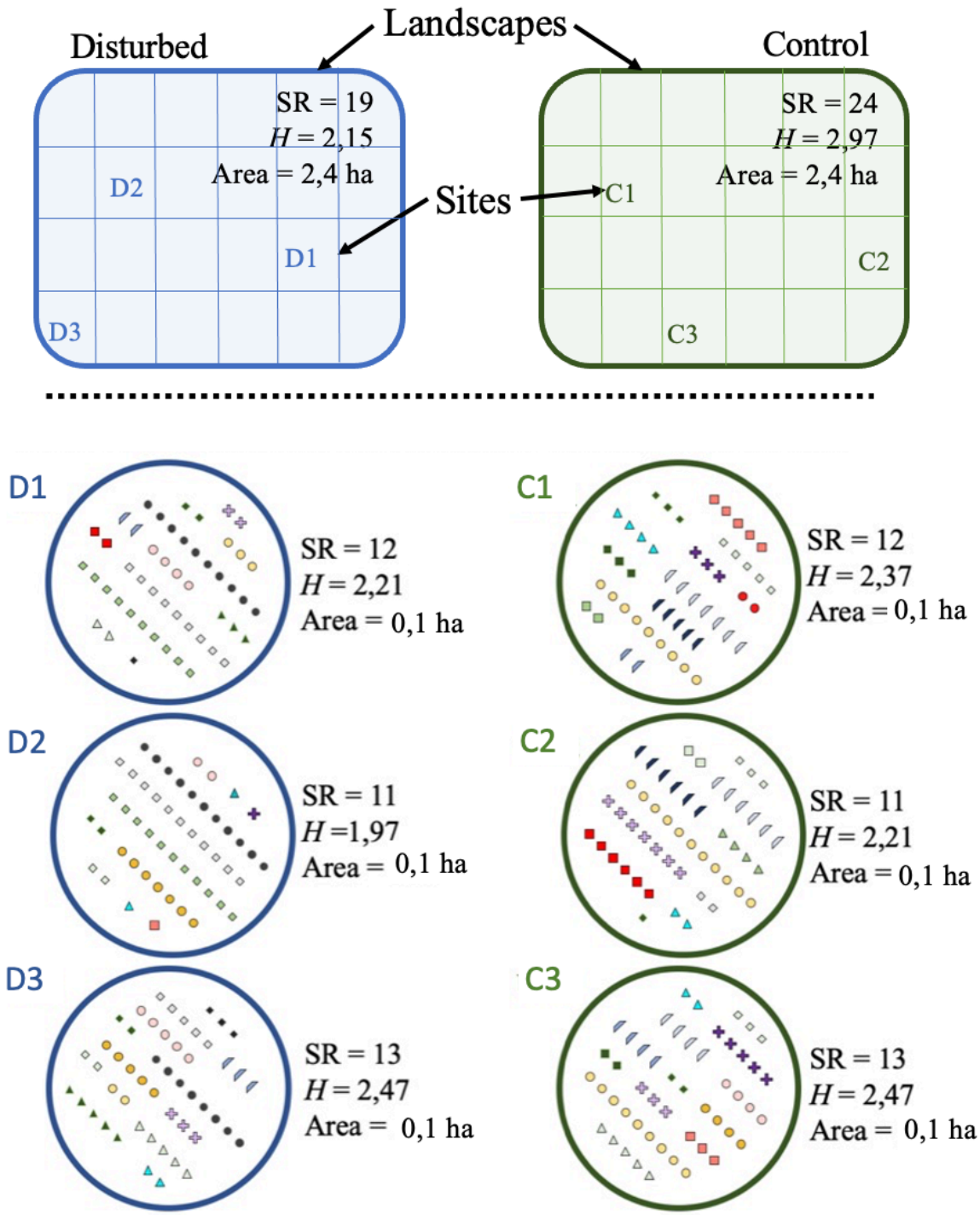


Figure S1. Representation of sampling scales (landscape and site scales) used in the theoretical experimental design II with communities (one experiencing disturbance and not the other) used for calculation and comparison of plant diversity metrics. Three sites (D1 to D3, for Disturbed; and C1 to C3, for Control) are sampled for each landscape. The associations between each symbol and the name of the plant species are listed in SI Table 1.

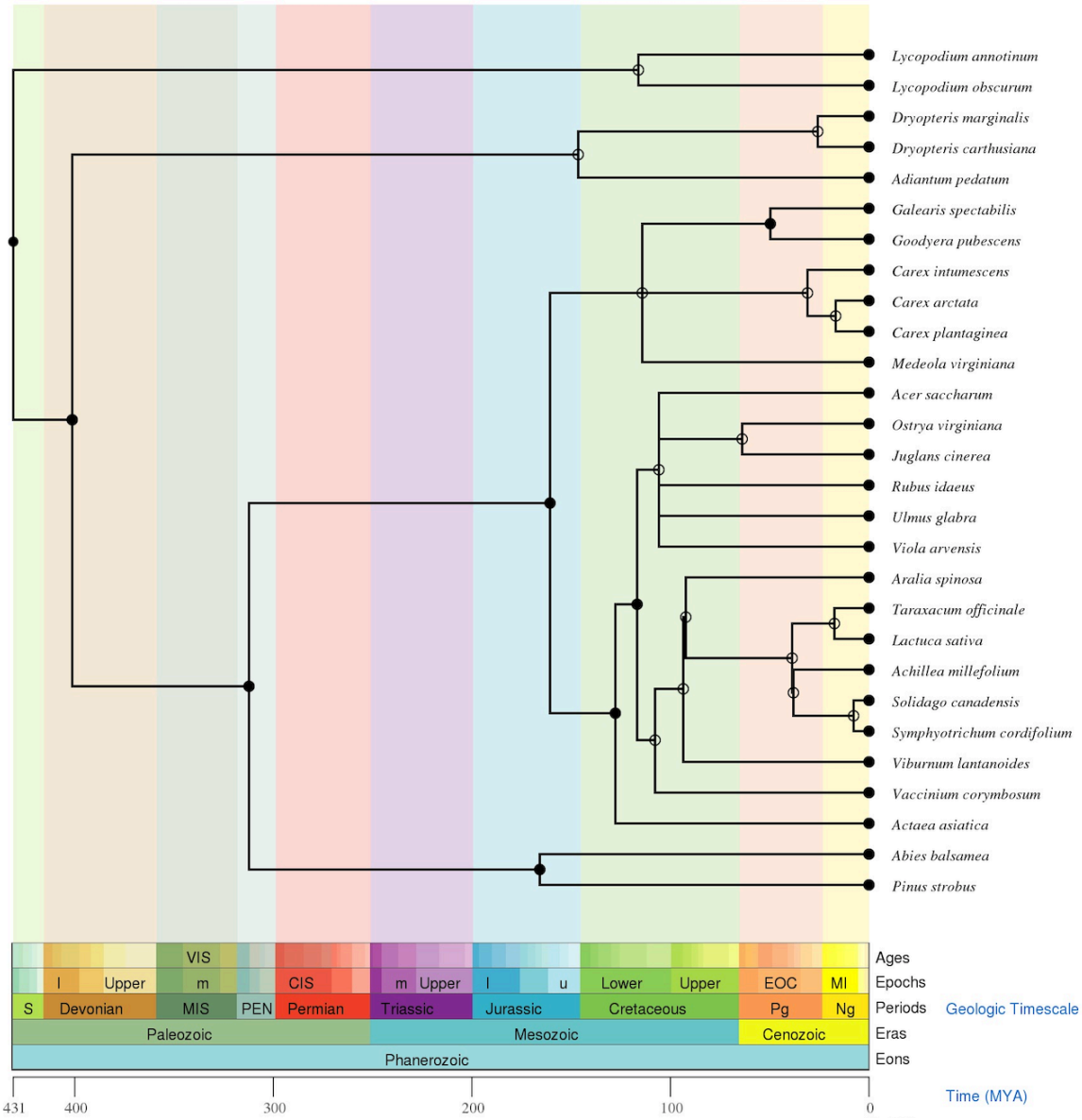
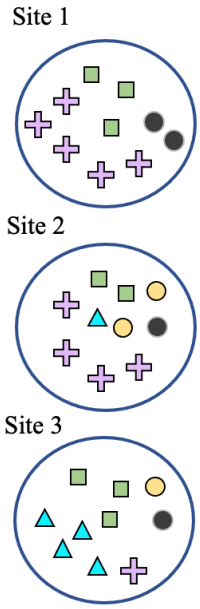


Figure S2. Representation of phylogenetic tree for the plant community (28 species) under study using TimeTree (Kumar *et al*., 2017).



	Mean abondance	Site 1 $R'i$	Site 2 $R'i$	Site 3 $R'i$	$mean\ R'i$
✚	3.33	1.50	1.20	0.30	1
■	2.67	1.12	0.75	1.12	1
▲	1.67	0	0.60	2.40	1
●	1.33	1.50	0.75	0.75	1
○	1	0	2	1	1

Figure S3. Example of calculation of *R'i* for each species in three different sites.

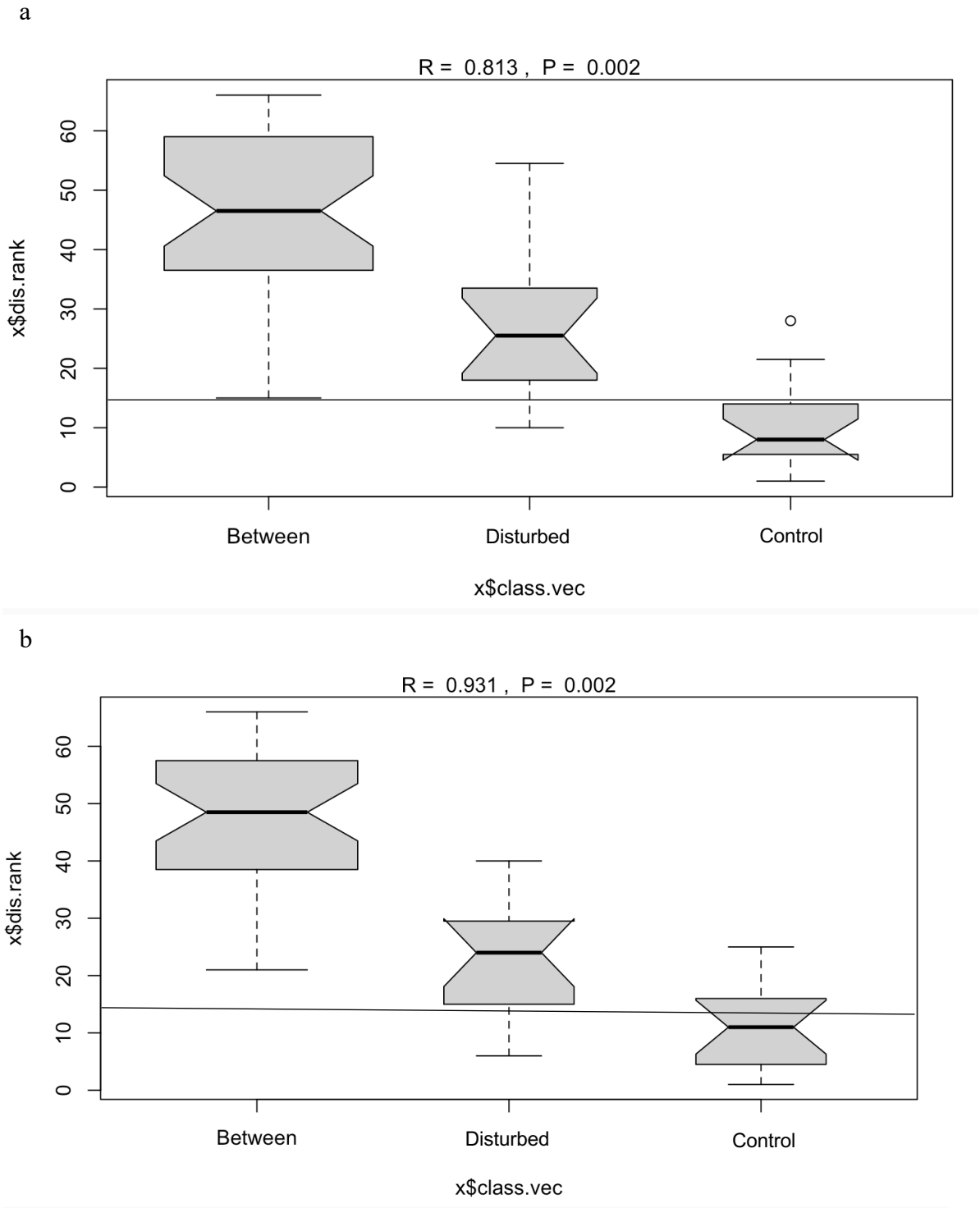


Figure S4. Box-and-whisker plots of the mean within-treatment dissimilarity (BC_{ij}) for plant community based on a) species identity and b) species functional traits, in disturbed or control treatment for the theoretical experiment I. Each value is the mean of all possible combinations of sites within the same treatment. R refer to dissimilarity *between (inter-treatment)* compare to *within (intra-treatment)* and P refer to the statistically significance of within dissimilarity following ANOSIM analysis.

CONCLUSION GÉNÉRALE

Force est de constater qu'on retrouve aujourd'hui très peu de forêts tempérées non-aménagées. Pour les forêts tempérées aménagées de l'est de l'Amérique du Nord, au cours des 40 dernières années, les stratégies de sylviculture ont passablement évolué, de la forêt jardinée par les coupes partielles à la sylviculture d'adaptation aux changements globaux (Comité d'experts, 2017; D'Amato *et al.,* 2021). À la lumière de l'état des connaissances obtenues dans les chapitres expérimentaux de cette thèse, il est légitime de se poser la question suivante : « Comment limiter la perte de biodiversité, de fertilité des sols, ainsi que de minimiser l'altération des fonctions des plantes et du microbiome, en aménageant ces forêts ? ».

Cette thèse a été effectuée dans le but de mieux comprendre comment l'écologie forestière peut être affectée par les aménagements sylvicoles à court, moyen et long terme. La nature du travail consistait à mesurer et analyser différentes variables associées à l'écologie forestière dans des forêts non-aménagées et dans des forêts aménagées de structure équienne (AÉ, coupe totale) et inéquienne (AI, coupe partielle) le long d'une chronoséquence (< 5 ans, 15 ans, 30 ans après coupe) dans 189 parcelles. De plus, une expérience en serre a été effectuée afin d'évaluer la croissance de semis d'arbres feuillus dans des sols associés à des forêts non-aménagées et à des forêts après coupe. L'approche privilégiée dans le cadre de cette thèse a été d'évaluer l'abondance des champignons et des bactéries du sol, la composition et la diversité taxonomique, fonctionnelle et phylogénétique des plantes du sous-bois et des champignons du sol, l'abondance des débris ligneux, ainsi que plusieurs propriétés physico-chimiques du sol dans les parcelles forestières. Cependant, cette méthode exhaustive a limité l'étendue géographique de

l'étude, ne permettant pas d'échantillonner des forêts tempérées sur une plus grande proportion de l'Est de l'Amérique du Nord.

Synthèse des principaux résultats

Les résultats de ce projet montrent comment et à quelle ampleur la diversité des plantes, une partie du microbiome du sol et plusieurs propriétés du sol sont modifiés dans le temps par différentes intensités de coupe forestière comparativement à des forêts non-aménagées (Figure 1).

Pour les plantes de la strate de sous-bois, plus de 30 ans après aménagement forestier, tant sous aménagement de forte (AÉ) ou de faible intensité (AI), nous avons observé une diminution de plus de 20% de la diversité phylogénétique. Cette perte de diversité était associée notamment à des plantes avec des traits fonctionnels particuliers (*e.g.,* très petites graines) et des plantes plus anciennes qui se reproduisent par spore. L'utilisation d'une chronoséquence a permis de cibler le «15 ans après coupe » comme une période de plus faible diversité dans les communautés de plantes de la strate de sous-bois, autant dans les parcelles avec coupe de faible intensité que celles de forte intensité. La période «5 ans après coupe» a pour sa part été identifiée comme une période où la composition, la structure et la diversité des traits fonctionnels des communautés végétales se sont montrées très sensibles aux coupes de fortes intensités.

Cette thèse s'est aussi intéressée à quantifier l'impact des types de récolte forestière sur le sol forestier. Cinq ans après coupe, les forêts aménagées présentaient des taux de nitrification nette potentielle plus élevés que les forêts non aménagées. Dans l'ensemble, les effets des coupes totales sous AÉ sur les propriétés chimiques du sol étaient plus

importants et soutenus à moyen et long terme comparativement aux coupes partielles sous AI (Figure 1). Le gradient hypothétique de diminution de la fertilité du sol testé dans l'expérience en serre a grandement affecté la croissance des semis des trois espèces d'arbres testés. Les sols provenant de forêts sous AÉ, avec une fertilité plus faible, étaient associés à des taux de croissance et une biomasse totale plus faibles chez les trois espèces, par rapport au sol de la forêt «non-aménagée» qui présentait la grande fertilité. Les résultats montrent que l'exploitation forestière peut avoir des effets néfastes majeurs sur la fertilité et la productivité des sols, à court, moyen et long terme.

Les résultats de l'analyse du microbiome du sol ont révélé une augmentation de l'abondance des bactéries, une diminution du ratio champignon/bactérie et une modification des guildes trophiques des champignons du sol après les coupes forestières. Une plus grande proportion de champignons parasites et pathogènes des plantes et des animaux a été mesurée peu après les coupes totales. Comme plusieurs des variables du microbiome du sol sont importantes pour comprendre les flux du C, ces informations sont nouvelles et pertinentes. Ces résultats suggèrent que des coupes forestières faites de manière trop intense (AÉ) ou trop fréquente (AI) peuvent avoir des conséquences importantes sur la biodiversité, la productivité des sols, la dynamique du C et la pollution des forêts (Figure 1). De plus, comme plusieurs forêts sont actuellement dans les stades 5, 15 ou 30 ans après coupes, ces résultats permettent d'entrevoir l'étendue des effets (ou pertes) à anticiper, comparativement à des forêts ou des territoires qui seraient non-aménagées.

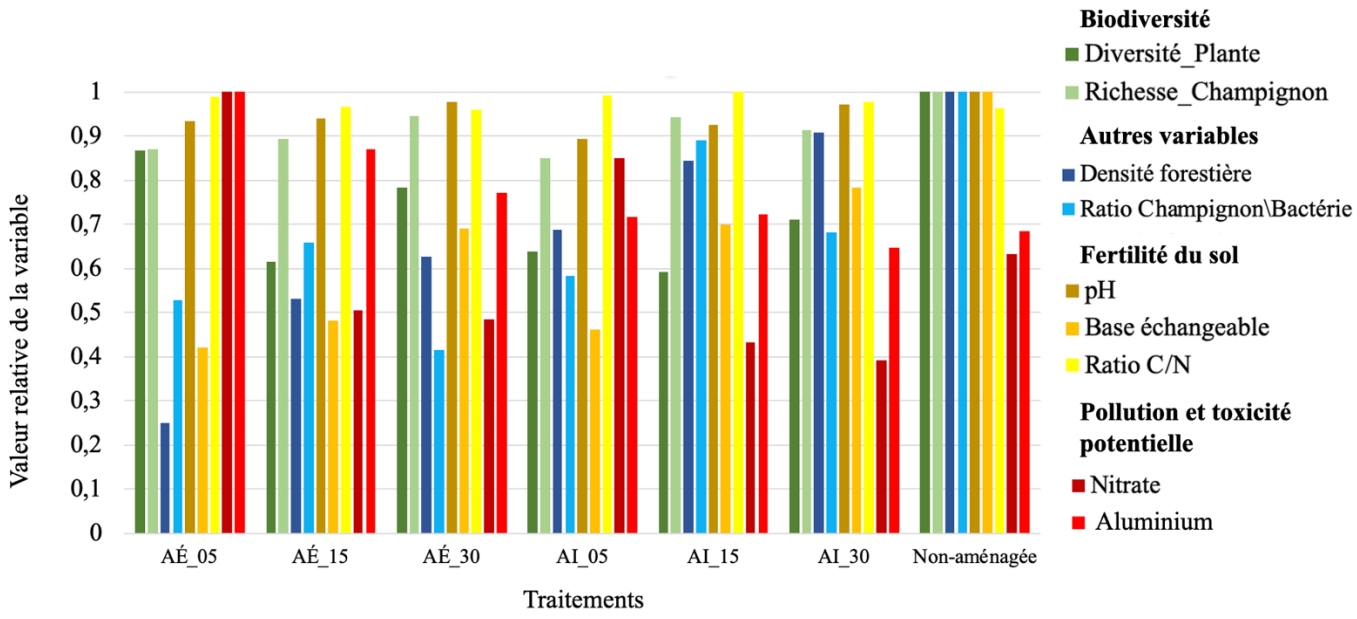


Figure 1. Synthèse des résultats de la thèse. Les valeurs relatives de chaque variable (par rapport à la moyenne la plus élevée entre les forêts non-aménagées et des forêts sous un système sylvicole équienne (AÉ) ou inéquienne (AI), 5 ans, 15 ans et 30 ans après coupe) sont présentées. La **Biodiversité** est représentée par la diversité phylogénétique des plantes de la state de sous-bois (Diversité_Plante) et la richesse totale en champignon du sol (Richesse_Champignon). La densité forestière de la strate gaule-canopée (Densité forestière), ainsi que le ratio champignon/bactérie du sol (Ratio Champignon/Bactérie) sont aussi présentés comme **Autres variables** importantes dans l'écologie forestière. La **Fertilité du sol** est représentée par le pH, la concentration en bases échangeables (Base échangeable) et le ratio C/N (Ratio C/N). La **Pollution et toxicité potentielle** est représentée par la concentration en aluminium (Aluminium) et en nitrates (Nitrate). Les valeurs de la fertilité du sol et de la pollution et toxicité potentielle sont des moyennes des horizons organique et minéral.

Ensemble, ces résultats témoignent de l'importance de la conservation et de l'augmentation des superficies des forêts «non-aménagées» comme une solution pour limiter la perte de biodiversité et de fertilité des sols, et lutter contre les changements climatiques. Sur ce dernier point, des études supplémentaires seraient nécessaires pour approfondir nos connaissances concernant le potentiel de séquestration et de stockage du C forestier des forêts non-aménagées et aménagées par différentes approches sylvicoles.

À l'échelle du peuplement en forêt tempérées aménagées dans les domaines bioclimatiques de l'érablière à tilleul et de l'érablière à caryer, parmi les pistes de solutions pour limiter la perte de biodiversité, la modification du microbiome et la diminution de la fertilité des sols, les résultats de la présente thèse pointent vers des coupes qui soient à la fois moins intensives et moins fréquentes (*e.g.*, AI avec des rotations plus longues que celles actuellement préconisées), tout en minimisant la perturbation des sols. Ce type d'aménagement pourrait aussi maintenir des volumes plus élevés de bois morts dans différentes classes de décomposition. La présente thèse (*e.g.,* Information supplémentaire II du Chapitre I et Chapitre III) suggère qu'il est important, pour minimiser les impacts négatifs des pratiques sylvicoles, de : 1) stabiliser le pH du sol dans le temps, 2) viser une structure forestière diversifiée incluant des arbres de grands diamètres, et 3) maintenir une composition forestière se rapprochant de celle des forêts non-aménagées (*e.g.*, abondance plus limitée du hêtre à grande feuille en sous-couvert, plus grande abondance d'essences compagnes mégatrophes comme le tilleul d'Amérique).

Outre ces résultats issus des chapitres I, II et III, cette thèse a aussi permis de documenter le choix des indices de diversité à sélectionner, leurs limites, ainsi que les informations qu'on peut en tirer (Chapitre IV). Ce chapitre théorique démontre les avantages d'intégrer des composantes dépendantes de l'espèce telles que la diversité phylogénétique ou fonctionnelle et des composantes spatiales alpha et beta dans l'évaluation de la diversité.

Finalement, certaines méthodes d'analyse ont été testées dans le cadre de cette thèse. Par exemple, l'approche de quantification de l'abondance de champignons du sol par la détermination de la fréquence des OTU par séquençage nouvelle-génération a été validée

en la comparant avec la méthode qPCR (Information supplémentaire, Chapitre III). Cette validation méthodologique est importante vue le nombre considérable d'études qui ont utilisé la fréquence d'OTU pour estimer l'abondance de différentes espèces, sans toutefois qu'elles aient validé cette estimation.

Limitation de l'étude

Le dispositif expérimental et l'expérience en serre

Le dispositif expérimental a permis d'analyser les effets des coupes menant à des forêts de structure équiennes et inéquiennes sur différentes variables écologiques d'intérêt comparativement à des forêts non-aménagées. Cependant, pour analyser clairement le rétablissement de ces variables le long d'une chronoséquence, sous AÉ, il aurait été souhaitable d'inclure des sites coupés depuis beaucoup plus de 30 ans de façon couvrir une rotation complète d'un peuplement forestier (*e.g.,* 60-90 ans). Une étude sur trois rotations de coupes partielles d'AI (*e.g.,* 60-90 ans) aurait aussi été nécessaire pour comparer plus équitablement ces deux types d'aménagements (i.e., coupes partielles de faible intensité plus fréquentes *vs* coupes totales intensives à longue rotation de récolte). Ainsi, dans la perspective d'obtenir des informations précises pouvant servir de recommandation forestière, une expérience similaire avec une chronoséquence plus longue est recommandée. De tels sites n'étaient pas disponibles dans l'aire d'étude de la présente thèse.

L'étude de la dynamique temporelle de la diversité des plantes de sous-bois, de la modification du microbiome et des propriétés du sol aurait été plus précise si les mêmes parcelles avaient été remesurées à différents intervalles de temps suivant les traitements

sylvicoles. Cependant, une substitution espace-pour-temps était la seule méthode disponible pour étudier cette dynamique temporelle à l'intérieur du dispositif expérimental que nous avons implanté en milieu forestier.

Dans l'expérience en serre, il aurait été souhaitable d'échantillonner davantage de sites forestiers ayant des conditions physico-chimiques similaires pour chaque traitement. De plus, il aurait été intéressant d'analyser les communautés microbiennes du sol pour pouvoir faire de plus amples relations entre la croissance des semis et le microbiome du sol.

L'étude des communautés de plantes de la strate de sous-bois

Peu de limitations ont été identifiées dans l'étude sur le terrain des communautés de plantes. Nous avons en effet pris soin de visiter les mêmes micro-parcelles de végétation à différentes périodes (*i.e.*, le printemps et l'été). De plus, l'aide d'un botaniste expert a permis d'identifier des espèces plus difficiles à classifier (*e.g.*, les carex). D'un autre côté, plusieurs données sur la phylogénie ou les traits des plantes étaient difficilement, voire pas du tout, accessible. Sans remplacement, l'arbre phylogénétique créé était hautement incomplet, avec plus de 90 espèces manquantes. Il ne permettait donc pas de calculer adéquatement la diversité phylogénétique. Ainsi, la phylogénie (ou les traits) d'espèces similaires a été utilisée. Cette méthode a permis de calculer la diversité phylogénétique et de faire l'étude des communautés de traits en utilisant toutes les espèces. Par contre, cette approche était accompagnée d'une plus faible précision des données.

L'étude des communautés de champignons du sol

La méthodologie utilisée dans notre étude des communautés de champignons du sol n'a pas permis de bien identifier les champignons mycorhiziens arbusclaires (CMA). Bien que les CMA étaient probablement très abondants dans les sols des forêts étudiées, les marqueurs privilégiés dans notre étude et le séquençage n'ont pas permis de les identifier clairement et, ainsi, d'en évaluer la dynamique après aménagement forestier. La possibilité d'utiliser des marqueurs moléculaires spécifiques pour l'identification et la quantification des CMA et des ECM avec le q-PCR a été explorée dans cette thèse. Malheureusement, lors de notre étude, il n'existait, à notre connaissance, aucun outil à notre portée permettant l'identification et la quantification de l'ensemble de ces champignons dans le sol (Berthiaume, 2014; Nadimi, Stefani & Hijri, 2016). Vue cette limitation et le fait que la proportion de champignons phylogénétiquement assignés variait d'une parcelle à l'autre et d'un traitement à l'autre, nous avons décidé d'étudier la modification de la proportion relative des différents groupes trophiques ou guildes. Récemment, de nouvelles avancées méthodologiques ont été faites dans le domaine (Nilsson *et al*., 2019; Miyauchi *et al*., 2020). De plus, le fait de ne pas avoir analysé l'horizon minéral dans le sol, où les CMA sont dominants par rapport aux ECM qui sont plus présents dans les couches organiques et superficielles du sol, a aussi limité l'analyse des CMA. Les contraintes et limites de cette méthodologie ont été mentionnées et prises en compte lors de l'interprétation de nos résultats (Nilsson *et al*., 2019). Bien évidemment, il aurait été intéressant de pouvoir étudier les guildes de champignons dans plusieurs horizons du sol.

Pistes de recherches futures pour mieux comprendre l'impact des coupes forestières

Liens entre la diversité végétale et les fonctions de l'écosystème forestier

La conservation des fonctions de l'écosystème forestier comme la productivité primaire et le recyclage des nutriments est souvent mise de l'avant comme argument pour démontrer l'importance de la diversité des plantes en forêt (*e.g.,* Hooper *et al.,* 2012). Cependant, des auteurs questionnent la preuve tangible des liens entre la diversité végétale et les fonctions de l'écosystème, notamment à petite échelle (*e.g.,* l'échelle d'une parcelle forestière) (Vellend *et al*., 2013). Une étude, à petite échelle, reliant la diversité des plantes en forêt aménagées et non-aménagées, à de nombreuses fonctions de l'écosystème serait ainsi un atout majeur à la compréhension de l'importance écologique de la biodiversité. Comme il est possible de faire des liens entre plusieurs fonctions de l'écosystème et les traits fonctionnels des plantes (Garnier & Navas, 2013), la comparaison d'une vaste sélection de traits, entre parcelles forestières aménagées ou non, permettraient d'amorcer cette analyse. Cependant, le manque d'information sur les traits fonctionnels de plusieurs espèces de plantes que l'on retrouve en forêt, et particulièrement en forêt non-aménagée, semble un frein à la compréhension des effets des coupes forestières sur la modification des fonctions de l'écosystème. Dans la présente thèse, le nombre de traits fonctionnels utilisés se limitait à quatre. Ainsi, une étude future pourrait s'attarder à mesurer une sélection de plusieurs traits fonctionnels de plantes que l'on retrouve en forêt non-aménagée. Cette étape permettrait ensuite de mieux comprendre les impacts tangibles des coupes forestières à petite échelle sur l'écosystème forestier.

Le C dans l'écosystème forestier

Dans un contexte de lutte aux changements climatiques et vu l'importance du C dans les sols forestiers (Lal, 2008; Pan *et al.,* 2011), des recherches plus approfondies apparaissent souhaitables pour mieux comprendre les effets de l'aménagement forestier en forêt feuillue tempérée sur la dynamique du C. En effet, on retrouve présentement dans la littérature scientifique d'intéressants constats, mais parfois contradictoires, concernant le rôle de l'aménagement forestier sur la séquestration et le stockage du C (*e.g.,* Ford & Keeton, 2017; Jones *et al.,* 2019; Goldstein *et al*., 2020). Il est aussi connu que l'accumulation de C dans le sol forestier en forêt boréale est davantage associée à l'activité des champignons près des racines (Clemmensen *et al*., 2013) qu'à la productivité forestière primaire. Omettre d'étudier et de considérer des composantes de l'écosystème forestier comme le sol et son microbiome pourrait entraîner des conclusions erronées concernant l'effet des coupes forestières sur la séquestration et le stockage du C. De plus, comme la présente thèse a identifié la structure forestière diversifiée (avec présence d'arbres de grands diamètres) comme une variable positivement corrélée avec la proportion de champignons symbiotiques en forêt tempérée, il serait intéressant de mieux comprendre les mécanismes qui peuvent expliquer cette corrélation (*e.g.,* l'importance de la production d'exsudats racinaires (notamment des sucres non-structuraux) chez les arbres de différents stage ontogénique). Une meilleure connaissance des liens entre la structure des forêts et le C séquestré et stocké dans les sols serait un atout indéniable pour l'aménagement durable des forêts.

Ainsi, en complément à la présente étude, le dispositif expérimental mis en place pourrait servir à documenter : 1- l'estimation du C aérien séquestré (e.g., utilisation des équations de Lambert *et al*., 2005), 2- la respiration microbienne dans les sols (notamment l'horizon

organique), 3- l'abondance (ou proportion) des champignons symbiotiques (incluant les champignons mychoriziens arbusculaires) à différentes profondeurs dans les sols, ainsi que 4- la production d'exudats racinaires (sucres non-structuraux) chez les arbres de différents stades ontogéniques. L'ensemble de ces mesures permettrait de mieux connaître les relations entre le C aérien séquestré par la végétation et des variables influençant le C qui est réémit dans l'air par le microbiome du sol (*e.g.*, par la respiration microbienne, la modification du ratio champignons/bactéries) ou stocké à plus long terme dans les sols (*e.g.*, par des champignons symbiotiques).

Ensemble, ces deux pistes de recherches futures permettraient de documenter ou de valider l'ampleur des conséquences des coupes sur l'écosystème forestier, ainsi que de démystifier les bénéfices écologiques de la conservation de ces forêts.

J'en profite pour faire trois suggestions qui permettraient, selon moi, d'améliorer la gestion des forêts.

1- Il faudrait éviter le terme «cloche de verre», mais plutôt parler de forêts non-aménagées par l'humain. Celles-ci ne sont pas fermées et peuvent être un noyau de biodiversité utile pour les forêts avoisinantes.
2- Quand on parle des forêts et du carbone, il serait préférable de bien distinguer le rôle écologique de ces forêts dans la séquestration/stockage de carbone (incluant les sols) de la ressource bois comme alternative de substitution à d'autres produits plus polluants.

3- Quand on fait référence aux «forêts non-aménagées», je suggère d'éviter le terme «vieilles forêts», puisque celles-ci peuvent avoir une structure (*i.e.,* densité, âge des arbres) très diversifiée.

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