

## **Table des matières**

Résumé.....	iii
Abstract.....	v
Liste des tableaux.....	x
Liste des figures .....	xi
Remerciements.....	xii
Avant-propos.....	xiii
Introduction générale .....	1
Le nouveau paradigme forestier.....	1
Les forêts du Québec.....	2
Les perturbations naturelles .....	2
Chablis.....	2
Épidémies de tordeuses des bourgeons de l'épinette .....	3
Feu.....	3
Les services écosystémiques .....	4
La biodiversité et les services écosystémiques.....	4
Le potentiel de la diversité fonctionnelle .....	5
Objectifs de la thèse .....	6
Chapitre 1: Stand height and cover type complement forest age structure as a biodiversity indicator in boreal and northern temperate forest management .....	9
Résumé.....	9
Abstract .....	10
Introduction .....	11
Methodology .....	13
Study area.....	13
Beta diversity analysis.....	14
Alpha diversity measures .....	15

Alpha diversity statistical analysis .....	16
Results.....	16
Beta diversity analysis.....	16
Alpha diversity analysis .....	17
Discussion .....	19
Conclusions .....	22
Acknowledgements .....	22
References .....	23
Tables and figures .....	30
Supplementary material.....	37
Chapitre 2: Response diversity, functional redundancy and post-logging productivity in northern temperate and boreal forests.....	51
Résumé .....	51
Abstract .....	52
Introduction .....	53
Methodology .....	55
Study area.....	55
Functional effect groups.....	56
Functional redundancy and response diversity .....	56
Ecosystem productivity metric .....	57
Statistical analysis .....	58
Results.....	60
Functional redundancy and response diversity .....	60
Species identity effects.....	61
Discussion .....	61
Conclusions .....	64
Acknowledgments.....	65

References .....	65
Tables and figures .....	73
Supplementary material.....	78
Chapitre 3: Mitigation of water loss and xylem resistance to cavitation influence the response of stand mortality to severe drought, but not productivity, in northern temperate and boreal forests .....	89
Résumé .....	89
Abstract .....	90
Introduction .....	91
Methodology .....	93
Study area.....	93
Identification of drought conditions .....	93
Productivity and mortality.....	94
Functional traits.....	95
Structural equation modelling .....	95
Results.....	96
Permanent sample plot dataset .....	96
Structural equation models.....	97
Discussion .....	99
Conclusion.....	101
Acknowledgments.....	102
References .....	102
Tables and figures .....	109
Supplementary material.....	114
Conclusion générale .....	119
Implication des résultats.....	120
Limites.....	122
Perspectives.....	123

Bibliographie.....	124
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## Liste des tableaux

<b>Table 1.1.</b> Stand-level age classes, height classes, cover types and canopy cover density classes considered .....	30
<b>Table 1.2.</b> Linear regression models of plot-level local contribution to beta diversity .....	31
<b>Table 1.3.</b> Coefficients from the top linear effects model of LCBD .....	32
<b>Appendix 1.A.</b> Functional trait data and sources. ....	37
<b>Table 2.1.</b> Candidate model sets built to test the influence of FR, RD and species identity effects on RD–post-disturbance productivity relationship.....	73
<b>Table 2.2.</b> Generalized linear mixed effect model coefficients from the top model .....	73
<b>Appendix 2.B.</b> Functional trait data and sources.....	79
<b>Appendix 2.C.</b> Extended candidate model set.....	85
<b>Table 3.1.</b> AIC <sub>c</sub> and p-values of chi-square goodness of fit tests for SEM models per bioclimatic domain and plot type with varying latent variable compositions.....	109
<b>Appendix 3.C.</b> Number and percentage of plots where mortality did not occur and number of plots where mortality was greater than 0 per bioclimatic domain and plot type .....	116

## Liste des figures

<b>Figure 1.1.</b> Map of the study area: western Québec, Canada .....	33
<b>Figure 1.2.</b> Proportion of plots whose local contribution to beta diversity (LCBD) is significant ..	34
<b>Figure 1.3.</b> Stand tree alpha diversity plotted per cover type .....	35
<b>Figure 1.4.</b> Unscaled results of the network visualization analysis.....	36
<b>Appendix 1.B.1.</b> Sugar maple bioclimatic domain stand tree diversity plotted per cover type .....	42
<b>Appendix 1.B.2.</b> Balsam fir bioclimatic domain stand tree diversity plotted per cover type.....	43
<b>Appendix 1.B.3.</b> Black spruce bioclimatic domain stand tree diversity plotted per cover type.....	44
<b>Appendix 1.B.4.</b> Sugar maple bioclimatic domain unscaled results of the network analysis .....	45
<b>Appendix 1.B.5.</b> Balsam fir bioclimatic domain unscaled results of the network analysis .....	46
<b>Appendix 1.B.6.</b> Black spruce bioclimatic domain unscaled results of the network analysis .....	47
<b>Appendix 1.C.1.</b> Deciduous sample plots per age and height class .....	48
<b>Appendix 1.C.2.</b> Mixedwood sample plots per age and height class .....	49
<b>Appendix 1.C.3.</b> Coniferous sample plots per age and height class .....	50
<b>Figure 2.1.</b> Map of the study area: Québec, Canada .....	75
<b>Figure 2.2.</b> Histograms of plot-level species composition .....	76
<b>Figure 2.3.</b> Balsam fir (a) and black spruce relative abundance (b) plotted against coniferous response diversity, and white birch relative abundance plotted against deciduous response diversity (c) .....	77
<b>Appendix 2.A.</b> Dendrogram of functional effect groups.....	78
<b>Figure 3.1.</b> Map of the study area.....	110
<b>Figure 3.2.</b> Histograms of plot-level data.....	111
<b>Figure 3.3.</b> Results of the structural equation models of each bioclimatic domain and plot type..	112
<b>Figure 3.4.</b> Total effects of observed variables on mortality and productivity across bioclimatic domains and plot types.....	113
<b>Appendix 3.A.</b> Boxplot of the proportion of dead biomass of the main taxonomic groups found within our study area per plot type and per bioclimatic domain .....	114
<b>Appendix 3.B.</b> Histograms of stand mortality (a) and productivity (b) per bioclimatic domain ...	115
<b>Appendix 3.D.</b> Alternative structural equation model of the non-drought Balsam fir-White birch bioclimatic domain.....	115
<b>Appendix 3.E.</b> Tree species leaf mass per unit area plotted against leaf area to sapwood ratio coloured according to taxonomical family.....	117

## **Remerciements**

Je tiens tout d'abord à remercier Frédéric Raulier, mon directeur de recherche, pour m'avoir accepté comme étudiant au doctorat dans son laboratoire. Sans lui je n'aurais jamais eu l'opportunité de faire cet ardu doctorat et de connaître la belle province du Québec. Je lui remercie en plus son appui lors de son congé maladie. Je lui souhaite une récupération rapide!

Je tiens également à remercier particulièrement Mathieu Bouchard et Élise Filotas, mes deux codirecteurs de recherche, pour m'avoir tellement aidé lors de l'absence de Frédéric et pour m'avoir toujours donné des idées intéressantes et des commentaires constructifs et rapides. J'ai vraiment aimé travailler avec vous et je n'aurais jamais fini mon doctorat sans votre tutelle. Je voudrais aussi remercier Isabelle Auger, Frédéric Doyon, Dylan Craven, Morgane Urli et les évaluateurs anonymes qui ont analysé mes manuscrites lors de leur publication pour leurs excellentes suggestions qui ont enrichi la qualité de ma thèse.

Ce projet a été possible grâce au financement du Fonds de recherche du Québec-Nature et technologies (FRQ-NT), du Fonds Produits forestiers Résolu, et du programme de Modélisation de la complexité des forêts qui est financé par le conseil de recherches en sciences naturelles et en génie du Canada (CRSNG) à travers le Programme de formation orientée vers la nouveauté, la collaboration et l'expérience en recherche (FONCER). J'aimerais aussi remercier le Ministère de l'Économie, de l'Innovation et des Exportations du Québec (MEIE), la Fondation Canadienne pour l'Innovation (FCI) et la FRQ-NT pour le financement de Calcul Québec et Compute Canada.

Je tiens évidemment à remercier mon père, ma mère, mes frères et les autres membres de ma famille pour m'avoir toujours supporté dans mes projets. Je les tiens toujours proche à mon cœur même s'ils sont restés au Portugal pendant mon doctorat. Je remercie aussi tous les amis que j'ai laissés au Portugal. Je ne vous ai pas oubliés même si on se voit que quelques fois par année!

Un merci tout spécial à Julia pour sa bonne disposition et sa patience, ainsi qu'à tous les bons amis que j'ai fait à Québec, en particulier Raf, Claude, mes coloc et toute la gang de l'escalade, pour tous les moments inoubliables qu'on a passé! Je remercie aussi tout le monde de mon département que j'ai rencontré. En plus, je voulais remercier tout le monde que j'ai rencontré à la résidence et que m'a tellement bien accueilli lors de mon arrivée au Québec. Finalement, je tiens à remercier toutes les personnes que je n'ai pas mentionnées et qui m'ont aidé d'une façon ou d'une autre àachever cette thèse!

## **Avant-propos**

Cette thèse est constituée par trois chapitres rédigés sous la forme d'articles scientifiques qui sont déjà ou seront bientôt publiés dans des revues scientifiques internationales. Alors, les trois chapitres sont écrits en anglais. Je suis le premier auteur de chacun de ces articles, car j'ai proposé les questions de recherche, j'ai fait les analyses statistiques et j'ai rédigé les manuscrits. Frédéric Raulier, Mathieu Bouchard et Élise Filotas y sont des co-auteurs pour m'avoir aidé lors du développement des objectifs de recherche, de l'analyse des données et de la rédaction des manuscrits. La version des articles inclus dans cette thèse est la version publiée ou soumise pour publication, dépendamment de l'état de publication des articles lors de la soumission de cette thèse.

Le premier article s'intitule « Stand height and cover type complement forest age structure as a biodiversity indicator in boreal and northern temperate forest management ». Cet article a déjà été publié : Ecological Indicators 72 (2017), 288-296.

Le deuxième article s'intitule « Response diversity, functional redundancy and post-logging productivity in northern temperate and boreal forests ». Cet article a été soumis à *Ecological Applications* en Mai 2017, reçu pour des corrections en octobre, resoumis en novembre 2017 et accepté avec des corrections mineures en Février 2018.

Le troisième article s'intitule « Mitigation of water loss and xylem resistance to cavitation influence the response of stand mortality to severe drought, but not productivity, in northern temperate and boreal forests» et sera prochainement soumis au Journal of Applied Ecology.

## **Introduction générale**

### **Le nouveau paradigme forestier**

Les attentes de la population en regard de l'aménagement forestier ont évolué graduellement lors des dernières décennies. Les forêts ne doivent plus être aménagées seulement pour la production de bois, car leur rôle important dans la production de plusieurs autres services écosystémiques, tels que la séquestration du carbone et l'écotourisme, est désormais reconnu (Millennium Ecosystem Assessment 2005). En plus d'être incapables de répondre aux besoins multicritères de cette nouvelle perspective d'aménagement forestier (Kangas et Kangas, 2005), les stratégies traditionnelles d'aménagement forestier ne permettent pas de gérer explicitement l'incertitude amenée par les changements climatiques (D'Amato et al., 2011).

Le développement de stratégies d'aménagement forestier adaptées est essentiel pour réduire la vulnérabilité des forêts à l'augmentation de la fréquence des extrêmes climatiques (Allen et al., 2010) et à l'expansion de la distribution géographique des insectes dommageables et maladies des arbres (Ramsfield et al., 2016). Une des principales stratégies suggérées est l'utilisation des peuplements biologiquement diversifiés pour améliorer le potentiel adaptatif des forêts, puisque les écosystèmes plus diversifiés sont normalement plus résilients aux perturbations (D'Amato et al., 2011). Le développement de ce genre de stratégies d'aménagement adaptatives repose largement sur l'utilisation d'indicateurs de biodiversité qui reflètent le fonctionnement de l'écosystème et sa réponse aux perturbations (Hisano, Searle, et Chen, 2017). Étant donné que nos connaissances sur ces relations dans les écosystèmes forestiers demeurent faibles (Mori, Lertzman, et Gustafsson, 2017), l'étude des liens entre la diversité forestière, le fonctionnement de l'écosystème et la réponse de l'écosystème aux perturbations naturelles et anthropogéniques est essentielle pour le développement de stratégies d'aménagement forestier plus efficaces.

Le but de cette thèse était d'améliorer nos connaissances sur les relations entre la diversité des arbres, la productivité primaire et sa réponse aux perturbations dans les forêts tempérées nordiques et boréales. En explorant ces relations, je souhaitais contribuer au développement de nouveaux indicateurs de biodiversité qui puissent être intégrés dans les stratégies d'aménagement forestier. À travers cet exercice j'ai cherché à évaluer le potentiel des stratégies d'aménagement forestier basés sur les traits fonctionnels des espèces pour améliorer les stratégies utilisées actuellement.

## **Les forêts du Québec**

Les forêts du Québec sont un habitat clé pour plus de 200 espèces d'oiseaux et plus de 60 espèces de mammifères (MFFP, 2015), et jouent un rôle fondamental pour la conservation de la diversité biologique. Ces mêmes forêts sont très importantes pour le développement économique de la province. L'exploitation forestière des forêts du Québec génère près de 14 milliards de dollars et est responsable de près de 59 000 emplois directs (MFFP, 2015). La conciliation des fonctions économiques et écologiques de ces forêts représente un enjeu important pour le futur.

Les forêts tempérées et boréales du Québec couvrent une surface de 761 100 km<sup>2</sup>, soit environ 2% des forêts à l'échelle globale (MFFP, 2015). Ces forêts couvrent un gradient important de climat, végétation, type de sol, topographie et perturbations naturelles, ce qui a mené à la définition formelle de six domaines bioclimatiques (Saucier et al., 2003). Les quatre premiers domaines bioclimatiques sont situés dans la zone tempérée et les deux autres dans la zone boréale. Du sud vers le nord, les forêts feuillues font partie des trois premiers domaines bioclimatiques : l'érablière à caryer cordiforme, l'érablière à tilleul et l'érablière à bouleau jaune. Le quatrième domaine bioclimatique, la sapinière à bouleau jaune, est une zone de transition entre la forêt tempérée et la forêt boréale, tandis que le cinquième domaine, la sapinière à bouleau blanc, correspond à la partie la plus au sud de la forêt boréale (Saucier et al., 2003). Les peuplements mixtes (mélanges conifères-feuillus) sont particulièrement communs dans ces deux derniers domaines. La pessière à mousses, le sixième domaine bioclimatique, est dominé par des conifères et est de loin le domaine bioclimatique couvrant la plus grande superficie, soit plus que tous les autres domaines combinés. La pessière à mousses s'étend jusqu'au 52<sup>e</sup> parallèle et représente la partie nord de la forêt boréale continue.

## **Les perturbations naturelles**

Des domaines bioclimatiques distincts ont évolué sous différents régimes de perturbations naturelles. Par conséquent, l'importance des principales perturbations naturelles varie selon le domaine bioclimatique (Saucier et al., 2003). Les trois perturbations naturelles principales au Québec sont le chablis, les épidémies de tordeuses des bourgeons de l'épinette (*Choristoneura fumiferana*) et les feux.

### **Chablis**

Le chablis, soit le déracinement ou le bris des arbres causés par des vents forts, joue un rôle clé dans la dynamique des forêts feuillues tempérées de l'Amérique du Nord. Les chablis peuvent être classés comme partiels lorsqu'ils affectent seulement quelques arbres dans un peuplement, ou comme des

totaux lorsqu'ils détruisent le peuplement au complet. Alors que traditionnellement l'impact des chablis dans les forêts boréales a été considéré comme minimal, des études récentes ont montré que les chablis peuvent avoir un impact important sur ces forêts lorsqu'on inclut les chablis partiels (Waldron, Ruel, et Gauthier, 2013). En plus de causer la mort des arbres, les chablis peuvent aussi modifier la structure des sols en influençant la quantité des nutriments, les niveaux d'humidité, la température et la disponibilité de la lumière au niveau du sol (Girard, De Grandpré, et Ruel, 2014).

### **Épidémies de tordeuses des bourgeons de l'épinette**

Les épidémies de tordeuses des bourgeons de l'épinette sont considérées comme une des perturbations naturelles les plus importantes dans les forêts boréales et sub-boréales du Québec (Bouchard et Pothier, 2010). Par exemple, la dernière épidémie (1976-1991; Boulanger et al., 2012) s'est étendue sur plus de 55 millions d'hectares de forêt dans l'Est américain, représentant la perte de 139 à 238 millions de mètres cubiques de sapins et d'épinettes au Québec (Morin et al., 2009). Malgré le fait que ces épidémies affectent surtout le sapin baumier (*Abies balsamea*), d'autres essences de conifères, tels que l'épinette noire (*Picea mariana*) et blanche (*Picea glauca*), sont aussi affectées et peuvent subir des pertes de croissance et de la mortalité (Bouchard et Pothier, 2010). Les épidémies de tordeuse se produisent à des cycles de 30 à 40 ans et durent généralement de 5 à 15 ans à l'échelle locale. Les épidémies ont une tendance à être spatialement synchrones sur des grandes superficies. Cependant, sachant que les arbres matures sont plus vulnérables et que les gaules des sapins baumiers prennent au moins 50 ans à devenir matures, ces épidémies ont généralement un impact important au niveau du peuplement à tous les 60 à 80 ans (Boulanger et al., 2012).

### **Feu**

Le feu est reconnu comme étant la perturbation naturelle la plus importante pour les forêts boréales nord-américaines (Gauthier et al., 2015), mais leur impact sur les forêts tempérées est historiquement plus faible. La fréquence des feux au Canada a baissé lors des dernières décennies, mais elle va probablement augmenter dans le futur à cause des changements climatiques (Bergeron et al., 2010). Ces variations spatio-temporelles de la fréquence et de l'intensité des feux peuvent être expliquées par plusieurs facteurs biotiques, environnementaux et anthropogéniques. Par exemple, parmi les facteurs qui peuvent expliquer ces différences, il faut savoir que les forêts dominées par des feuillus sont plus résistantes aux feux (Girardin et al., 2013), que le gradient est-ouest de la précipitation augmente considérablement l'intervalle de retour de feu dans l'est du Québec (Mansuy et al., 2014), et que les techniques de suppression des feux ont été améliorées (Girardin et al., 2013).

## **Les services écosystémiques**

Les services écosystémiques peuvent être définis comme étant les contributions directes et indirectes des écosystèmes au bien-être humain (Braat et de Groot, 2012). Ce terme a été popularisé par l'Évaluation des Écosystèmes pour le Millénaire (Millennium Ecosystem Assessment; MEA 2005) et prend de plus en plus d'importance dans la discussion sur la conservation environnementale et la gestion des ressources naturelles (de Groot et al., 2010).

On peut séparer les services écosystémiques fournis par les forêts en quatre catégories: (i) les services d'approvisionnement, qui comprennent les produits tangibles comme le bois et la nourriture ; (ii) les services de régulation, qui sont les avantages immatériels assurés par le bon fonctionnement des écosystèmes, comme la régulation du climat et la filtration de l'air ; (iii) les services socioculturels, qui comprennent les avantages intangibles obtenus par l'Homme dans ses interactions avec la Nature, comme le tourisme de la nature ; et (iv) les services de soutien, qui incluent tous les services nécessaires au soutien des autres services, comme la formation du sol et la pollinisation (Millennium Ecosystem Assessment 2005). Les services écosystémiques sont influencés par des facteurs anthropogéniques, tels que l'accroissance de la population mondiale, les fluctuations de l'activité économique et les changements sociopolitiques et par des facteurs non anthropogéniques, comme la biodiversité et le climat (Millennium Ecosystem Assessment 2005). Nos connaissances sur l'influence de ces variables sur l'approvisionnement des services écosystémiques sont toutefois limitées (Adams, 2014).

## **La biodiversité et les services écosystémiques**

La biodiversité est un concept complexe composé par plusieurs composants distincts, dont la diversité compositionnelle (le nombre d'espèces), structurelle (le degré de l'organisation physique, spatiale ou interspécifique) et fonctionnelle (la variabilité des mécanismes et des processus de fonctionnement des espèces présentes) (Redford et Richter, 1999). Étant donné que les services écosystémiques peuvent être influencés par chacune de ces composantes (Balvanera et al., 2006), établir le rôle exact de la biodiversité dans le maintien des services écosystémiques est compliqué. En fait, Mace et al., (2012) ont suggéré que la biodiversité joue un rôle essentiel dans tous les niveaux de la hiérarchie des services écosystémiques, parce que : (i) la biodiversité régule les processus fondamentaux qui soutiennent le fonctionnement des écosystèmes ; (ii) la biodiversité en soi est un service écosystémique parce que l'Homme en tire des avantages directs ; et (iii) la biodiversité est un bien valorisé à une échelle mondiale.

Malgré le fait que les relations entre les services écosystémiques et la biodiversité n'ont toujours pas été décrites d'une façon exhaustive, des études récentes ont montré que la performance des services écosystémiques est intrinsèquement liée à la biodiversité. Par exemple, Lefcheck et al., (2015), une méta-analyse de 94 études, a trouvé que la biodiversité améliore la performance de plusieurs fonctions de l'écosystème indépendamment du niveau trophique et du type d'habitat, Paquette et Messier, (2011) ont trouvé un effet significatif de la biodiversité sur la productivité des forêts tempérées et boréales, et Gamfeldt et al., (2013) ont montré que la performance de plusieurs services écosystémiques est influencée par le nombre d'espèces d'arbres dans les forêts aménagés.

### **Le potentiel de la diversité fonctionnelle**

Actuellement, le concept de diversité fonctionnelle représente une des principales avenues de recherche en écologie, en particulier au niveau de la façon dont la biodiversité est mesurée (McGill et al., 2006). Selon cette nouvelle façon d'appréhender la biodiversité, plutôt que de se contenter de mesurer la richesse et l'abondance des espèces, on quantifie également certains traits fonctionnels des espèces, ce qui nous permet d'analyser explicitement des liens entre les espèces et leurs fonctions (Villéger, Mason, et Mouillot, 2008). Parmi les traits fonctionnels habituellement considérés, on peut définir deux catégories selon le rôle qu'ils jouent dans le cycle de vie de l'espèce : les traits d'effet, qui déterminent l'influence des espèces sur les processus de l'écosystème, et les traits de réponse, qui permettent de quantifier la réponse des espèces aux changements environnementaux et aux perturbations (Suding et al., 2008). Puisqu'elle permet de quantifier la relation directe entre les traits fonctionnels et le fonctionnement de l'écosystème, la diversité fonctionnelle est la composante de la biodiversité qui est la plus susceptible de refléter l'impact des modifications environnementales sur les services écosystémiques (Cadotte, Carscadden, et Mirochnick, 2011).

En fait, plusieurs études ont montré l'importance des relations entre la diversité fonctionnelle et le fonctionnement des forêts. Par exemple, Ziter et al., (2013) ont trouvé une corrélation significative entre la diversité fonctionnelle des plantes et les stocks de carbone des forêts tempérées nordiques, tandis que Paquette et Messier, (2011) ont montré que la diversité fonctionnelle influence positivement la productivité des forêts tempérées nordiques et boréales. La diversité fonctionnelle influence aussi la réponse des peuplements forestiers aux perturbations, puisqu'elle réduit l'impact négatif du climat sur la croissance et le recrutement des arbres (Ruiz-Benito et al., 2017), en plus d'augmenter la résilience des forêts au feu (Spasojevic et al., 2016).

Quelques inconvénients limitent toutefois l'utilisation du concept de diversité fonctionnelle dans un contexte d'aménagement forestier. D'abord, une stratégie d'aménagement qui viserait une augmentation de la diversité fonctionnelle pourrait théoriquement conduire à sacrifier des espèces qui seraient plus menacées (rares) que d'autres ou des espèces d'intérêt commercial, puisque le concept de diversité fonctionnelle ne considère pas explicitement la valeur des espèces individuelles (Villéger, Mason, et Mouillot, 2008). L'utilisation d'indices peut également compliquer la communication des résultats d'études portant sur les traits fonctionnels pour un public et des utilisateurs (aménagistes) habitués de réfléchir en termes d'espèces. Deuxièmement, nos connaissances sur l'influence des traits fonctionnels sur le fonctionnement des écosystèmes comportent des lacunes significatives. Par exemple, l'interaction entre les traits fonctionnels et leur variabilité intra-spécifique, deux sujets peu étudiés, peuvent avoir des fortes conséquences sur la capacité adaptative des arbres et le fonctionnement des écosystèmes (Aubin et al., 2016). Finalement, le nombre important de traits et de mesures de diversité fonctionnelle qui sont actuellement disponibles, et le fait que plusieurs de ces mesures soient fortement corrélées, peut compliquer le choix des traits et des mesures adéquates pour un contexte donné (Mason et al., 2013).

Malgré tout, les nouvelles études et innovations dans le domaine de la diversité fonctionnelle tendent à réduire graduellement les inconvénients associés à l'utilisation de ce concept, particulièrement au niveau de l'information disponible. Des bases de données d'accès libre, comme la base de données TRY (Kattge et al., 2011), sont dorénavant disponibles et sont continuellement enrichis par des études détaillées permettant ainsi de mieux cibler les traits à considérer. De plus, le développement des logiciels d'accès libre dédiés au calcul de la diversité fonctionnel, c'est-à-dire le package « FD » du logiciel R (Laliberté et al., 2014), facilitent l'analyse de ce type de données. De plus, des manuels de sélection de traits fonctionnels (Aubin et al., 2016) et de mesures de diversité fonctionnelle (Mason et al., 2013) aident les chercheurs à choisir les mesures et les trait fonctionnels les plus adaptés aux objectifs de leurs études. Malgré l'importance de la diversité fonctionnelle pour la compréhension du fonctionnement de l'écosystème, les avancées récentes dans son analyse, et le besoin des aménageurs forestiers d'assurer un aménagement durable des forêts, le concept de diversité fonctionnelle n'a toujours pas été incorporé de façon efficace dans l'aménagement forestier.

## **Objectifs de la thèse**

L'objectif de cette thèse était d'explorer la possibilité d'intégrer le concept de diversité fonctionnelle des arbres dans l'aménagement durable des forêts tempérées nordiques et boréales. Étant donné que la diversité fonctionnelle des arbres influence la réponse de l'écosystème aux perturbations

environnementales et anthropogéniques, il est essentiel de comprendre ces relations et de développer des indicateurs de biodiversité plus efficents qui peuvent être intégrés dans des stratégies d'aménagement forestier (Mori, Lertzman, et Gustafsson, 2017).

Dans le premier chapitre, j'ai testé l'hypothèse que la structure de l'âge de la forêt est un indicateur pouvant saisir toutes les composantes de la biodiversité locale et à l'échelle du paysage. Ce dernier est un des indicateurs de biodiversité les plus utilisés dans l'aménagement forestier à l'échelle mondiale (Montréal Process Working Group, 2015), mais il n'a pas été développé pour représenter toutes les composantes de la biodiversité (Hunter et Malcolm, 1990). Dans ce chapitre, ainsi que dans les deux autres chapitres de ma thèse, j'ai utilisé le réseau de placettes échantillons temporaires et permanentes du Québec pour vérifier mes hypothèses car ces placettes couvrent un grand gradient climatique, compositionnel et spatio-temporel (MFFP, 2016). Dans un premier temps, j'ai utilisé des modèles de régression multiple et des développements récents dans l'évaluation de la diversité bêta pour examiner si cet indicateur expliquerait la variabilité de la diversité des arbres à l'échelle du paysage. J'ai également évalué l'influence de la hauteur et du type de couvert sur la diversité bêta des arbres. Dans un deuxième temps, j'ai utilisé des techniques de bootstrapping et des tests non paramétriques de Mann-Whitney pour évaluer la relation entre les caractéristiques du peuplement (l'âge, la hauteur et le type de couvert) et la diversité compositionnelle, structurelle et fonctionnelle des arbres à une échelle locale.

Dans les deux autres chapitres, j'ai étudié les interactions entre la diversité fonctionnelle des peuplements et les effets des perturbations totales (chapitre 2) et partielles (chapitre 3). Dans le deuxième chapitre, j'ai testé l'hypothèse que la redondance fonctionnelle et la diversité des réponses sont significativement liées à la productivité après coupe. De plus, ces indicateurs ont été calculés séparément pour les conifères et les feuillus pour tester l'hypothèse que ces groupes fonctionnels différents ont des impacts distincts sur la diversité après coupe. L'influence de plusieurs autres variables sur la productivité après coupe, comme le climat, les caractéristiques du peuplement, le nombre d'espèces et l'importance des espèces dominantes, a aussi été testée. J'ai utilisé des séries temporelles de dix ans de l'EVI (*Enhanced Vegetation Index*), un indicateur de productivité mesuré par des satellites (Huete et al., 2002), pour quantifier la variable réponse.

Dans le troisième chapitre, j'ai étudié l'effet de la diversité fonctionnelle des arbres sur l'atténuation de l'impact de la sécheresse extrême sur la mortalité des arbres et la productivité de l'écosystème. Spécifiquement, j'ai examiné trois traits fonctionnels qui sont reliés à trois mécanismes distincts de tolérance à la sécheresse : (i) le rapport du poids sec de la feuille à la surface foliaire, qui influence la

perte en eau de l'arbre (Poorter et al., 2009); (ii) la pression du xylème conduisant à une perte de 50% de sa conductivité par cavitation, une mesure reliée à la résistance du xylème à la cavitation (Choat et al., 2012) ; et (iii) le rapport de la surface foliaire à la surface de l'aubier, qui influence l'efficacité de l'utilisation de l'eau (McDowell et al., 2008). J'ai utilisé la modélisation par équations structurelles pour définir la tolérance à la sécheresse comme une variable latente (c'est-à-dire une variable hypothétique pour laquelle aucune mesure directe n'est disponible, mais dont l'existence peut être vérifiée par des mesures sur d'autres variables observées ; Grace et al., 2012) avec les trois traits fonctionnels mentionnés ci-dessus. J'ai testé l'hypothèse que cette variable latente représente soit la tolérance à la sécheresse (définie comme la capacité d'une espèce de survivre à une sécheresse extrême; Aubin et al., 2016), soit la résistance à la sécheresse (c'est-à-dire, la capacité d'une espèce de maintenir sa productivité lors des sécheresses extrêmes; Volaire, 2018).

# **Chapitre 1: Stand height and cover type complement forest age structure as a biodiversity indicator in boreal and northern temperate forest management**

## **Résumé**

L'âge des peuplements forestiers est un des indicateurs de biodiversité les plus utilisés dans l'aménagement forestier à l'échelle mondiale. Historiquement, l'âge a été proposé comme un indicateur de biodiversité avec le but de protéger des espèces rares associées aux vieilles forêts. Bien que cet indicateur n'ait pas été développé dans l'optique d'évaluer toutes les composantes de la biodiversité, il est souvent utilisé dans ce but. Dans cette étude, j'ai analysé la diversité alpha (à l'échelle locale) et bêta (à l'échelle du paysage) des arbres des placettes-échantillons temporaires localisées dans l'ouest Québécois pour examiner la possibilité de complémenter l'âge des peuplements forestiers avec d'autres indicateurs de biodiversité. Mes analyses ont montré que le type de couvert et la hauteur prédisent mieux la diversité bêta des arbres que l'âge. En plus, mes analyses démontrent que les placettes qui appartiennent à des classes d'âge différentes peuvent être similaires au niveau de leur diversité alpha. L'impact de la classe de hauteur sur la diversité alpha des arbres était plus fort que prévu, puisque cette variable était plus importante que l'âge dans les forêts de conifères et complémentait l'âge dans les forêts mixtes et feuillues. Mes résultats suggèrent que l'âge des peuplements forestiers ne devrait pas être utilisée comme le seul indicateur de biodiversité dans les stratégies d'aménagement durable des écosystèmes forestiers. En outre, quelques vieux peuplements secondaires peuvent également contribuer à la protection de la biodiversité. Je propose que de meilleurs compromis entre l'exploitation forestière, le fonctionnement de l'écosystème et la protection environnementale puissent être atteints si un indicateur basé sur l'âge des peuplements forestiers est complémenté par l'ajout du type de couvert et de la hauteur du peuplement, et si d'autres indicateurs du fonctionnement de l'écosystème basés sur la biodiversité soient développés et implémentés.

## **Abstract**

Forest age structure is one of the main indicators of biodiversity in temperate and boreal forests worldwide. This indicator was mainly designed for the conservation of a subset of rare or sensitive species related to the oldest age classes: it was not designed to capture variability across the entire biodiversity spectrum, but is often considered as such. In this study, we analysed alpha and beta diversity in temporary plots of western Quebec, Canada, to examine the need to develop biodiversity indicators complementary to existing forest age structure targets. Our analysis revealed that considered individually, stand characteristics such as cover type and height are better predictors of changes in site-level contribution to tree beta diversity than age. We also show that plots belonging to different age classes can be similar in terms of tree alpha diversity. Height class was found to have a more significant impact on tree alpha diversity than expected: height was more important than age in coniferous forests, and in deciduous and mixedwood stands it frequently complemented the impacts associated with age to better explain the observed diversity patterns. Our results suggest that forest age structure target levels should not be used as the sole indicator of ecosystem sustainability, and that some mature secondary stands can provide significant contributions to biodiversity. We propose that more efficient trade-offs between forest exploitation, ecosystem functioning and environmental conservation can be attained if: (i) forest age structure targets are complemented by cover type and stand height; or (ii) complementary biodiversity indicators of ecosystem sustainability are implemented.

## **Introduction**

Forests provide several fundamental ecosystem services worldwide (Gamfeldt et al., 2013). They contribute to climate change mitigation through the sequestration of CO<sub>2</sub> (Canadell & Raupach, 2008), help sustain local livelihoods (Scherr et al., 2003), provide fresh water supplies (Jones et al., 2009), and harbour numerous endangered species (Myers et al., 2000). Due to the ecological and socio-economic importance of forest ecosystems, a number of management practices at the international and governmental levels have been proposed to help ensure the sustainability of their exploitation. These range from voluntary mechanisms, such as the United Nations Programme on Reducing Emissions from Deforestation and Forest Degradation (UN-REDD) and forest sustainability certifications granted, for instance, by the Forest Stewardship Council, to governmentally-enforced regulations. While the facultative sustainability mechanisms mentioned above are quite widespread (Auld et al., 2008), only governmentally-enforced practices are truly mandatory.

By agreeing to the Montréal Process (Montréal Process Working Group, 2015), a group of countries accounting for 90% of the world's temperate and boreal forests have agreed to adopt a number of recommendations and follow several indicators for the conservation and sustainable management of temperate and boreal forests. One of the main recognized indicators is forest age structure, of which the proportion of the oldest age classes is the most critical component in a forest management context. Granting oldest stands such an influential position is not without cause. Older forests are associated with critical habitats for species of conservation concern (Drapeau et al., 2016), improved recreational value (Englin et al., 2006) and increased carbon stores (Goulden et al., 2011). These broad links to forest management objectives, coupled with its fairly inexpensive estimation process and its straightforward implementation within timber supply models (Buongiorno & Gilless, 2003), likely justify the widespread use of forest age as a proxy of biodiversity.

Still, targets using age structure do not necessarily capture all facets of biodiversity, and could be complemented or even replaced by different indicators of ecosystem sustainability (Chapin III et al., 1996). In particular, variables other than stand age have been documented to have a significant impact on biodiversity. Height class and canopy cover density are linked to stand structural development (Harper et al., 2002), and cover type (deciduous, mixedwood or coniferous trees) is an indicator of the type of species community found in the study area. Recent studies also show that for many potentially sensitive species, habitat quality is not primarily related to forest age, but to particular micro-habitats that could be present or not within a given forest age class. For example, Thompson

et al., (2016) found that the presence of large white pines was more important than stand age for cavity nesters in central Ontario mixedwood forests, and Luszcz et al., (2016) found that some forest-dwelling bat species in southwestern British Columbia were influenced by forest composition, but not by stand age. These studies confirm that the assumption that relationships between biodiversity and forest stand characteristics are driven primarily by forest age is an oversimplification. This suggests that there is a need to develop complementary indicators that are adapted to capture the effect of forest management practices on overall forest biodiversity.

Biodiversity can be considered as a triumvirate of compositional, structural and functional attributes (Redford & Richter, 1999), and it can be further classified as alpha (local diversity), gamma (regional diversity) and beta diversity (spatial differentiation) (Whittaker, 1972). Measurements of tree biodiversity at the stand- or site-scale, such as species richness and Shannon's diversity, are indicators of alpha diversity. Equally important to consider when examining the performance of biodiversity indicators are the variation in biodiversity between sites at the landscape level, which relates to beta diversity (Whittaker, 1972). Recently, total variance of the sampled community data has been proposed as a useful indicator of beta diversity that is independent from alpha diversity measurements (Legendre & de Cáceres, 2013), which is very advantageous when partitioning diversity into alpha and beta components (Jost, 2007). This methodology also allows researchers to estimate each site's local contribution to beta diversity (LCBD), an indicator of the ecological uniqueness of a site with regards to its contribution to beta diversity. LCBD could therefore complement alpha diversity indicators by identifying sites worth protecting due to their unusual species compositions and degraded sites that require ecological restoration interventions. Despite its recent origin, LCBD studies have already been published in areas as distinct as limnology (Anton-Pardo et al., 2015) and urban forestry (Yang et al., 2015).

The concept of functional diversity, which is the variation or dispersion of functional traits in an ecological group (Laliberté & Legendre, 2010), could potentially complement more traditional biodiversity indicators, such as the previously mentioned species richness and Shannon's diversity. The implementation of functional diversity is still poorly developed within a forest management context (Mori et al., 2016). Functional traits refer to the phenotypic attributes of an organism linked to its effect on ecosystem processes and its response to environmental changes (Hooper et al., 2005; Mori et al., 2013). Functional diversity is considered to be the component of biodiversity most significantly linked to overall ecosystem service performance (Balvanera et al., 2006) and it has been found to be a good predictor of temperate and boreal forest productivity (Paquette & Messier, 2011).

Moreover, functional diversity has been proposed as a proxy for quantifying ecological resilience because of its ability to capture the capacity of communities to respond to a range of disturbances (Standish et al., 2014; Suding et al., 2008).

The aim of this study was to examine the potential of developing a biodiversity indicator complementary to conventional forest age structure targets. In order to do this, we used data from temporary sampling plots of western Québec (eastern Canada) to assess how these targets, originally designed to protect a subset of sensitive species within boreal and northern temperate hardwood forests, capture: (i) variability of diversity at the landscape scale using a novel indicator of beta diversity, local contribution to beta diversity (LCBD); and (ii) variability of overall compositional, structural and functional biodiversity at the site level (alpha diversity). First, we estimated beta diversity, determined each plot's LCBD and assessed which variables best explained variability in LCBD. Then, we calculated three measures of tree alpha diversity (site-level compositional, structural and functional diversity) and we compared the influence of stand-level variables (age included) on these measures of tree diversity. We further explored the forest management implications of our results.

## Methodology

### Study area

We used data from temporary sample plots located in western Québec, Canada (Figure 1.1). These plots are distributed across a latitudinal gradient that ranges from the northern temperate forest to the southern boreal forest and encompass a number of distinct climates, forest communities, prevalent natural disturbances and forest management practices. Six distinct bioclimatic domains are included in this latitudinal gradient: sugar maple (*Acer saccharum*)-basswood (*Tilia americana*), sugar maple-bitternut hickory (*Carya cordiformis*), sugar maple-yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*)-yellow birch, balsam fir-white birch (*Betula papyrifera*) and black spruce (*Picea mariana*)-feathermoss (Robitaille and Saucier, 1998). Sample points located to the north of the northern limit of the harvestable boreal forest were excluded from our analyses.

A total of 99,429 sampling plots from this database were used. Within each circular plot of 400 m<sup>2</sup>, all trees with a diameter at breast height (DBH) greater than 9 cm are identified, their DBH measured and the overall percentage of defoliation estimated (MFFP, 2015). At the centre of each 400 m<sup>2</sup> plot is a smaller 40 m<sup>2</sup> circular plot where saplings (DBH ≤ 9 cm) are identified and counted by DBH class. Plots are sampled randomly according to a stratified sampling design: 15 plots are sampled per

strata, which are defined according to forest age and composition. Sampling effort varies between main vegetation zones (deciduous, coniferous and mixed). Stand age class is determined through visual inspection of the plot and core-based ageing of three trees per plot, cover type is estimated according to the basal area occupied by coniferous species (deciduous: <25%; mixedwood: 25 to 50%; coniferous: >75%), and height class is the mode of the photo-interpreted height of all trees in the plot. Data examined was collected between 1970 and 2012.

### Beta diversity analysis

Beta diversity was estimated according to the methodology proposed by Legendre & de Cáceres, (2013) using the R scripts provided therein. Beta diversity was measured as the total variance of community data from dissimilarity matrices using chord-transformed relative abundance data obtained from species' basal area per hectare. The chord-transformation is done according to the following equation (1.1):

$$y'_{ij} = \frac{y_{ij}}{\sqrt{\sum_{j=1}^p y_{ij}^2}},$$

where  $y'_{ij}$  ( $y_{ij}$ ) is the chord-transformed (untransformed) relative abundance data of species  $j$  at site  $i$  for all species  $p$  (Legendre & Gallagher , 2001). Plot-level local contribution to beta diversity (LCBD), a comparative indicator of site ecological uniqueness, was then obtained by partitioning total beta diversity among sites. The significance of the contribution of each plot to beta diversity was also tested through a permutation analysis of 5000 iterations. This method performs random, independent permutation of species abundance data among plots to test the null hypothesis that species are independently distributed at random among the plots (Legendre & de Cáceres, 2013).

Simple linear regression models were built with LCBD as the response variable and two components: climate and stand-level characteristics. We included climate variables in our analyses since our study area covers two forest biomes (Prentice, 1990). Two baseline scenarios were considered: one with only a climate component (average annual temperature and annual precipitation) and one with the additive effects of the four stand characteristics considered in this study: age, height, density and cover type (Table 1.1). Ten models were built that contained all individual and two-way combinations (excluding interactions) of the previously mentioned stand characteristics variables (Table 1.1). This same list of ten models was then rerun with the climate component as an additive effect. Model selection was done using the Akaike Information Criteria (AIC; Burnham & Anderson 2002). Plot-level estimates of climate variables were estimated using BioSIM (ver. 10; Régnière et al., 2014), a

software tool that interpolates climate data from the nearest weather stations to specific points of interest by considering the physical distances between them, plot-level geographical coordinates and altitude.

No influential plots were detected (Cook's distance of all plots was inferior to 1). No collinearity was found between average annual temperature and annual precipitation ( $R^2 = 0.26$ ). Visual inspection of the residuals and the QQ-plot suggests homogeneity of the variances and normality of the residuals across all models. All variance inflation factors (VIFs) were smaller than 5 and were thus lower than a commonly used threshold of 10 (Marquardt, 1970).

### **Alpha diversity measures**

Three distinct measures of tree alpha diversity (i.e. local scale) were estimated for each sampling plot: species richness, Shannon's diversity index and functional dispersion. These encompass all three components of biodiversity: compositional, structural and functional, respectively (Redford & Richter, 1999). Species richness corresponds to the number of tree species per plot. Shannon's diversity index has been widely used to estimate stand structure (e.g. Boucher et al., 2006; Buongiorno et al., 1994) and was estimated with the proportion of basal area per hectare using 10-cm DBH classes (and an open-ended class for trees larger than 80 cm). Higher Shannon diversity values correspond to more uneven-sized stands while stands with lower values tend to be more even. Shannon's diversity is strongly influenced by maximal tree size, which is higher in the south of our study area. Functional dispersion was calculated with the "FD" R language package, version 1.0-12 (Laliberté & Legendre, 2010). Functional dispersion is a multi-trait index that estimates the average distance within the functional trait space between individual species and the centroid of all species. This index was estimated using 13 categorical and continuous functional traits related to tree productivity and environmental characteristics: average maximum height, growth rate, leaf size, wood density, wood decay resistance, vegetative reproduction capacity, seed mass, shade tolerance, drought tolerance, waterlogging tolerance, leaf longevity, leaf mass per area and nitrogen content per leaf mass unit. Species' distances to the stand centroid were weighted using stand-level basal area per hectare. The number of dimensions of the functional space was estimated according to the framework proposed by Maire et al., (2015), by generating a species traits' Gower's distance dissimilarity matrix, performing a principal coordinate analysis, and selecting the number of functional spaces with the lowest mean squared deviation. Most trait values were assembled by a previous study (Paquette et al., 2015) and missing values were collated from other online data sources (Appendix 1.A). Shrub

species that can grow to tree-like dimensions were removed from the analysis because individuals of these species that are under 7 meters tall were not sampled.

### **Alpha diversity statistical analysis**

A total of 99,429 sample plots were analysed. These were grouped in 40 groups according to their age, height and cover type (Table 1.1). Group size varied between 118 and 9,771 plots. Cover type and height class were chosen because they were the two top performing variables from the beta diversity analysis and grouping stands according to these variables is thus likely to group together biologically equivalent sites that have similar species compositions when compared with a mean site (Legendre & de Cáceres, 2013). Groups with less than 100 sample plots were removed from the analysis.

The three biodiversity measures were compared across all groups using nonparametric Mann-Whitney U tests in order to account for the non-normal distribution of the data in some groups. As nonparametric tests can be sensitive to unequal sample sizes (Zimmerman, 1987), we bootstrapped the Mann-Whitney U test 1000 times using sample sizes of 100 plots. Two groups were considered to be statistically equivalent in terms of tree diversity if, for each of the three biodiversity indicators (species richness, Shannon's structural diversity and functional dispersion), over 50% of the replicates were not significantly different at a p-value of 0.05. These results were visualized using a network analysis-based approach (Proulx et al., 2005): each group was classified as a single node in the network and links between the nodes represented biodiversity equivalency. In order to ensure that our results were not confounded by the effects of climate, we repeated these analyses for each major bioclimatic domain: (i) sugar maple-bitternut hickory, sugar maple-basswood and sugar maple-yellow birch; (ii) balsam fir-yellow birch and balsam fir-white birch; and (iii) black spruce-feathermoss (Appendix 1.B).

Statistical analyses were done using the R software environment v. 3.2.3. (R, 2015) and network visualization was done using the “igraph” R language package, version 1.0.1 (Csárdi and Nepusz, 2006).

## **Results**

### **Beta diversity analysis**

Positive gradients of local contribution to beta diversity (LCBD) were found for both height and density classes: plots that were either taller or had more dense canopies were more prone to generating

significant contributions to beta diversity than shorter or less dense ones (Figures 1.2b, 1.2d). From all the analysed variables, the plots with the tallest trees were the ones most probable to contribute significantly to beta diversity. Plot age class did not have a clear influence on the significance of the contribution to beta diversity (Figure 1.2a). Among cover types, deciduous plots were the ones more likely to provide significant beta diversity, and mixedwood plots were slightly less likely to do so (Figure 1.2c).

The linear model that had the lowest AIC score and that explained the most variance in LCBD was the one that included the climate component, height and cover ( $R^2 = 0.27$ ; Table 1.2). In the top model, coniferous and mixedwood stands were negatively associated with LCBD when compared with deciduous stands, while height was positively associated with LCBD (Table 1.3). Cover type was present in the three top models. Age and density were the stand characteristics variables that performed the worst (Table 1.2). Stand characteristics appear to be more important at explaining LCBD than the climate variables we considered: the model with climate variables alone performed worse than the one that only included cover type and height. The additive model with all 4 stand characteristics considered in this study (age, height, density and cover type) performed better than all models that contained climate variables and just one stand characteristic, but performed worse than those that included climate variables and two stand characteristics. Climate variables alone (average annual temperature and annual precipitation) explained 17.06% of the observed variance in LCBD, although the contribution of precipitation was minimal (Table 1.2).

### **Alpha diversity analysis**

A total of 53 tree species were sampled across all sample plots, with a maximum of 15 tree species recorded and an average of  $4.75 \pm 2.08$  tree species per plot ( $\pm$  corresponds to standard deviation). Observed plot-level Shannon's structural diversity varied between 0 and 1.79 and had a plot average value of  $1.09 \pm 0.36$ . Plot-level functional dispersion estimates varied between 0 and 0.27 and had an average value of  $0.13 \pm 0.06$ . A functional dispersion value of 0 corresponds to plots where only a single tree species was recorded.

Among the deciduous forest groups, species richness ( $\overline{SR} = 5.24 \pm 0.33$ ) was quite homogeneous, regardless of age or height class (Figure 1.3a). Functional dispersion ( $\overline{FDIS} = 0.118 \pm 0.012$ ) was more variable, although no clear patterns with age and height class were observed. Shannon's diversity, however, varied substantially between groups of different age classes ( $\overline{H'_{all}} = 1.16 \pm 0.13$ ;

$\overline{H'_{50y}} = 1.02 \pm 0.10$ ;  $\overline{H'_{70y}} = 1.18 \pm 0.04$ ;  $\overline{H'_{90y}} = 1.21 \pm 0.08$ ;  $\overline{H'_{120y}} = 1.29 \pm 0.04$ ), and variability between groups of different height appeared only within age classes (Figure 1.3b).

Mixedwood stand groups were the richest in functional diversity ( $\overline{FDis} = 0.165 \pm 0.005$ ) but, as with deciduous stands, age and height did not appear to have a substantial impact (Figure 1.3a). On average, taller mixedwood groups had more species ( $\overline{SR_{all}} = 5.55 \pm 0.59$ ;  $\overline{SR_{\geq 22m}} = 6.40 \pm 0.41$ ), and the impact of age on species richness was only substantial when height classes were accounted for (Figure 1.3a). These roles were reversed with regards to Shannon's diversity: age appeared to be the most important variable affecting Shannon's diversity and the effect of height was only apparent when age classes were also considered ( $\overline{H'_{all}} = 1.18 \pm 0.14$ ). Stands belonging to the oldest age class had particularly higher structural diversity than other stands ( $\overline{H'_{120y}} = 1.32 \pm 0.06$ ; Figure 1.3b).

Among the coniferous stands, species richness ( $\overline{SR_{all}} = 3.52 \pm 1.30$ ;  $\overline{SR_{\geq 22m}} = 6.15 \pm 0.36$ ), Shannon's structural diversity ( $\overline{H'_{all}} = 0.903 \pm 0.214$ ;  $\overline{H'_{\geq 22m}} = 1.353 \pm 0.004$ ) and functional dispersion ( $\overline{FDis_{all}} = 0.099 \pm 0.037$ ;  $\overline{FDis_{\geq 22m}} = 0.151 \pm 0.003$ ) increased with height, and stands belonging to the tallest height class were more biodiverse (Figure 1.3). The impact of age was only apparent when height classes were taken into account. Disregarding the tallest plots, coniferous stands were the poorest in terms of biodiversity for all three measures.

The alpha diversity network formed by linking equivalent groups presented a non-trivial structure with 18 components (i.e. the number of independent linked nodes) of different size and connectivity (Figure 1.4). In comparison, a network where equivalence between nodes is based on age class groups, would have consisted of only four components (one for each age class), each fully connected. When equivalence was based on the three biodiversity measures, stand groups were solely connected to stand groups of the same cover type, as shown by the absence of links crossing different shaded areas in Figure 1.4. Regarding height and age, stand groups were almost exclusively linked with those of adjacent classes, resulting in components having, on average, two nodes of degree 1. Only one pair of stand groups belonging to the oldest age class was classified as equivalent in terms of biodiversity. These two groups belonged to adjacent height classes. As revealed by the number of dark green nodes linked to nodes of a different colour, six stand groups from the oldest age class were not significantly different from stand groups of other age classes from the same or from the succeeding height class (Figure 1.4). Two of these groups were related to more than one type of younger stand groups, which corresponded to the shortest oldest classes within deciduous and mixedwood forests (as identified by the number 3) and to the age class 61-80 years (as identified by yellow). Height appeared to be a

particularly important indicator of biodiversity within the coniferous forest (Figures 1.3, 1.4; blue shaded area), where all connections were established between equally tall stands of different ages and where no stands of the same age class were linked. This is shown by the links between nodes of the same number. Eight stand groups were significantly distinct from all other stands in terms of biodiversity, but no pattern was apparent within this subset.

## Discussion

Developing management strategies that accomplish better trade-offs between forest exploitation and ecosystem sustainability has become a major preoccupation for forest ecologists and managers. Age structure targets, currently employed in many forest management systems in boreal and northern temperate forests, were not designed to capture all facets of biodiversity (compositional, structural and functional), and may be limited indicators of forest ecosystem function and resilience. In this study, we analysed alpha and beta tree diversity to examine the need to develop complementary forest management biodiversity indicators that would help better reflect ecosystem sustainability.

We found a very weak correlation between stand age and significant contributions to tree beta diversity. Indeed, stands belonging to the tallest height category were much more likely to be biologically unique than those belonging to the oldest age class. This is possibly because older stands are not necessarily more unique and more niches are available in taller stands. For instance, old boreal stands within our study area are often dominated by one or two species, namely black spruce and balsam fir (unpublished data). Despite their age, they are unlikely to provide significant contributions to tree diversity on a landscape scale. Therefore, stands in the tallest height class are much more likely to represent distinct ecological communities not easily found elsewhere within the same landscape.

Separating the impact of climate from that of stand-level characteristics on biodiversity is challenging due to their correlation. We have addressed this issue by considering climate as a predictor when modelling site-level contribution to beta diversity and by running the same list of models with and without this climate component. Stand-level characteristics, particularly cover type and, to a lesser degree, stand height, appeared to explain changes in beta diversity better than climate throughout our study area. Climate does have an important impact on forest communities: it influences key stand attributes such as height, and it dictates the characteristics of predominant natural disturbances (e.g., Bergeron et al., 2004). However, stand cover is a direct consequence of the type of ecological community: coniferous and deciduous stands represent inherently distinct communities, regardless of climate. This effect is further amplified when other stand characteristics are considered

simultaneously. For instance, stands of different heights support distinct types of communities, and stands of different heights and cover types even more so. Hence, while climate exerts a considerable effect on site-level contribution to beta diversity, the stand characteristics of the ecological communities themselves have a more significant impact at the scale of our study area (i.e. at a regional scale).

Overall, age class on its own mainly influenced Shannon's diversity within deciduous and mixedwood stands, which supports previous findings on the influence of forest age on tree structural diversity (e.g. Harper et al., 2003). Differences in structural diversity were much better explained when age class was considered simultaneously with that of height. This synergy between age class and height has two possible explanations. First, different stands of the same type can follow distinct successional pathways (Bergeron et al., 2014). For instance, the traditional successional pathway within boreal mixedwood stands can be accelerated by partial disturbance of the initial broadleaf cohort. Indeed, in the “three cohort” model, broadleaf-dominated stands slowly transition to mixed stands and then progress to conifer stands dominated by spruce, balsam fir or white cedar (Bergeron, 2000). Hence, two similarly-aged stands can be significantly distinct in terms of species composition and forest structure. Second, numerous age-independent, height-influencing variables can have substantial impacts on stand-level attributes and biodiversity. Particularly, soil characteristics (Laliberté et al., 2013), climate (Albert and Schmidt, 2010) and pollution (Grantz et al., 2003) all influence site-level productivity and, consequently, stand height.

Coniferous stands belonging to the tallest height class had higher biodiversity values than all other coniferous stand groups. This occurred likely because these stands are predominantly found in the more biodiverse southern part of our study area, while all other coniferous stands are much more evenly spread (Appendix 1.C). The results from the tallest coniferous class notwithstanding, in coniferous stands, the impacts of age and height on tree diversity were even more disparate than in deciduous and mixedwood stands: height classes were strikingly relevant, whereas the impact of age on tree diversity was somewhat lacking. This could be caused by the significant role successional changes appear to play in boreal forest productivity: Anyomi et al., (2014) showed that, within the northern part of our study area, site index, a height-based productivity measure, is mainly determined by species composition and stand structural diversity, instead of direct climatic effects. Stands can follow distinct successional pathways and, within the same pathway, can progress at different speeds. Consequently, stand age is not necessarily a good indicator of successional stage. Stand height however, is directly influenced by successional stage and is also directly linked to stand-level

productivity. As more productive sites tend to be more species rich (Mittelbach et al., 2001), stand height should be taken into account when selecting sites that contribute disproportionately to ecosystem function. The greater importance of this variable within the coniferous forest is likely caused by the existence of less productive sites to the north of our study area: as there is greater productivity variability among sites, stands of the same age are more likely to belong to different height classes than in areas where productivity is less variable. These findings are unlikely to be significantly affected by management type or bioclimatic domain, as we repeated the alpha diversity analysis independently for each bioclimatic domain. These domains are subjected to distinct management strategies: while partial cutting is predominant in the south, clear cutting is much more common in the north (Appendix 1.B).

Our analysis reinforces the importance of considering compositional, structural and functional diversity when comparing distinct forest communities. Employing indicators of all these three components was essential to accurately detect significant intergroup differences between deciduous, mixedwood and coniferous stand groups. A single biodiversity measure would have been unable to detect most of these differences, regardless of the type of biodiversity considered. Using only functional diversity and compositional or structural biodiversity would have enabled us to detect most differences between groups, but would have prevented us from properly assessing intergroup diversity. Functional diversity was essential in distinguishing deciduous from mixedwood stands, as these two usually possess similar structural and compositional diversity, but mixedwood stands tend to be significantly richer in functional diversity.

Forests are obviously not managed at the stand level nor at the scale of our study area: forest on public land in North America is usually divided into several forest management units (FMUs) of varying sizes (Kaya et al., 2016). It is within these FMUs, or subunits when FMUs are particularly large, that forest age structure targets can be applied (Bettinger et al., 2009). Stand cover, height and age characteristics vary between FMUs. Hence, stand group contributions to biodiversity are likely to change among them. For instance, coniferous stands in a deciduous-dominated landscape are much more likely to contain species rarely found elsewhere within that FMU than within an FMU located in a coniferous-dominated landscape. While the main findings of this study are likely to hold within each FMU, more detailed interactions among stand groups are likely to change. Such FMU-specific differences could be analysed using the methodology applied here in order to inform decision makers and lead to more sustainable forest management.

Our results suggest that forest management strategies that are uniquely based on forest age structure targets might not be sufficient to maintain ecosystem sustainability. Such targets were designed with the idea that stands older than rotation age will be harvested and therefore such stands will become an issue for biodiversity in forests managed for timber (Bergeron et al., 2002). Numerous studies have found that some rare or endangered species do rely on older forests to survive (e.g. Molina et al., 2006) and therefore minimum amounts of older forests need to be maintained in managed forests. This is one of the main reasons forest age structure targets have been implemented in forest management and they appear to perform remarkably in that regard. However, they were not designed with the objective of maintaining overall ecosystem sustainability and, as such, they are not its most accurate indicator.

## **Conclusions**

Better understanding differences between biodiversity levels of different forest age classes and examining the potential of juvenile and mature secondary stands to harbor significant levels of biodiversity are both highly relevant areas of research that should lead to more efficient trade-offs between forest exploitation, ecosystem functioning and environmental conservation. We recommend that forest management should be improved by complementing forest age structure targets with the inclusion of additional, significant and easily measurable variables, such as cover type and stand height, and by developing complementary biodiversity indicators more directly related to ecosystem sustainability. We also recommend that further research should: (i) examine the relationships between stand variables easily available from forest inventories, such as stand height, and biodiversity indicators of other taxa; and (ii) focus on integrating indicators of biodiversity related to ecosystem structure and function in the design of forest management strategies and models of annual allowable cut estimations.

## **Acknowledgements**

This work was funded by the Fonds de recherche du Québec, Nature et technologies (FRQ-NT). We would like to thank the Forest Complexity Modelling program, which is funded by NSERC through its CREATE program, and the Fonds Produits forestiers Résolu for supporting this project. We would also like to thank the Canada Foundation for Innovation (CFI), the Ministère de l'Économie, de l'Innovation et des Exportations du Québec (MEIE), the RMGA and the Fonds de recherche du Québec - Nature et technologies (FRQ-NT) for funding the operation of the Guillimin supercomputer.

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doi:10.1080/00220973.1987.10806451

## Tables and figures

**Table 1.1.** Stand-level age classes, height classes, cover types and canopy cover density classes considered. Age is measured in years, height in meters and canopy cover density in percentage of crown cover.

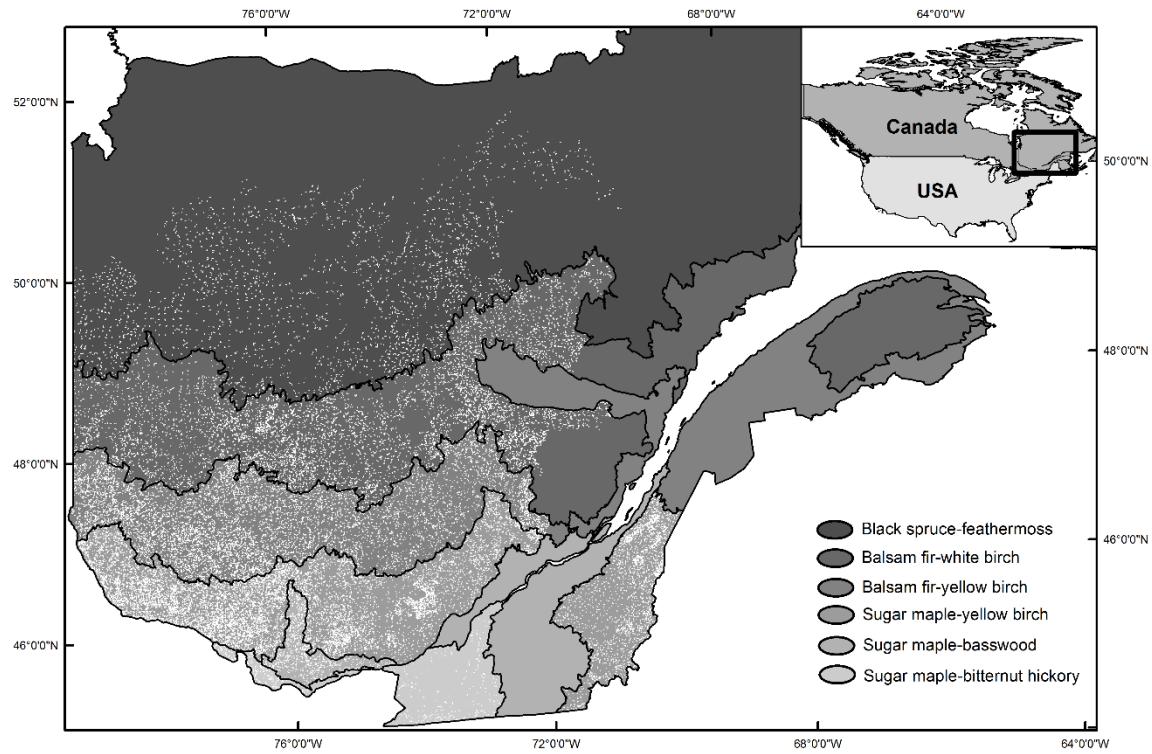
Age class		Height class		Cover type		Density class	
<b>50</b>	41y ≤ age ≤ 60y	<b>4</b>	7m ≤ height < 12m	<b>F</b>	Deciduous	<b>D</b>	25% ≤ dens < 40%
<b>70</b>	61y ≤ age ≤ 80y	<b>3</b>	12m ≤ height < 17m	<b>M</b>	Mixedwood	<b>C</b>	40% ≤ dens < 60%
<b>90</b>	81y ≤ age ≤ 100y	<b>2</b>	17m ≤ height < 22m	<b>C</b>	Coniferous	<b>B</b>	60% ≤ dens < 80%
<b>120</b>	age ≥ 101y	<b>1</b>	height ≥ 22m			<b>A</b>	dens ≥ 80%

**Table 1.2.** Linear regression models of plot-level local contribution to beta diversity (LCBD). Explanatory variables include average annual temperature (Tavg), annual precipitation (precip), age class (age), cover type (cover), height class (height) and canopy cover density (density). R squared is the adjusted R squared in %. ΔAIC is the AIC difference between the top model and the corresponding model.

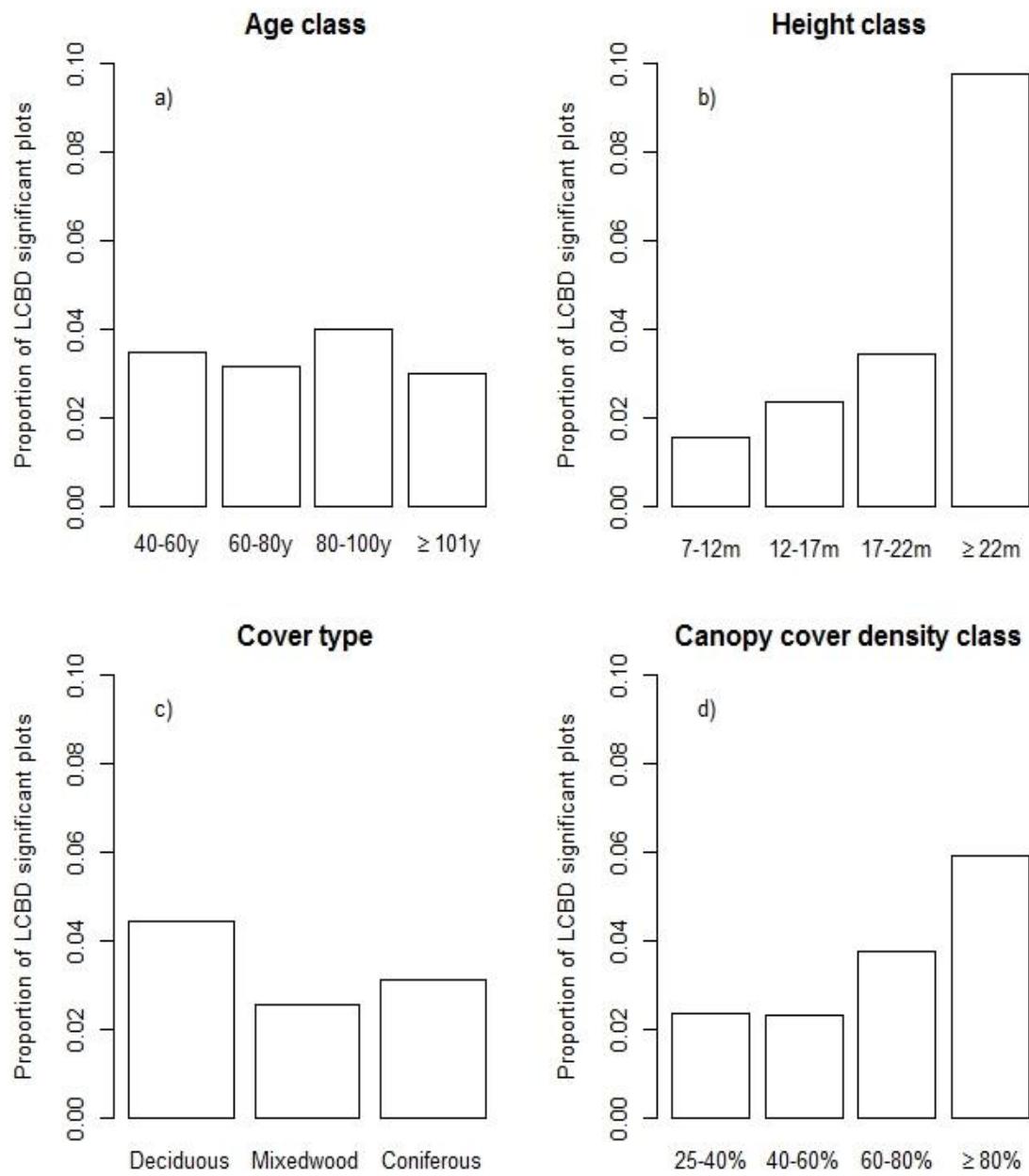
Model structure	R squared	AIC	ΔAIC
<b>LCBD ~ Tavg + Precip + Height + Cover</b>	27.08	419480.6	0
<b>LCBD ~ Tavg + Precip + Age + Cover</b>	25.25	421941.1	2460.5
<b>LCBD ~ Tavg + Precip + Density + Cover</b>	25.05	422210.5	2729.9
<b>LCBD ~ Tavg + Precip + Cover</b>	24.42	423045.3	3564.7
<b>LCBD ~ Tavg + Precip + Height + Density</b>	23.72	423963.3	4482.7
<b>LCBD ~ Tavg + Precip + Age + Height</b>	22.45	425603.4	6122.8
<b>LCBD ~ Age + Height + Cover + Density</b>	22.13	426008.5	6527.9
<b>LCBD ~ Tavg + Precip + Height</b>	21.99	426180.5	6699.9
<b>LCBD ~ Tavg + Precip + Age</b>	20.71	427804.7	8324.1
<b>LCBD ~ Height + Cover</b>	20.44	428136.5	8655.7
<b>LCBD ~ Tavg + Precip + Density</b>	19.01	429903.3	10422.8
<b>LCBD ~ Tavg + Precip + Age</b>	18.25	430825.3	11344.7
<b>LCBD ~ Tavg + Precip</b>	17.06	432254.8	12774.2
<b>LCBD ~ Tavg</b>	16.96	432376.2	12895.7
<b>LCBD ~ Height + Density</b>	16.67	432732.7	13252.1
<b>LCBD ~ Density + Cover</b>	16.27	433200.7	13720.1
<b>LCBD ~ Age + Cover</b>	15.51	434094.5	14613.9
<b>LCBD ~ Cover</b>	14.79	434933.7	15453.1
<b>LCBD ~ Age + Height</b>	14.41	435387.4	15906.8
<b>LCBD ~ Height</b>	13.57	436345.9	16865.3
<b>LCBD ~ Age + Density</b>	6.93	443699.4	24218.8
<b>LCBD ~ Density</b>	4.83	445912.9	26432.3
<b>LCBD ~ Precip</b>	1.89	448931.2	29450.6
<b>LCBD ~ Age</b>	1.34	449489.1	30008.5

**Table 1.3.** Coefficients from the top linear effects model of LCBD. SE denotes standard error. The reference level for the cover type variable is deciduous and the reference level for the height class is height greater than or equal to 22m.  $H$  stands for height. \* denotes significant variables.

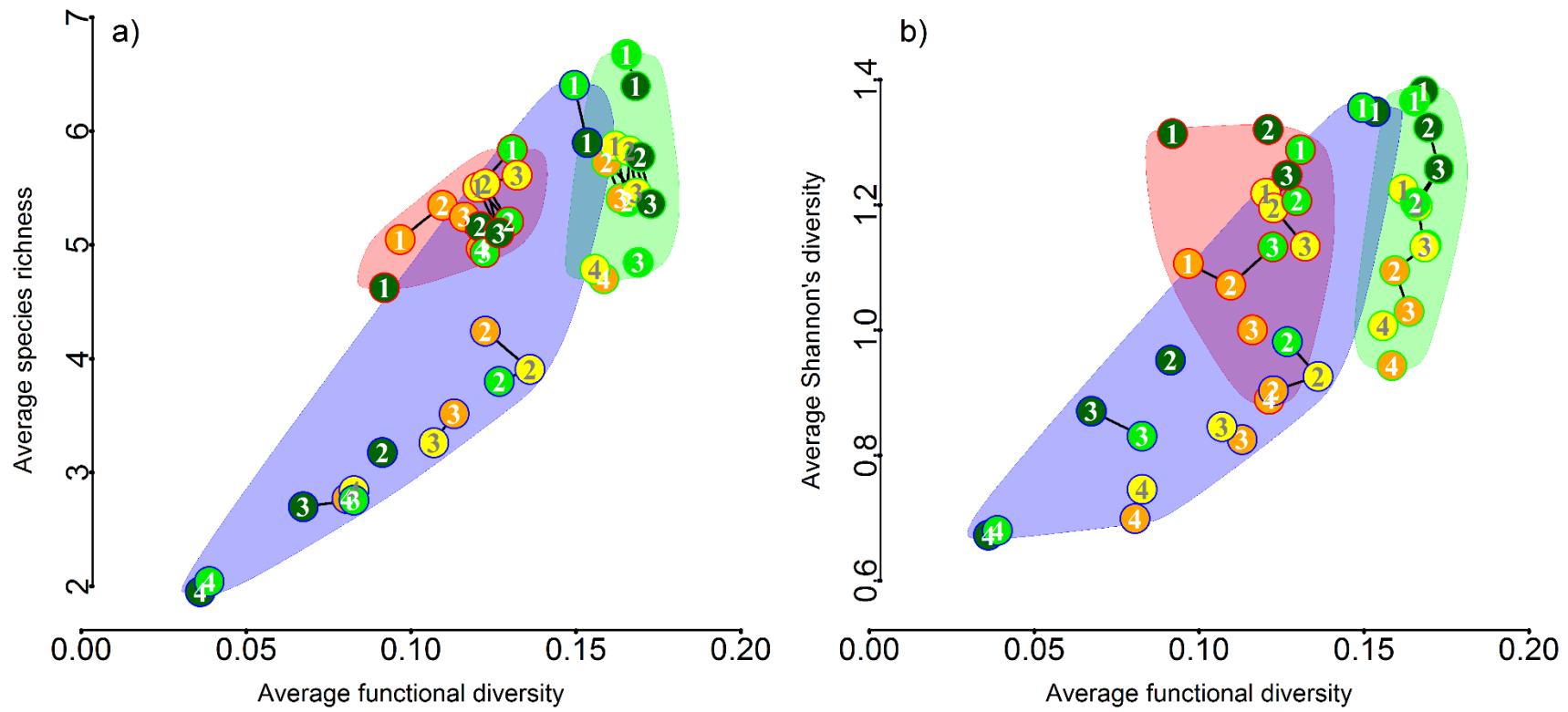
		<i>Estimate</i>	<i>SE</i>	<i>p-value</i>
	<i>Intercept</i>	10.3941	0.0649	<b>0*</b>
	<i>Temperature</i>	0.4517	0.0050	<b>0*</b>
	<i>Precipitation</i>	0.0006	0.0001	<b>0*</b>
<i>Cover type</i>	<i>Mixed</i>	-1.3585	0.0163	<b>0*</b>
	<i>Coniferous</i>	-0.9998	0.0202	<b>0*</b>
	<i>17m ≤ H &lt; 22m</i>	-0.8089	0.0262	<b>0*</b>
<i>Height class</i>	<i>12m ≤ H &lt; 17m</i>	-1.4483	0.0272	<b>0*</b>
	<i>7m ≤ H &lt; 12m</i>	-1.5769	0.0346	<b>0*</b>



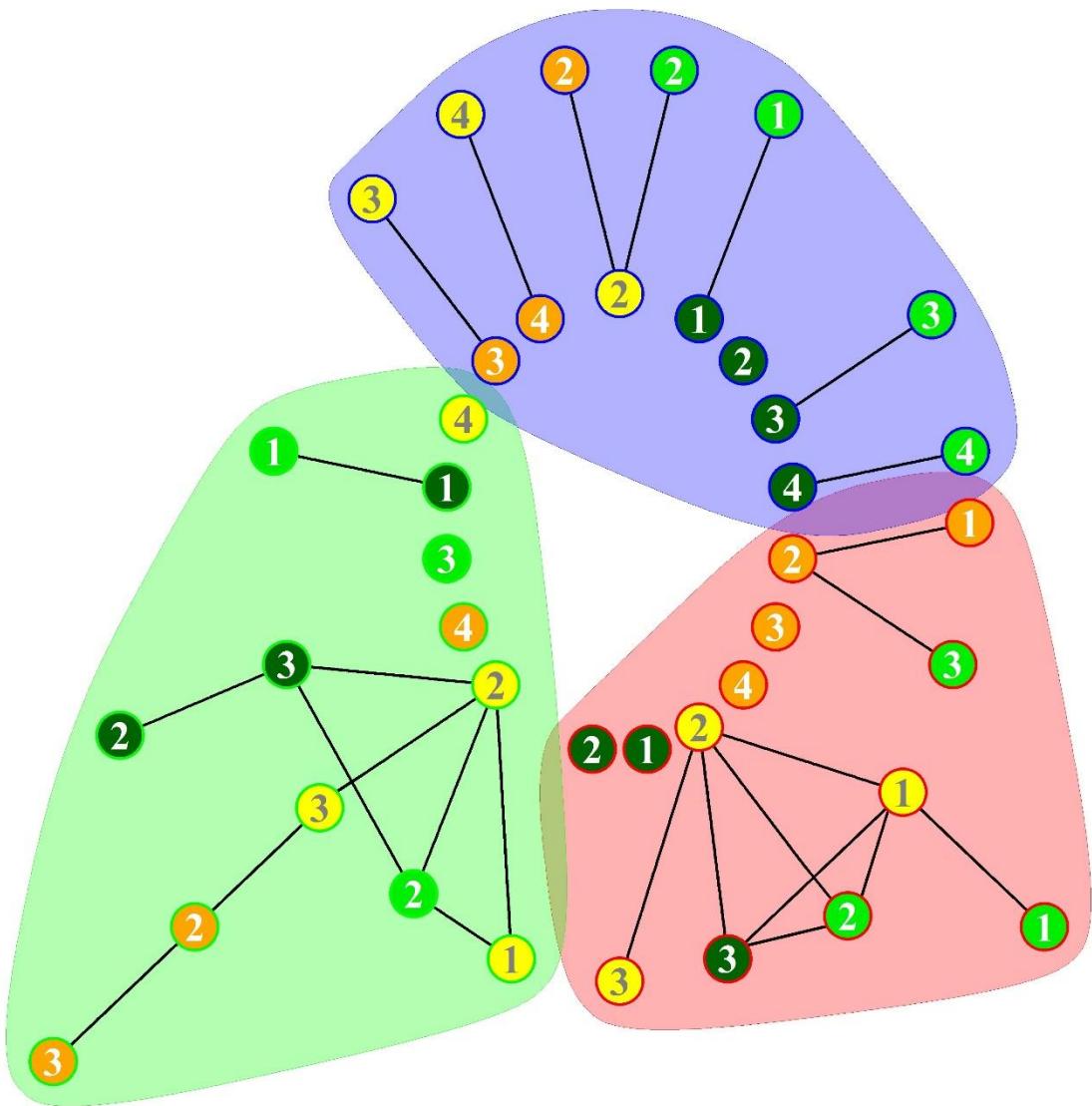
**Figure 1.1.** Map of the study area: western Québec, Canada . White points represent permanent and temporary sample plots. Black lines delimit bioclimatic domains.



**Figure 1.2.** Proportion of plots whose local contribution to beta diversity (LCBD) is significant according to: a) age class; b) height class; c) cover type; and d) canopy cover density class. P-values were calculated from 5000 permutations following the previously described methodology. All intervals are open below and closed above.



**Figure 1.3.** Stand tree alpha diversity plotted per cover type according to: (a) functional diversity and species richness; and (b) functional diversity and Shannon's structural diversity. Nodes linked by black lines have non-significant differences in terms of three tree diversity measures (species richness, Shannon's structural diversity and functional dispersion) according to our network-based analysis. The unscaled network can be seen in Figure 1.4 Node colours represent stand age classes (**orange**: 41-60 years; **yellow**: 61-80 years; **green**: 81-100 years; **dark green**: over 100 years old). Numbers represent height classes (1: height  $\geq 22m$ ; 2:  $17m \leq \text{height} < 22m$ ; 3:  $12m \leq \text{height} < 17m$ ; 4:  $7m \leq \text{height} < 12m$ ). Background shading and node frame colour represent cover type (**red**: deciduous stands; **green**: mixedwood stands; **blue**: coniferous stands).



**Figure 1.4.** Unscaled results of the network visualization analysis . Symbol labelling follows the code described in Figure 1.3.

## Supplementary material

### Appendix 1.A. Functional trait data and sources.

	maxH	GR	LS	WD	WDR	VR	SM	ST	DT	WT	LL	LMA	NLM
<i>Abies balsamea</i>	25	1	1	0,34	1	1	2,151762203	5	1	2	4,7	151	1,66
<i>Acer negundo</i>	20	3	4	0,44	1	1	3,555348061	3,5	3	2,8	1,609	37,04	2,5
<i>Acer nigrum</i>	30	2	3	0,52	1	1	4,189654742	3	3,4	1,5	1,609	70,63	1,83
<i>Acer pensylvanicum</i>	10	1	3	0,44	1	1	3,737669618	3,5	2	1	1,609	42,65	2,22
<i>Acer rubrum</i>	25	3	3	0,49	1	1	3,044522438	3,4	1,8	3,1	1,717	71,09	1,91
<i>Acer saccharinum</i>	35	3	3	0,44	1	1	5,539115853	3,6	2,88	3,37	1,609438	36	2,36
<i>Acer saccharum</i>	35	1	3	0,56	1	1	4,189654742	4,8	2,3	1,1	1,705	70,63	1,83
<i>Acer spicatum</i>	5	2	3	0,44	1	2	3,017773404	3,3	2	2	1,609438	30,6	2,49
<i>Alnus rugosa</i>	5	2	2	0,37	1	2	0,350656872	1	2	2,9	1,569	67,14	2,98
<i>Betula alleghaniensis</i>	25	3	2	0,55	1	1	0,703097511	3,2	3	2	1,705	46,08	2,2
<i>Betula papyrifera</i>	25	3	2	0,48	1	1	0,285178942	1,5	2	1,3	1,281	77,88	2,31
<i>Betula populifolia</i>	12	3	2	0,45	1	1	0,104360015	1,5	2,3	1	1,792	58,44	1,79
<i>Carpinus caroliniana</i>	8	1	2	0,58	1	0	2,63905733	4,6	2	2,3	2,041	49,05	2,15
<i>Carya cordiformis</i>	25	1	4	0,6	1	0	7,979681302	2,1	4	2,5	1,609	44,05	2,6
<i>Carya ovata</i>	25	1	4	0,64	1	2	8,421883012	3,4	3	1,38	1,722767	68,39116	2,09
<i>Celtis occidentalis</i>	12	2	2	0,49	1	1	4,65646348	3,5	3,85	2,65	1,704748	82,64463	2,8919
<i>Cornus alternifolia</i>	10	2	4	0,58	1	1	4,039856377	2	1,77	1,02	1,609438	40	1,7
<i>Fagus grandifolia</i>	25	1	2	0,56	1	2	5,659482216	4,8	1,5	1,5	1,609	61,22	2,04
<i>Fraxinus americana</i>	30	2	4	0,55	1	1	3,828641396	2,5	2,4	2,6	1,74	76,75	2,12
<i>Fraxinus nigra</i>	20	2	4	0,45	1	1	4,077537444	3	2	3,5	1,609	71,94	2,1
<i>Fraxinus pennsylvanica</i>	25	3	4	0,53	1	1	3,496507561	3,1	3,9	3	1,609	87,72	1,8
<i>Juglans cinerea</i>	25	3	4	0,36	1	0	9,623839785	1,9	2,4	1,3	1,609	60,98	2,6
<i>Juglans nigra</i>	30	3	4	0,51	3	1	9,338173743	1,9	2,38	1,83	1,609438	32,78689	2,96
<i>Juniperus virginiana</i>	15	1	1	0,44	3	1	2,341949817	1,28	4,65	1,19	3,627633	333,3333	1,64
<i>Larix laricina</i>	25	3	1	0,48	2	0	0,955511445	1	2	3	1,792	120	1,36

<i>Ostrya virginiana</i>	12	1	2	0,63	1	1	2,772588722	4,6	3,3	1,1	1,609	37,04	2,2
<i>Picea abies</i>	40	1	1	0,38	1	0	2,091864062	4,5	1,8	1,2	4,277	235,18	1,19
<i>Picea glauca</i>	25	1	1	0,35	1	0	1,147402453	4,2	2,9	1	3,912	302,86	1,28
<i>Picea mariana</i>	20	1	1	0,41	1	2	0,741937345	4,1	2	2	3,807	294,12	1,12
<i>Picea rubens</i>	25	2	1	0,38	1	0	1,458615023	4,4	2,5	2	4,637	304,67	1,15
<i>Pinus banksiana</i>	20	3	1	0,42	1	0	1,504077397	1,4	4	1	3,296	243,9	1,24
<i>Pinus resinosa</i>	25	3	1	0,39	1	0	2,272125886	1,9	3	1	3,584	294,12	1,17
<i>Pinus rigida</i>	30	3	1	0,47	1	2	2,162823151	2	4	2	3,496508	204,499	1,16
<i>Pinus strobus</i>	30	3	1	0,36	2	0	2,890371758	3,2	2,3	1	2,996	121,92	1,42
<i>Pinus sylvestris</i>	28	2	1	0,395	1	0	1,801809805	2	4,34	2,63	3,338748	243,3905	1,304714
<i>Populus balsamifera</i>	25	3	2	0,37	1	1	0,262364264	1,3	1,8	2,6	1,281	83,46	1,95
<i>Populus deltoides</i>	30	3	3	0,35	1	1	0,832909123	1,8	1,6	3	1,609	88,18	2,39
<i>Populus grandidentata</i>	20	3	2	0,39	1	1	0,165514438	1,2	2,5	2	1,609	70,45	2,5
<i>Populus tremuloides</i>	25	3	2	0,37	1	1	0,139761942	1,2	1,8	1,8	1,582	82,02	2,16
<i>Prunus pensylvanica</i>	12	3	3	0,36	1	1	3,496507561	1	2	1	1,609	50	2,4
<i>Prunus serotina</i>	22	3	2	0,47	3	0	4,553876892	2,5	3	1,1	1,705	72,3	2,48
<i>Prunus virginiana</i>	9	3	2	0,36	1	1	4,521788577	2,6	2,9	1,1	1,609	84,03	2,8
<i>Quercus alba</i>	35	1	3	0,6	3	0	8,172164452	2,9	3,6	1,4	1,609	81,21	2,39
<i>Quercus bicolor</i>	22	3	3	0,64	3	0	8,237743804	3	3,4	2,6	1,609	86,98	2,33
<i>Quercus macrocarpa</i>	15	1	3	0,58	3	0	8,707978827	2,7	3,9	1,8	1,792	92,74	2,27
<i>Quercus rubra</i>	25	2	3	0,56	2	1	8,197263371	2,8	2,9	1,1	1,792	84,2	2,06
<i>Sorbus decora</i>	10	1	4	0,42	1	1	1,271538124	2,6	1,77	1,27	1,609438	63,97	2,17
<i>Thuja occidentalis</i>	15	1	1	0,3	3	2	0,832909123	3,5	2,7	1,5	3,497	223	1,02
<i>Tilia americana</i>	35	2	3	0,32	1	1	2,772588722	4	2,9	1,3	1,609	60,81	2,94
<i>Tsuga canadensis</i>	30	1	1	0,4	1	0	2,312535424	4,8	1	1,3	4,094	122,55	0,99
<i>Ulmus americana</i>	35	3	3	0,46	1	1	2,00148	3,1	2,9	2,5	1,775	79,47	2,07
<i>Ulmus rubra</i>	25	3	3	0,48	1	1	2,493205453	3,3	3	1,7	1,609	59,88	2,5
<i>Ulmus thomasii</i>	25	2	2	0,57	1	1	2,014903021	3,2	2	1	1,609	64,1	2,3

## **Label codes**

**maxH:** Average maximum height (meters)

**GR:** Growth rate (1: slow; 2: moderate; 3: rapid)

**LS:** Leaf size (1: needle/scale; 2: small <10cm; 3: large; 4: compound)

**WD:** Wood density (g/cm<sup>3</sup>)

**WDR:** Wood decay resistance (1: not; 2: moderate; 3: resistant; 4: very resistant)

**VR:** Vegetative reproduction capacity (0: never; 1: possible; 2: common)

**SM:** Seed mass (mg)

**ST:** Shade tolerance (1: very intolerant, 2: intolerant, 3: medium tolerance, 4: tolerant, 5: very tolerant)

**DT:** Drought tolerance (1: very intolerant, 2: intolerant, 3: medium tolerance, 4: tolerant, 5: very tolerant)

**WT:** Waterlogging tolerance (1: very intolerant, 2: intolerant, 3: medium tolerance, 4: tolerant, 5: very tolerant)

**LL:** Leaf longevity (months)

**LMA:** Leaf mass per area (g/m<sup>2</sup>)

**NLM:** Nitrogen content per leaf mass unit (%)

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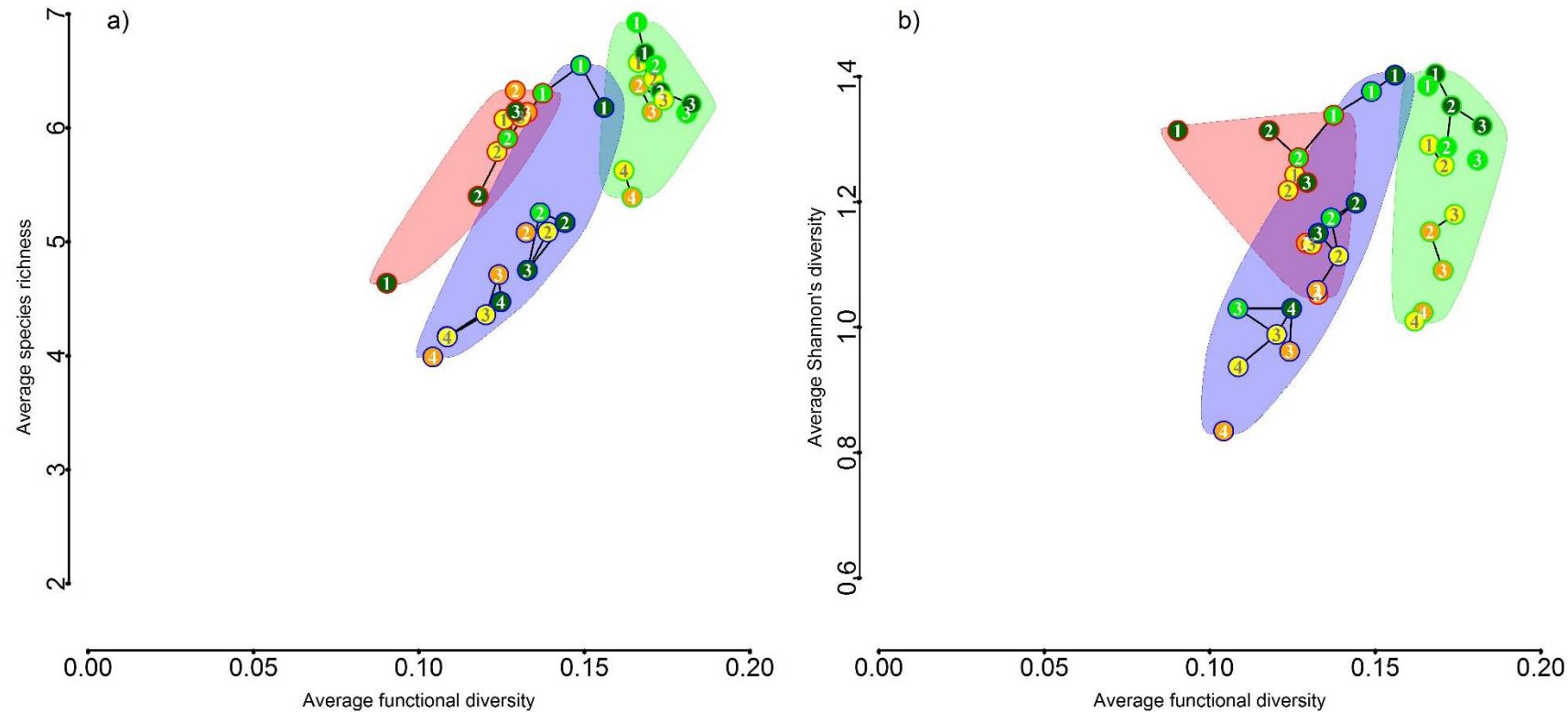
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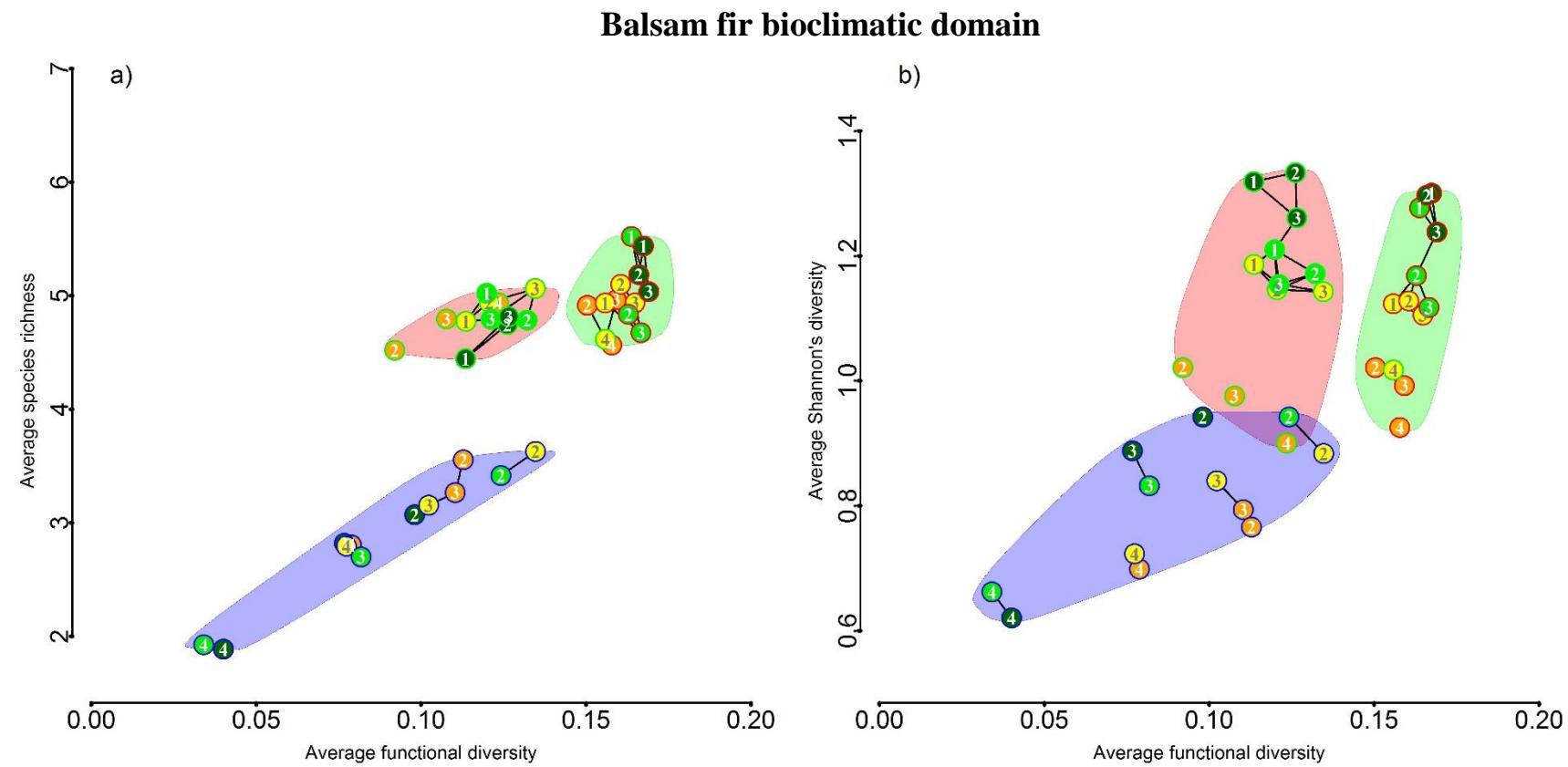
## Appendix 1.B. Scaled and unscaled network analyses by bioclimatic domain

**Appendix 1.B.1.** Sugar maple bioclimatic domain stand tree diversity plotted per cover type according to: (a) functional diversity and species richness; and (b) functional diversity and Shannon's structural diversity.

**Sugar maple bioclimatic domain**

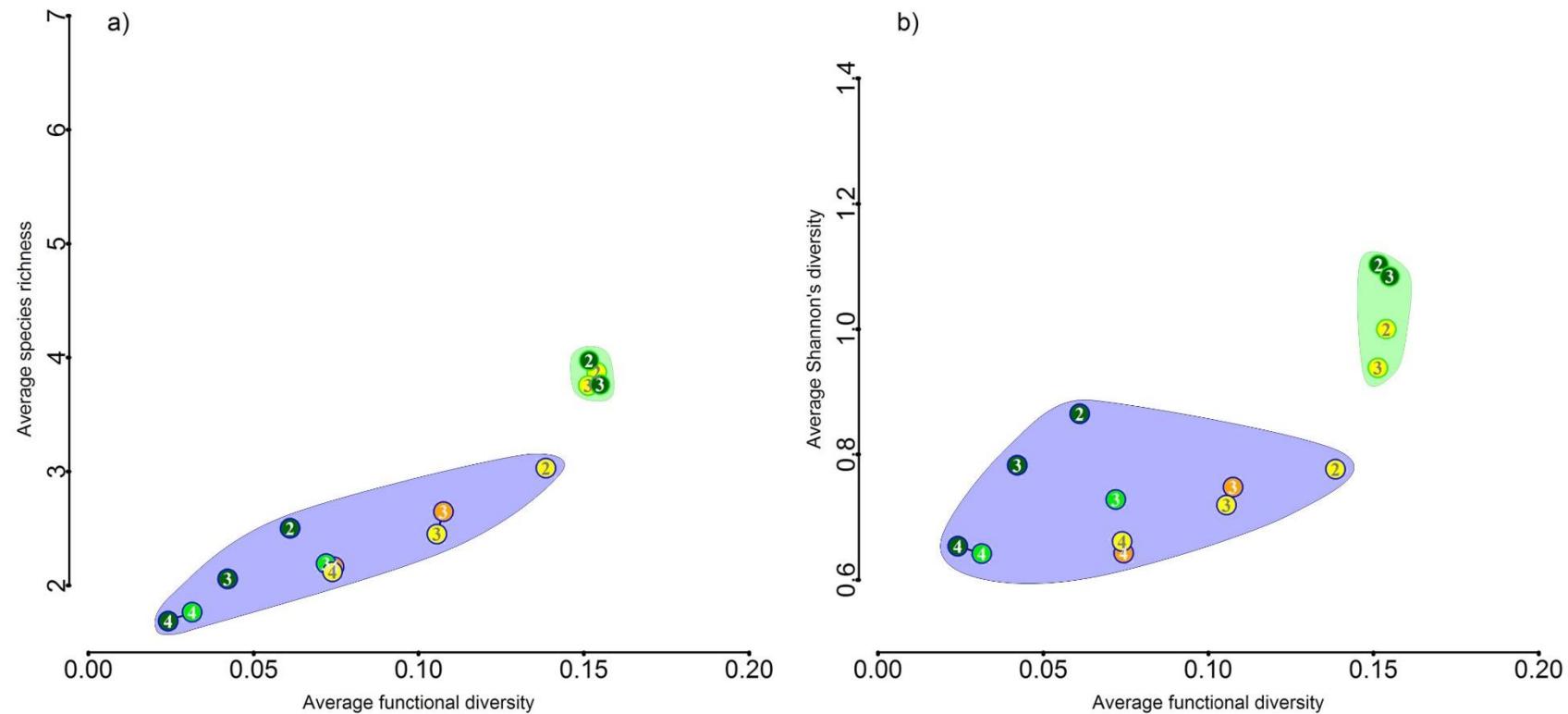


**Appendix 1.B.2.** Balsam fir bioclimatic domain stand tree diversity plotted per cover type according to: (a) functional diversity and species richness; and (b) functional diversity and Shannon's structural diversity for the Balsam fir bioclimatic domain.



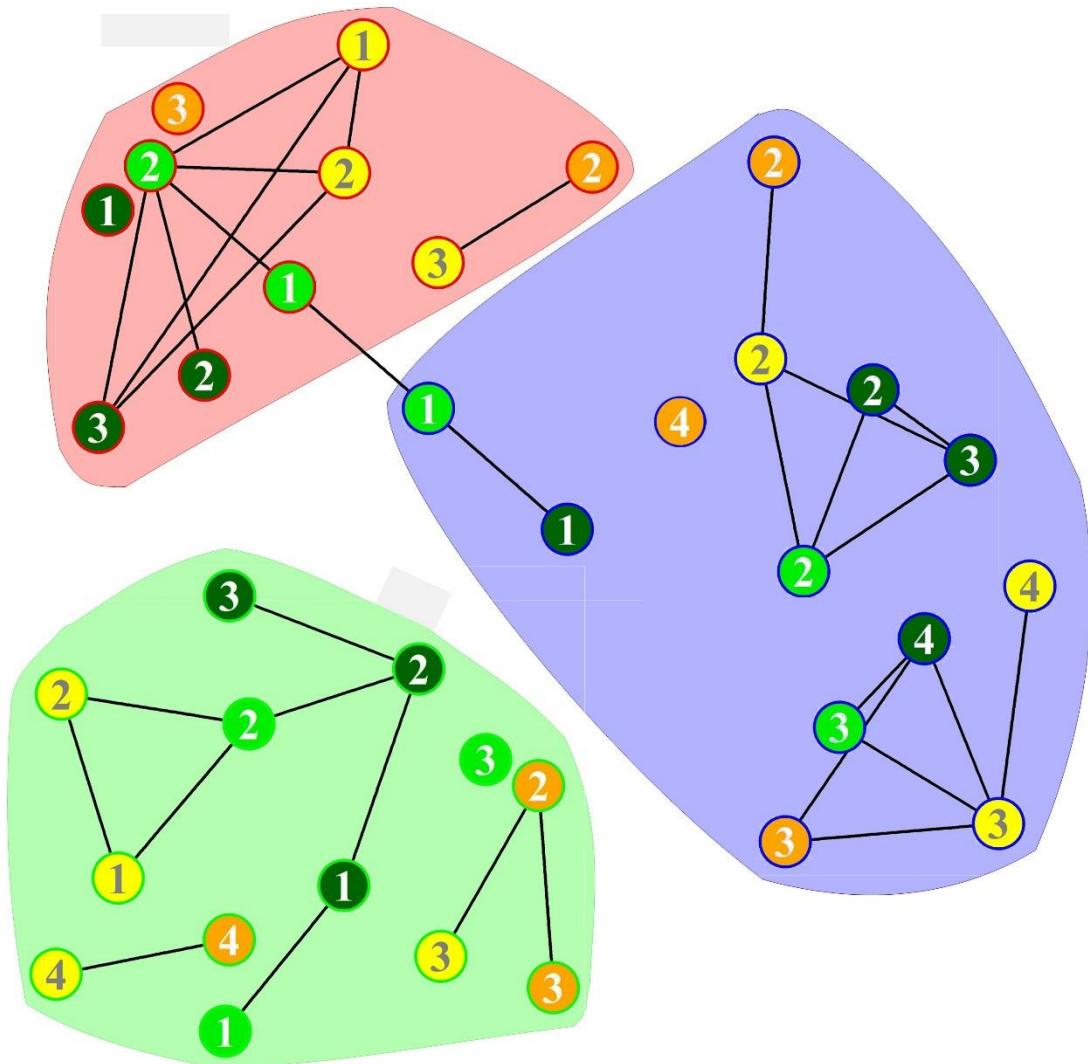
**Appendix 1.B.3.** Black spruce bioclimatic domain stand tree diversity plotted per cover type according to: (a) functional diversity and species richness; and (b) functional diversity and Shannon's structural diversity.

### Black spruce bioclimatic domain



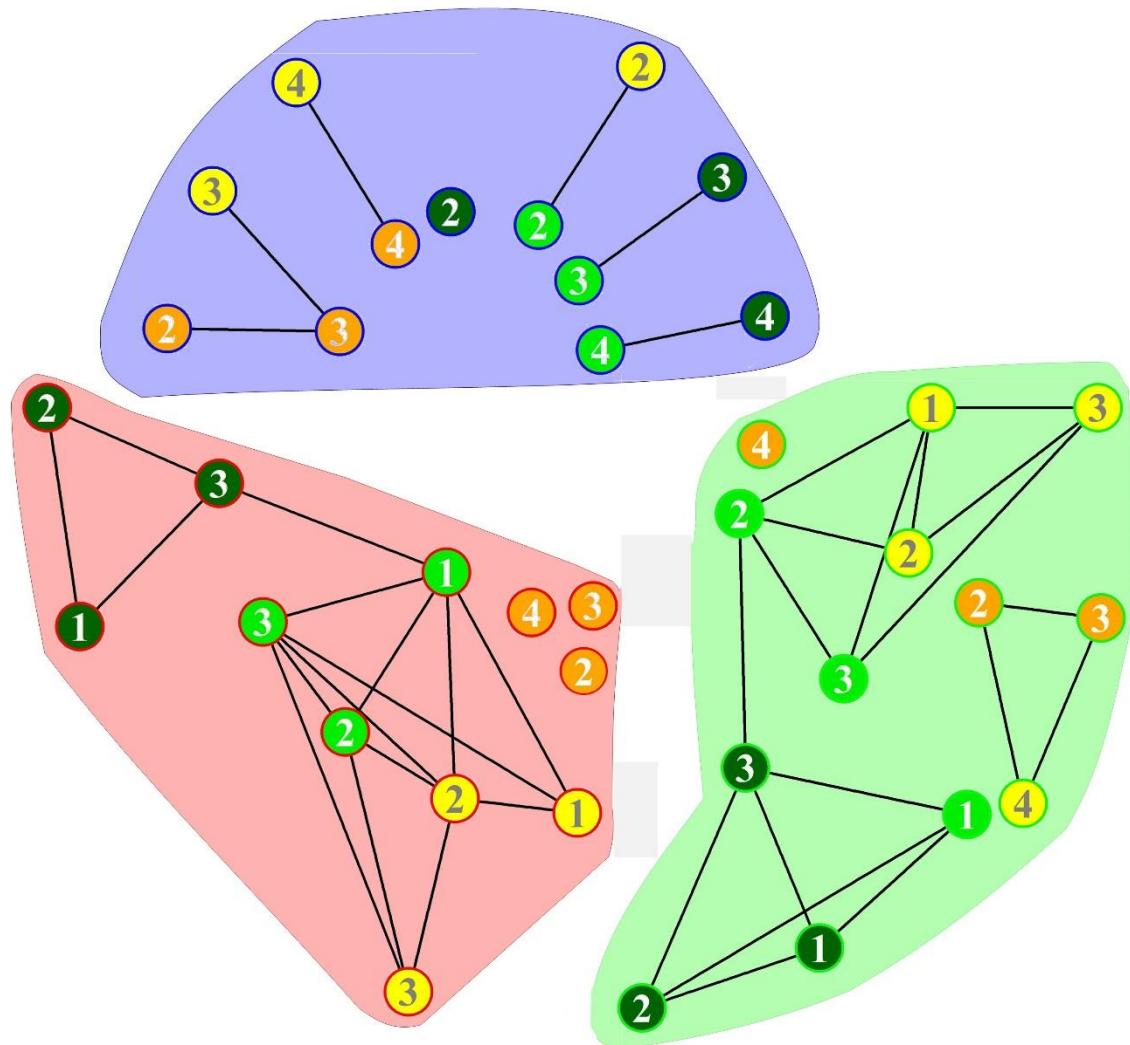
**Appendix 1.B.4.** Sugar maple bioclimatic domain unscaled results of the network analysis.

Sugar Maple

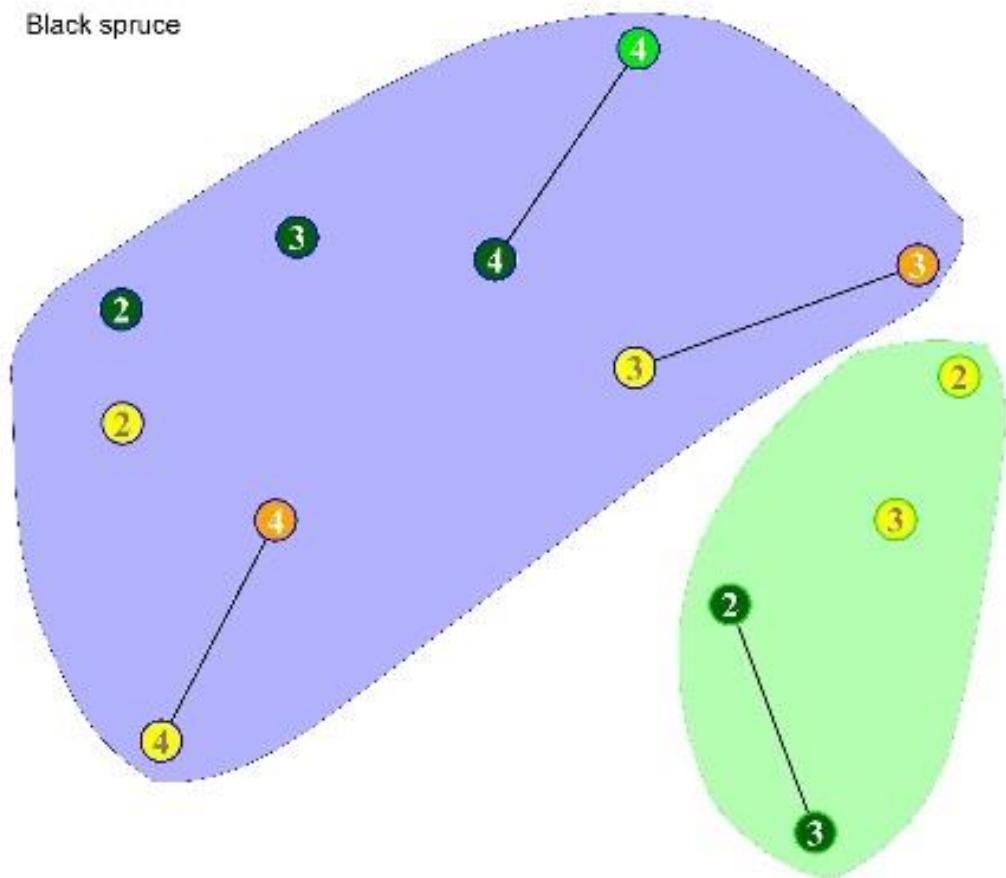


**Appendix 1.B.5.** Balsam fir bioclimatic domain unscaled results of the network analysis.

Balsam fir

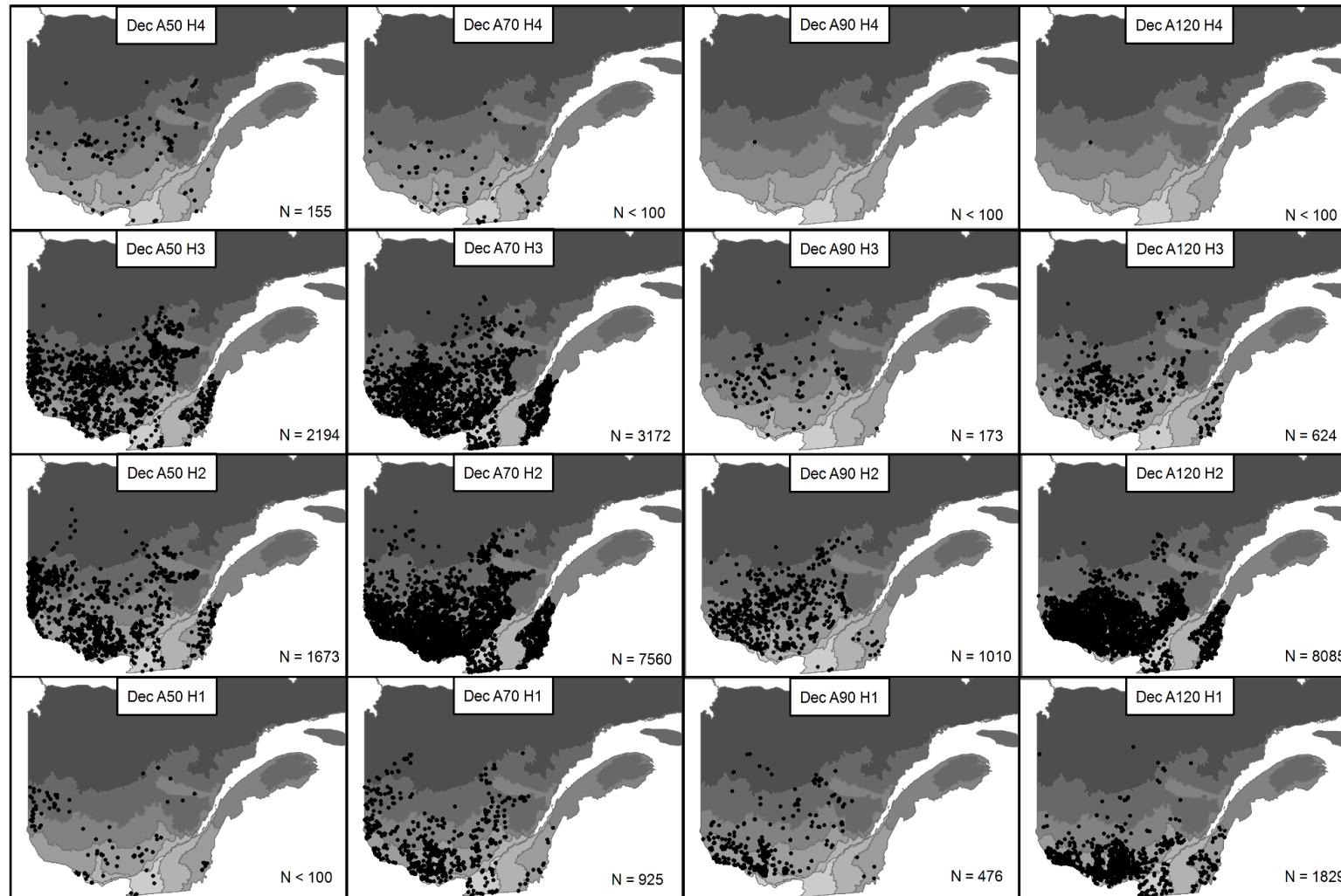


**Appendix 1.B.6.** Black spruce bioclimatic domain unscaled results of the network analysis.

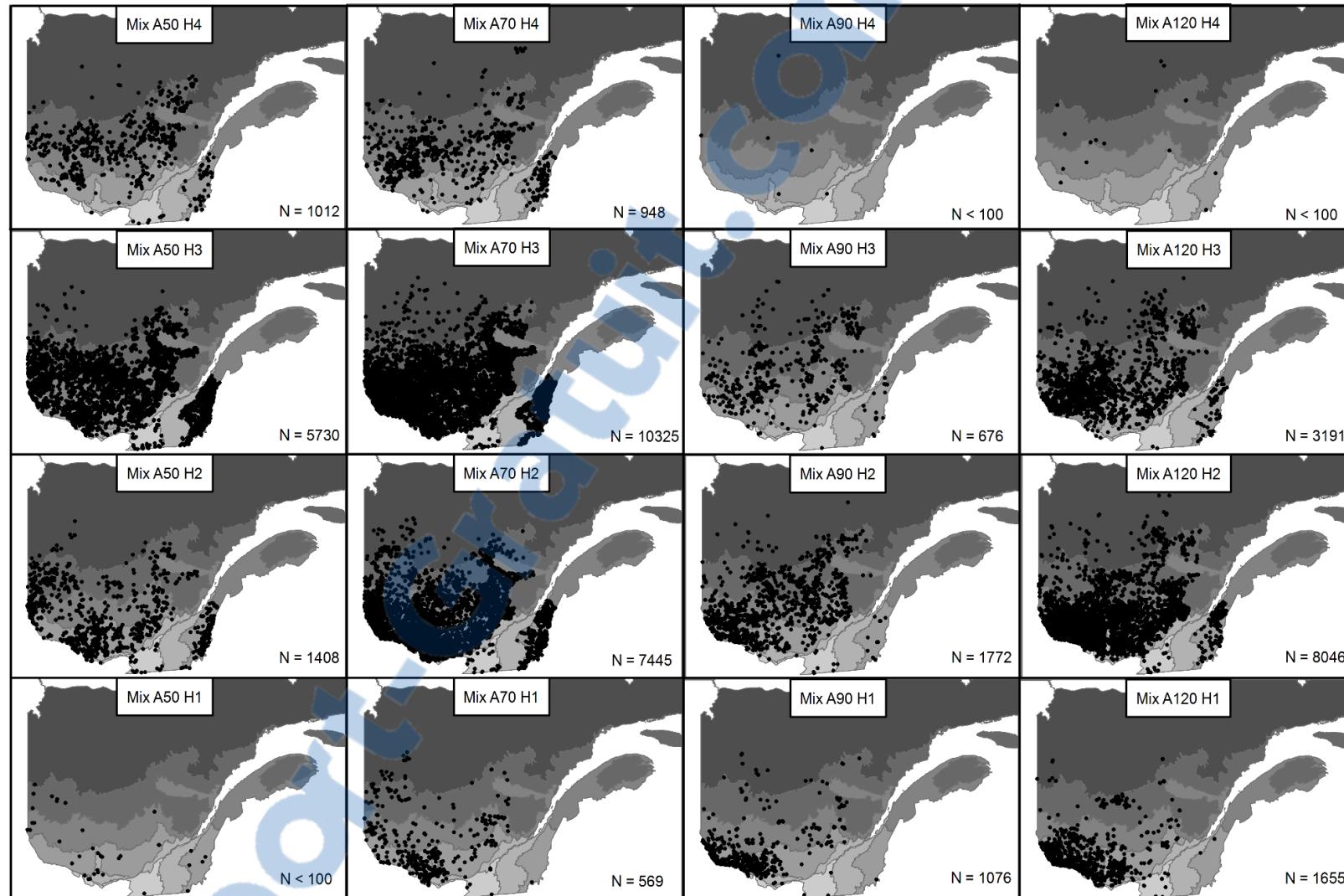


### Appendix 1.C. Map of plots per cover type, age class and height class

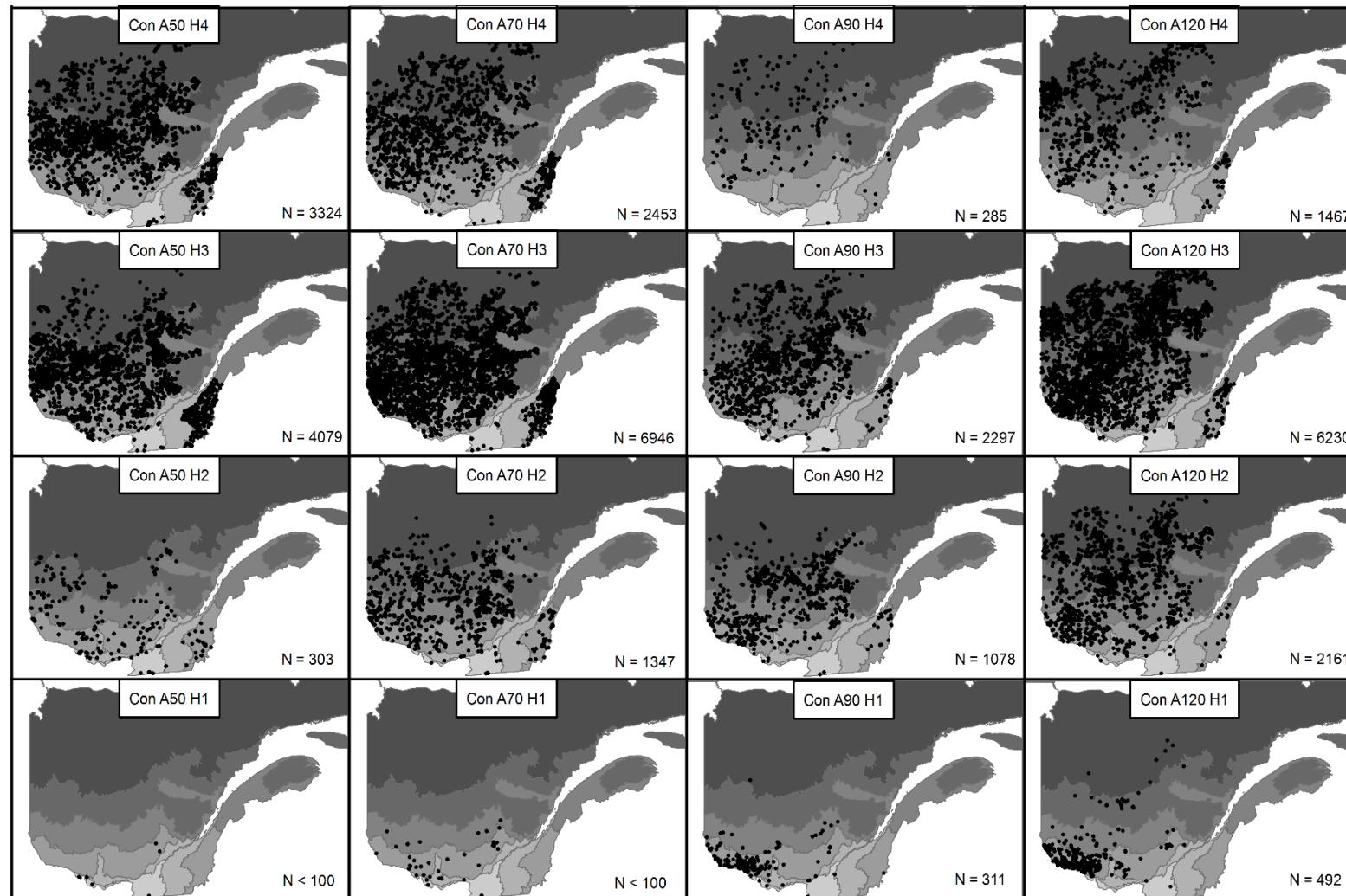
**Appendix 1.C.1.** Deciduous sample plots per age and height class. In the title of each subplot *Dec* stands for deciduous, *A* stands for age class and *H* stands for height class. N is the number of plots per group. The classes are the same as the ones identified in the manuscript.



**Appendix 1.C.2.** Mixedwood sample plots per age and height class. In the title of each subplot *Mix* stands for mixedwood, *A* stands for age class and *H* stands for height class. N is the number of plots per group. The classes are the same as the ones identified in the manuscript.



**Appendix 1.C.3.** Coniferous sample plots per age and height class. In the title of each subplot *Con* stands for coniferous, *A* stands for age class and *H* stands for height class. N is the number of plots per group. The classes are the same as the ones identified in the manuscript.



## **Chapitre 2: Response diversity, functional redundancy and post-logging productivity in northern temperate and boreal forests**

### **Résumé**

Le développement d'indicateurs de résilience des écosystèmes est essentiel pour l'amélioration des stratégies d'aménagement durable des forêts. Des études récentes suggèrent que la redondance fonctionnelle (RF) et la diversité des réponses (DR), deux indicateurs de la diversité des arbres associés au fonctionnement de l'écosystème, pourraient être utilisées comme indicateurs de la résilience des communautés forestières face à diverses perturbations. L'objectif de ce chapitre était d'examiner la relation entre ces deux indicateurs et la productivité suivant une coupe totale dans les forêts du Québec. La productivité a été mesurée par la variabilité saisonnière du Enhanced Vegetation Index, une mesure courante de la productivité primaire de la biomasse végétale estimée à partir d'images satellites. De plus, j'ai testé l'hypothèse que les essences de feuillus et de conifères contribuent de façon distincte à la productivité après coupe en mesurant les deux indicateurs de diversité séparément pour chaque groupe d'essences. Le rôle de la richesse spécifique et des effets d'identité des espèces sur la réponse de la productivité après coupe ont aussi été examinés.

Cette analyse a démontré la nature complémentaire des indicateurs traditionnels de diversité et des indicateurs basés sur les traits fonctionnels lors de l'analyse de la réponse des communautés forestières à une perturbation sévère. J'ai trouvé une relation significative et positive entre la DR avant-coupe des feuillus et la productivité après coupe, ainsi qu'une relation significative et négative entre la DR des conifères et la productivité. Cette relation négative avec la productivité après coupe est probablement causée par la régénération plus lente des conifères et par la courte taille de l'intervalle de temps analysé. Les effets négatifs d'identité causés par l'épinette noire reflètent probablement la plus grande susceptibilité des peuplements dominés par cette espèce à des facteurs menant à une réduction de la productivité après coupe, comme la paludification et l'invasion par des éricacées. La diversité des réponses était un meilleur indicateur de la productivité après coupe que la redondance fonctionnelle. Cette étude est parmi les premières à trouver une relation significative négative entre la DR et le fonctionnement d'un écosystème, c'est-à-dire la DR de communautés des conifères et leur productivité après coupe.

## **Abstract**

The development of efficient ecosystem resilience indicators has been identified as one of the key research priorities in the improvement of existing sustainable forest management frameworks. Two indicators of tree diversity associated with ecosystem functioning have recently received particular attention in the literature: functional redundancy (FR) and response diversity (RD). We tested the hypothesis that these indicators could be used to predict post-logging productivity in forests of Québec, Canada. We analysed the relationships between pre-logging FR and RD in temporary sample plots and post-logging productivity, measured as seasonal variation in Enhanced Vegetation Index obtained from MODIS satellite imagery. The effects of the deciduous and coniferous tree components in our pre-disturbance diversity assessments were isolated in order to examine the additional hypothesis that they have different impacts on post-disturbance productivity. The role of tree species richness and species identity effects were also examined.

Our analysis revealed the complementary nature of traditional biodiversity indicators and trait-based approaches in the study of biodiversity-ecosystem functioning relationships in dynamic ecosystems. We report a significant and positive relationship between pre-disturbance deciduous RD and post-disturbance productivity, as well as an unexpected significant negative effect of coniferous RD on productivity. This negative relationship with post-logging productivity likely results from slower coniferous regeneration speeds and from the relatively short temporal scale examined. Negative black spruce-mediated identity effects were likely associated with increased stand vulnerability to paludification and invasion by ericaceous shrubs that slow down forest regeneration. Response diversity outperformed functional redundancy as a measure of post-disturbance productivity most likely due to the stand-replacing nature of the disturbance considered. To the best of our knowledge, this is among the first studies to report a negative significant relationship between a component of RD and ecosystem functioning, namely coniferous RD and forest ecosystem productivity after a stand-replacing disturbance.

## **Introduction**

Natural and anthropogenic transformations of forest ecosystems threaten their capacity to sustain the provision of numerous ecological services (MacDicken et al., 2015, Thom and Seidl 2016). In the face of such uncertainty, the development of efficient resilience indicators capable of predicting ecosystem response to disturbances has been identified as one of the key research priorities in the improvement of existing sustainable forest management frameworks (Mori et al., 2016). Specifically, developing indicators capable of predicting primary productivity following natural and anthropogenic disturbances could be a very useful step towards that goal. While primary productivity is not the only ecosystem service provided by forests, it is considered to be a main concern of forest management (Mori et al., 2016), since it is one of the key supporting ecosystem processes other services depend on (Millennium Ecosystem Assessment 2005). For instance, primary productivity regulates the strength of cascading effects of large herbivores on community function and structure (Pringle et al., 2007), and directly influences carbon dynamics (Hulvey et al., 2013). Preventing the decline of forest productivity following harvesting is therefore of particular interest to forest managers (Bose et al., 2014).

Tree diversity has been shown to play a fundamental role in temperate and boreal forest productivity (Liang et al., 2016). In these types of forest, species richness positively influences biomass production across all vegetation layers (Zhang et al., 2017). This relationship is stronger for overstory tree species richness, which is also positively associated with ecosystem multifunctionality and understory plant species richness (Gamfeldt et al., 2013). Primary productivity is also significantly affected by the traits of the dominant species due to species identity effects (Grossman et al., 2017). While compositional and functional tree diversity have been shown to contribute to forest productivity (Zhang et al., 2012), these two components of biodiversity can be independent of one another and have distinct impacts on ecosystem functioning. For instance, in an experimental study where functional diversity was allowed to vary independently from tree species richness, Tobner et al., (2016) showed that stands with identical species richness and greater functional diversity can be significantly more productive. Such discrepancies can be further magnified when the impact of disturbances is considered: following the flooding of a grassland experimental study, species richness reduced plant community resistance to flood while functional traits drove post-disturbance increase in biomass (Fischer et al., 2016).

Functional diversity is particularly suited to studying biodiversity-ecosystem functioning relationships under disturbances because they define mechanistic links between biodiversity and function, including responses to disturbances (Cadotte et al., 2011). However, due to the large number

of indicators available (Laliberté & Legendre 2010), indicator selection is highly dependent on the objective of the study. Two particularly promising functional diversity-based indicators of ecosystem resilience to disturbances have been highlighted by recent reviews on this subject: functional redundancy (FR) and response diversity (RD; e.g. Mori et al., 2016, 2013). The concept of FR is based on the insurance hypothesis put forward by Yachi and Loreau (1999): ecosystem functioning should be less affected by the absence or extinction of a species that can be replaced by another one that contributes similarly to ecosystem functioning, than by one for which no analogue is readily available. RD represents the different capacity that species within a given functional effect group (i.e. species that perform similar functions) have to respond to disturbances (Mori et al., 2013). In theory, greater inter-specific variation in responses to environmental fluctuations within each functional effect group should prevent disturbances from eliminating the majority of a given functional group, thus ensuring the preservation of the corresponding ecosystem functions (Elmqvist et al., 2003).

To date, empirical evidence demonstrating the ability of RD and, to a lesser degree, FR, to be adequate indicators of resilience to disturbances is still scarce, especially for forest ecosystems (Mori et al., 2016). The few real-world studies that do exist tend to be limited in scope and scale (Mori et al., 2013), or tend to indirectly test the linkages between functional traits and ecosystem functioning (e.g. Laliberté et al., 2010). Additionally, studies of the importance of RD in other taxa are not always conclusive (e.g. Cariveau et al., 2013). Although experimental studies on the relationships between FR, RD and ecological resilience are more common, they usually focus on grassland ecosystems (e.g. Pillar et al., 2013) and their ability to infer real-world biodiversity-ecosystem functioning relationships is restricted. Among other issues, such studies typically exclude disturbances that substantially influence biodiversity-ecosystem functioning relationships (Brose and Hillebrand 2016).

We present a large-scale empirical study of northern temperate and boreal forest plots in Québec (eastern Canada) aiming to improve our understanding of the real-world relationships between pre-disturbance functional diversity indicators (functional redundancy, response diversity) and post-disturbance productivity trajectories within a management-relevant context. We treat deciduous and coniferous species as two functional effect groups because they contribute differently to ecosystem productivity, they are easily identified by forest managers, and changes in their composition should greatly influence ecosystem processes and services (see *Functional effect groups* section in the methodology). We examined forest plots recovering from logging to test the hypothesis that pre-disturbance coniferous and deciduous functional redundancy and response diversity are good indicators of post-disturbance productivity. We calculated these functional diversity indexes per

functional effect group in order to test the additional hypothesis that these groups have different impacts on post-disturbance productivity. We also controlled for tree species richness and species identity effects in order to assess whether trait-based approaches improve our understanding of biodiversity-ecosystem functioning when these traditional approaches are considered. In order to test this hypothesis, we built 10-year time series of EVI (enhanced vegetation index), a remotely sensed primary productivity indicator (Huete et al., 2002), for forest plots of Québec that were clear-cut immediately before the beginning of the time series. We further discussed underlying mechanisms driving these relationships and explored the management implications of our results.

## Methodology

### Study area

We quantified pre-disturbance tree functional diversity metrics from temporary sampling plots selected from the Quebec provincial forest inventory programs conducted between 1992 and 2009 (MFFP 2016). Among these plots, a subset was selected according to four criteria. First, plots had to have been clear cut between 2000 and 2006 after they had been measured, so that an uninterrupted 10-year post-disturbance time series of MODIS data was available. Hence, the 10-year time series started between 2000 and 2006 and ended between 2011 and 2015. Second, in order to test the hypothesis that functional effect groups were important for determining post-disturbance productivity, plots needed to include at least one species from each group (deciduous and coniferous species). Both groups had to be present because Rao quadratic diversity, the measure used to calculate response diversity, can only be calculated when all functional groups are present. Otherwise, missing values are generated (Laliberté & Legendre 2010). Third, we discarded plots sampled over 10 years before they were clear cut. For all other plots, we considered unlikely that forest communities underwent key changes within 10 years if no stand-replacing disturbances occurred. Finally, only temporary plots located in MODIS (Moderate-resolution imaging spectroradiometer) 250 m pixels where over 80% of the area had undergone the same disturbance were kept. If the majority of a neighboring MODIS pixel had been clear cut but the pixel in which the temporary plot was positioned had not, the plot was associated with the neighboring MODIS pixel instead.

A total of 796 plots were selected according to these criteria (Figure 2.1). These plots were spread across a latitudinal gradient that encompasses multiple bioclimatic domains: sugar maple-bitternut hickory (*Carya cordiformis*), sugar maple-yellow birch (*Betula alleghaniensis*), balsam fir (*Abies balsamea*)-yellow birch, balsam fir-white birch (*Betula papyrifera*) and black spruce (*Picea mariana*)-feathermoss (Robitaille and Saucier 1998). Each plot consisted of a circular area of 400 m<sup>2</sup>.

Within this area, all trees whose diameter at breast height (DBH) was greater than 9 cm were recorded and their DBH was measured (MFFP 2016). A smaller 40 m<sup>2</sup> circular plot in which all saplings (DBH ≤ 9 cm) were identified and counted by DBH class was located at the center of each 400 m<sup>2</sup> plot. Sampling effort varied between main vegetation zones (deciduous, coniferous and mixed) and followed a random stratified design (MFFP 2016).

### Functional effect groups

We adopted a hierarchical effect-response functional trait framework to analyse the relationships between tree functional redundancy, response diversity and ecosystem productivity (e.g. Laliberté *et al.*, 2010). We first employed an unsupervised hierarchical clustering algorithm to identify functional effect groups using 6 effect traits: (i) average maximum height; (ii) leaf phenology (whether species lose all foliage seasonally or not); (iii) nutrient uptake strategy (presence of arbuscular mycorrhiza, ectomycorrhizal, or both); (iv) nitrogen content per leaf mass unit; (v) wood density; and (vi) leaf mass per area (R's stats package *hclust* algorithm; R Core Team 2016). These traits are publicly available (e.g., Paquette *et al.*, 2015) and have been suggested as effect traits associated with tree growth, photosynthetic rate and productivity (Cornelissen *et al.*, 2003). The clustering algorithm followed Ward's minimum variance method and was applied to a Gower dissimilarity matrix (caret R package, version 6.0-62; Kuhn, 2015). A visual inspection of the resulting dendrogram (Appendix 2.A) revealed two main functional effect groups: coniferous and deciduous species.

Considering deciduous and coniferous species as having distinct effects on forest productivity and, more generally, on function, makes sense for a number of reasons. First of all, species within these two groups support distinct animals (e.g., Drapeau *et al.*, 2000) and can be conceived of as ‘umbrella’ species that reflect functional diversity in the understory layers (Fourrier *et al.*, 2015). Secondly, coniferous species have greater leaf mass per area, which is associated with longer leaf lifespan, increased leaf defences and reduced decomposition, growth and maximum photosynthetic rates (Appendix 2.B; Cornelissen *et al.*, 2003). Thirdly, wood density, which is associated with carbon storage capacity, relative growth rate and stem defences (Cornelissen *et al.*, 2003), tends to be greater in deciduous species (Appendix 2.B). Finally, coniferous species have a narrower range of average maximum height (Appendix 2.B), a functional trait that has been linked to competitive vigour, stress response strategies and aboveground biomass (Cornelissen *et al.*, 2003).

### Functional redundancy and response diversity

We measured each deciduous and coniferous pre-disturbance functional redundancy (FR) and response diversity (RD) on each identified plot following the framework and code provided by Ricotta

et al., (2016). FR was estimated with the six previously mentioned effect traits used to establish the functional effect groups: average maximum height, leaf phenology, nutrient uptake strategy, nitrogen content per leaf mass unit, wood density and leaf mass per area. The following seven functional response traits were used to estimate RD: average maximum height, growth rate, wood density, vegetative reproduction capacity, seed mass, shade tolerance and capacity to establish seed banks. These response traits are directly associated with tree regeneration speed and strategies: these influence tree species ability to colonize sites after disturbance and are key aspects of post-disturbance recovery (Cornelissen et al., 2003). Deciduous and coniferous response diversity were calculated for each plot as the Rao quadratic diversity, according to the following equation (2.1):

$$RD = \sum_i p_i \sum_j p_j \delta_{ij},$$

where  $RD$  is the Rao quadratic diversity,  $p_i$  is the relative abundance of species  $i$ ,  $p_j$  is the relative abundance of species  $j$ , and  $\delta_{ij}$  is the pairwise functional dissimilarity between species  $i$  and  $j$ . If there is only a single species in the plot, species  $j$  equals species  $i$ . This functional dispersion-based indicator estimates the average distance between two randomly selected individuals within the functional trait space (Botta-Dukat 2005). Functional redundancy was calculated as 1 minus the ratio of Rao quadratic diversity and the Simpson index according to the following equation (2.2):

$$FR = 1 - \frac{Q}{D},$$

where  $FR$  is functional redundancy,  $Q$  is Rao quadratic diversity, and  $D$  is the Simpson index. Thus, this indicator compares the observed functional diversity with that of the most functionally distinct community possible that shares an identical abundance distribution (Ricotta et al., 2016). Hence, plots dominated by a single species have a FR of 1 and a RD of 0. Gower dissimilarity matrices were chosen because they can handle both missing values and mixed variable types (continuous, ordinal and categorical). These two metrics were not re-measured after clear-cutting took place (post-disturbance period). Species response trait values were weighted by basal area relative abundance. Most trait values were collected by a previous study (Paquette et al., 2015). Missing values and additional variables were collated from other online data sources (Appendix 2.B).

### **Ecosystem productivity metric**

Post-disturbance 10-year productivity time series were built using 16-day MODIS EVI (enhanced vegetation index) data. EVI is a productivity indicator based on the surface reflectance of solar radiation that has clear links to primary productivity (Pettorelli et al., 2005). The MODISTools R

package (Tuck et al., 2014) was used to download each temporary plot's 250 m pixel EVI and pixel reliability data from the MOD13Q1 MODIS product (Didan et al., 2015). The original 16-day time series data were smoothed using TIMESAT (Jönsson and Eklundh 2004). EVI data contribution to the smoothing functions was weighted using the complementary reliability layer and outliers were removed by multiplying the weights from a seasonal trend decomposition with the original weights. Asymmetric Gaussian functions were then fit to the data. This type of function was chosen because it has been found to be among the top two performing smoother functions for this kind of dataset (Hird and McDermid 2009) and appeared to perform slightly better than the double logistic function for our dataset. The seasonal variation of EVI (maximum EVI – minimum EVI; svEVI), a productivity measure that has been shown to be significantly correlated with gross primary productivity in North America (Sims et al., 2006), was then calculated. In order to remove any badly smoothed data from the dataset, svEVI points above the 0.999 and below the 0.001 percentiles of the distribution were removed.

### Statistical analysis

Autoregressive linear regression models of svEVI (nlme R package; Table 2.1; Pinheiro et al., 2015) were built with the following explanatory variables: (i) yearly climate variables; (ii) pre-disturbance stand characteristics; (iii) year of logging; (iv) site post-disturbance land cover class at the year 2013 (deciduous, coniferous or shrubland); (v) pre-disturbance tree species richness; (vi) pre-disturbance relative abundance of the most abundant tree species of each functional group (black spruce and white birch); (vii) pre-disturbance coniferous and deciduous FR and RD; (viii) number of years since disturbance as a numeric variable; and (ix) a binary categorical variable (set at 1 for 2 to 5 years after disturbance and 0 for the remaining years) that was introduced to allow the models to more realistically consider the relationships between FR, RD and time since disturbance observed in the data. The first year after disturbance was not included in this categorical variable because the noise introduced by the time lag between the time since disturbance and the first growing season (from a few weeks up to several months) had a greater impact on the first measurement of productivity.

Plot-level yearly climate variables (average annual temperature, annual precipitation, growing degree days over 5°C, potential evapotranspiration, water balance and growing season length) were calculated using BioSIM (version 10; Régnière et al., 2014), a software tool that uses geographical coordinates, elevation, slope and aspect to interpolate climate data. Pre-disturbance stand characteristics (age class, height class, density class and cover type) were directly measured in the sampling plots (MFFP 2016). The top 3 principal components of climate and pre-disturbance stand characteristics were then extracted through Principal Component Analysis (PCA). For the PCAs, a

categorical variable (cover type) was transformed into three binary variables, ordinal variables were first transformed into numeric variables according to the middle point of each class, numeric variables were log-transformed, and data were centered by subtracting the mean and scaled by dividing the predictor values by the standard deviation (caret R package, version 6.0-62; Kuhn, 2015).

Considering that site productivity is greatly influenced by different post-logging regeneration trajectories, post-disturbance land cover class was estimated using the land cover type 3 of the MODIS MCD12Q1 product (Friedl et al., 2010). This MODIS product provides an estimate of the land cover class at a spatial resolution of 500m, which is larger than the one svEVI was estimated at, but is still likely to reflect the type of regeneration of the disturbed area. Although this MODIS product was not available for the whole time series (it ended in the year 2013 and was not available for the whole time series up to that year), its value by the year 2013 was included in the regression models as an indicator of the type of vegetation the disturbed area was likely regenerating into.

Since the identity of the tree species present can have considerable impacts on ecosystem processes (Hooper and Vitousek 1997) and it has been suggested that primary productivity can be substantially influenced by the traits of the dominant species (Grime 1998), the possible influence of species identity effects on post-disturbance productivity was also assessed. In order to do this, within-group pre-disturbance basal area relative abundance of the most abundant species within each functional group (deciduous: white birch; coniferous: black spruce) was added to the candidate model set.

A total of 10 autoregressive linear regression models with svEVI as the response variable were built. Models shared all previously mentioned variables except FR, RD and species relative abundances. These variables were added to distinct models as combinations of two groups of variables: (i) functional diversity metrics (FR and RD, FR only and RD only); and (ii) species relative abundance (none, black spruce and white birch). A null model with tree species richness but without FR, RD nor species relative abundance was also included in the candidate model set. As we were comparing models with a similar random effect structure and different fixed effect structures, models were fit with log-likelihood maximization (Burnham & Anderson 2002). All input variables were standardized to a mean of 0 and a standard deviation of 0.5 in order to set all effect sizes on comparable scales and facilitate their interpretation (Grueber et al., 2011). The temporal correlation structure of our dataset was accounted for by specifying unique plot ID as a random effect with an autocorrelation structure of order 1. The best models were selected according to the  $AIC_c$  change (second-order Akaike Information Criterion; Burnham & Anderson 2002). Model variances were

homogenous, the model residuals were normal and no multicollinearity was detected among explanatory variables (all variance inflation factors were lower than 2; Marquardt, 1970).

## Results

### Functional redundancy and response diversity

The model including coniferous and deciduous pre-disturbance response diversity and black spruce relative abundance was the top model within the main candidate model set (Table 2.1; AIC<sub>c</sub> weight = 0.97). Our analysis also shows that functional diversity can complement species richness and species identity effects in explaining post-disturbance productivity: the top model was more parsimonious than models that did not include either functional diversity or species richness, and models that considered the tree community as a whole, instead of splitting it into two functional effect groups (Appendix 2.C). The fixed component of the top model explained approximately 48% of the observed variation and the whole model explained approximately 71% (Table 2.1). All models were substantially more parsimonious than the null model that did not consider FR, RD nor any species identity effects (Table 2.1).

Our analyses revealed a significant negative relationship between coniferous RD and post-disturbance productivity (Table 2.2). Two dominant species mixtures likely mediate this relationship. First, black spruce-balsam fir dominated stands are common throughout our study area (Figure 2.2h). These plots tend to have relatively low levels of pre-disturbance coniferous RD and high levels of post-disturbance productivity (top parabola in Figures 2.3a & b). Second, balsam fir-white spruce stands are also relatively common and have high levels of pre-disturbance coniferous RD and low levels of post-disturbance productivity (bottom parabola in Figure 2.3a).

We found a significant positive relationship between pre-disturbance deciduous RD and post-disturbance productivity (Table 2.2). This result supports the initial hypothesis that increased RD should lead to increased post-disturbance productivity. While significant, the p-value of this relationship is relatively close to the commonly accepted significance threshold of 0.05. The p-value is only marginally significant probably because of the large number of plots whose deciduous component is dominated by a single deciduous species, namely white birch (Figures 2.2a & e): these plots have low values of deciduous RD and post-disturbance productivity (Figure 2.3c). Deciduous and coniferous functional redundancy were not present in the top model of our candidate model set (Table 2.1).

### **Species identity effects**

Since functional effect groups were often dominated by a single species, species identity effects were widespread in our study area. The pre-disturbance deciduous effect group of approximately 38% of all plots ( $n = 299$ ) was dominated by a single species (white birch). This resulted in a large number of plots with maximal pre-disturbance deciduous functional redundancy (FR; Figure 2.2a) and minimal pre-disturbance deciduous response diversity (RD; Figure 2.2c). White birch is a species of particular interest, since it dominated the deciduous component in 25.6% of the plots in our dataset ( $n = 204$ ; Figure 2.e).

The coniferous functional effect group was less dominated by any single species, but significant species identity effects were still present. Hence, fewer plots had maximal levels of pre-disturbance coniferous FR (Fig. 2b) and minimal levels of pre-disturbance coniferous RD (Fig. 2d). Nevertheless, black spruce and balsam fir were particularly dominant within the coniferous functional effect group: over three quarters of the coniferous basal area was occupied by black spruce and balsam fir in 69.6% of our plots ( $n = 554$ ; Fig. 2h).

Black spruce identity effects appear to play an important role in post-disturbance productivity: black spruce relative abundance was a significant variable negatively correlated with post-disturbance productivity (Table 2.2). Black spruce relative abundance also appears to be negatively associated with coniferous RD, as plots where black spruce was less dominant tended to have greater levels of pre-disturbance coniferous RD (Figure 2.3b). Direct white birch identity effects on post-disturbance productivity do not appear to be significant: models containing this variable were considerably less parsimonious than the top model (Table 2.1).

### **Discussion**

The complementarity between traditional species-oriented biodiversity indicators, such as species richness, and functional diversity indicators reported in this study highlights the contribution of trait-based approaches to the study of biodiversity-ecosystem functioning relationships. While the complementarity between these facets of biodiversity and tree productivity has been reported elsewhere (e.g. Paquette & Messier 2011), few studies have explicitly addressed these relationships with respect to disturbances. For example, a simulation study of a temperate central European forest found that the positive effects of tree species richness on net primary productivity resilience to simulated natural disturbances was likely mediated by changes in functional diversity (Pedro et al., 2015). However, direct effects of changes in functional diversity were not assessed. As functional

diversity indicators can be independent of species richness (Ricotta et al., 2016), it is important to take into account both contributions when studying biodiversity-ecosystem relationships.

The absence of pre-disturbance functional redundancy (FR) from the top model is possibly due to the severity of the analysed disturbance. According to Yachi & Loreau (1999), FR should be an efficient indicator of ecosystem resilience to disturbances because the impact of the loss of a given species on ecosystem functioning should be reduced when there are multiple species performing similar functions. Indeed, this hypothesis appears to hold when partial disturbances are considered (e.g. Pillar et al., 2013). However, as our results suggest, this is unlikely to be the case when severe stand-replacing disturbances occur: as these types of disturbances tend to extirpate all species from a given area, a larger pool of species performing similar functions is unlikely to improve post-disturbance performance of those ecosystem functions.

In the face of such severe disturbances, response diversity (RD) is more likely to influence post-disturbance ecosystem functioning. Instead of measuring how similarly species perform a given ecosystem function, this indicator quantifies how species within the same functional group respond to various types of disturbances (Elmqvist et al., 2003). As disturbance response is trait-dependent (Mori et al., 2013), an appropriate trait selection can allow researchers to successfully quantify species responses to stand-replacing disturbances. The relevance of this variable is supported by the significant negative and positive relationships reported between coniferous and deciduous RD and post-disturbance productivity, respectively. The observed differences in effect direction likely result from the different regeneration speeds of these two functional groups and the relatively short temporal scale examined (up to 10 years after clear cutting took place). Considering that, following severe disturbances, deciduous species tend to occupy the upper canopy cover faster than the main shade-tolerant coniferous species within our study area (Pothier and Auger 2009), we are more likely to detect the effect of multiple deciduous regeneration strategies on post-disturbance productivity within such a relatively short period of time. As their coniferous counterparts are slower to recover, we were probably only able to detect the effect of a limited number of regeneration strategies on post-disturbance productivity. A bias in the relationships between the seasonal variation of EVI and gross primary productivity across vegetation composition types could have also potentially influenced the observed results: while the EVI-gross primary productivity relationship is strong in coniferous forests, it is generally stronger in deciduous forests (Huete et al., 2010). These results might also have been affected by the response traits used: even though all chosen response traits are associated with tree regeneration speeds and strategies (Cornelissen et al., 2003), their importance might vary according to forest type.

Black spruce-mediated identity effects influenced the magnitude of the effect of coniferous RD and FR on post-disturbance productivity. The observed negative black spruce-productivity relationship is supported by the mass-ratio hypothesis, which proposes that some ecosystem functions are mainly dictated by the dominant species (Grime 1998). This hypothesis has previously been proposed as an alternative mechanism to explain productivity in grassland ecosystems (Sasaki and Lauenroth 2011) and has been promoted as an important underlying process driving productivity in forests (Mori et al., 2016, Grossman et al., 2017). Black spruce-dominated stands are at a considerably greater risk of decreased productivity due to paludification and invasion by ericaceous shrubs (Thiffault et al., 2013). For instance, mixed trembling aspen-black spruce stands are less vulnerable to paludification than pure black spruce stands as a result of increased nutrient cycling (Légaré et al., 2005), while ericaceous shrubs produce slowly-decomposing litter that sequesters soil nitrogen (Joanisse et al., 2009), compete with black spruce for soil resources and excrete harmful allelochemicals (Yamasaki et al., 2002). Therefore, the observed negative relationship between black spruce abundance and post-disturbance productivity likely reflects this increased risk of paludification and invasion by ericaceous shrubs. A study comparing black spruce, trembling aspen and jack pine-dominated stands also found that black spruce-dominated stands were the least productive in terms of annual aboveground net primary productivity (Reich et al., 2001).

While our results suggest that common species play a more critical role in ecosystem functioning, the number and nature of the services in question needs to be taken into account before strong conclusions are drawn. In the literature, it is unclear whether common or rare species are more important in dictating biodiversity-ecosystem functioning relationships. Common species appear to be more influential when productivity is the ecosystem function under consideration (e.g. Vile et al., 2006), but some regulating and recreational services appear to be more dependent on rare species (e.g. Zavaleta, 2004). These relationships are further complicated when multifunctionality, one of the main objectives of sustainable forest management (Gustafsson et al., 2012), is directly acknowledged. Even though primary productivity directly influences other ecosystem functions (e.g. carbon storage; Hulvey et al., 2013), multifunctionality was not directly considered in our analyses. Further studies are needed to disentangle these complex relationships, as the few published scientific articles on this issue have found evidence on the importance of both rare (Soliveres et al., 2016) and dominant species (Lohbeck et al., 2016) in driving ecosystem multifunctionality.

Ideally, further real-world studies should also focus on larger spatial and temporal scales and should take cross-scale interactions into account, as extrapolating from small-scale, short-term experiments might lead to erroneous conclusions (Brose and Hillebrand 2016). In fact, cross-scale interactions are

known to influence local and regional ecosystem functioning stability (Loreau et al., 2003). For instance, Higgins and Scheiter, (2012) showed that the impacts of abrupt, small-scale regime shifts in vegetation cover are decreased at a landscape-level due to their asynchrony and Craven et al., (2016) demonstrated how interactions between local response diversity and habitat connectivity affect landscape-level resilience of a temperate forest. Furthermore, a multi-trophic, large-scale study recently showed that ecosystem functioning drivers at small scales likely differ from those at larger scales: while identity and niche complementarity effects drove small-scale ecosystem productivity, ecosystem functioning at larger scales was only directly associated with total biomass and species richness (Barnes et al., 2016). The influence of temporal scales should also be considered: mechanisms driving ecosystem function may vary across time (Loreau and de Mazancourt 2013) and short-term post-disturbance productivity does not necessarily equate to long-term productivity. The use of novel methodologies, such as structural equation modelling (e.g. Barnes et al., 2016) and probability density-based functional diversity indexes (Carmona et al., 2016), should allow future research to improve our understanding of complex cross-scale biodiversity-ecosystem functioning relationships and help inform policy and ecosystem management.

## Conclusions

Our study is one of the first to use real-world data of sampled forest plots spread across a large spatial area to analyse the direct relationships between post-disturbance productivity and two functional diversity indicators associated with ecosystem resilience: functional redundancy and response diversity. We found significant response diversity-ecosystem productivity relationships after logging in forested ecosystems, including a negative effect of coniferous response diversity. We also report negative black spruce-mediated identity effects that likely resulted from increased stand vulnerability to paludification and post-disturbance invasion by ericaceous shrubs.

Our results reveal the complementary nature of traditional biodiversity indicators and trait-based approaches in the study of biodiversity-ecosystem functioning relationships in dynamic forest ecosystems. Regarding the functional diversity indicators studied, these results suggest that response diversity is a more appropriate indicator of ecosystem productivity recovery after logging within northern temperate and boreal forests than functional redundancy. This is likely due to the capacity of response diversity to quantify the effect of species' disturbance response strategies. The relatively short time scale considered and the use of a single ecosystem function, primary productivity, must be taken into account when analyzing these results. Future work should focus on disentangling the complex relationships between biodiversity and multiple ecosystem functions and on assessing these

relationships at multiple spatial and temporal scales, as these are essential aspects to take into account in sustainable ecosystem management frameworks.

## Acknowledgments

This work was funded by the Fonds de recherche du Québec, Nature et technologies (FRQ-NT). We would like to thank the Forest Complexity Modelling program, which is funded by NSERC through its CREATE program, and the Fonds Produits forestiers Résolu for supporting this project. We would also like to thank the Canada Foundation for Innovation (CFI), the Ministère de l'Économie, de l'Innovation et des Exportations du Québec (MEIE), the RMGA and the Fonds de recherche du Québec – Nature et technologies (FRQ-NT) for funding the operation of Calcul Québec's Guillimin supercomputer. The MOD13Q1 and the MCD12Q1 MODIS products were retrieved from the online SOAP web service, courtesy of the NASA EOSDIS Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota. Finally, we would like to thank Isabelle Auger, Frédérik Doyon and Dylan Craven for their useful comments and suggestions.

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## Tables and figures

**Table 2.1.** Candidate model sets built to test the influence of FR, RD and species identity effects on RD–post-disturbance productivity relationship.

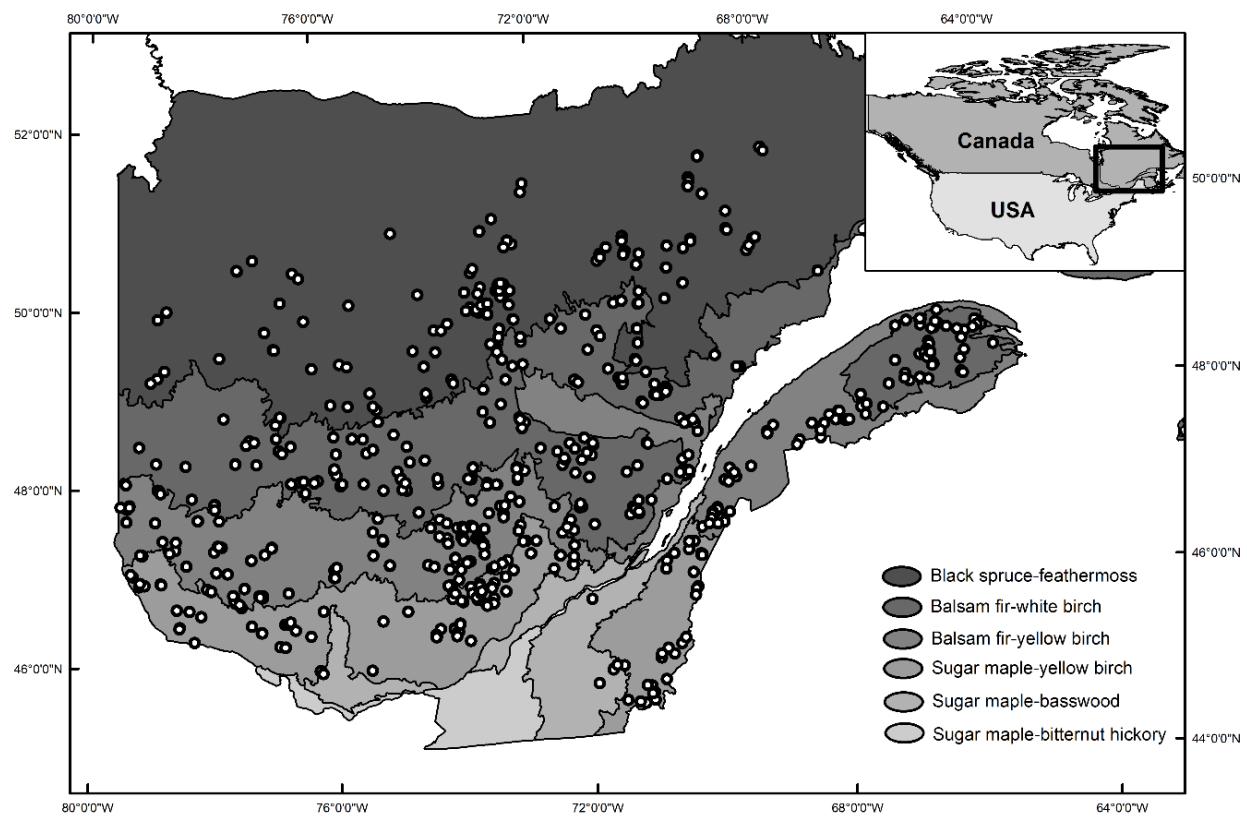
<i>Model parameters</i>											
<i>Time after disturbance</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Early years</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Year of logging</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Climate</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Stand chars</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Tree species richness</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Land cover</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Coniferous FR</i>		X	X		X	X		X	X		
<i>Deciduous FR</i>		X	X		X	X		X	X		
<i>Coniferous RD</i>	X		X	X		X			X		
<i>Deciduous RD</i>	X		X	X		X			X		
<i>Black spruce</i>	X	X	X								
<i>White birch</i>						X	X	X			
<i>Marginal R2</i>	0.48	0.49	0.48	0.47	0.47	0.46	0.47	0.46	0.47	0.45	
<i>Conditional R2</i>	0.71	0.71	0.71	0.7	0.71	0.7	0.7	0.7	0.71	0.7	
$\Delta AIC_c$	0	7.98	9.11	22.3	28.54	29.13	32.48	37.63	38.23	51.19	
$AIC_c Wt$	0.97	0.02	0.01	0	0	0	0	0	0	0	
<i>k</i>	19	21	19	18	20	18	19	19	21	16	

**Time after disturbance** is the number of growing seasons after clear cut; **Early years** is a binary categorical variable with value 1 for years 2 to 5; **Year of logging** is the calendar year when the stand was clear-cut; **Climate** represents the top 3 principal components of the previously described PCA of climate variables; **Stand chars** represents the top 3 principal components of the previously described PCA of stand characteristics variables; **Tree species richness** is the pre-disturbance number of tree species; **Land cover** is the MODIS post-disturbance land cover at year 2013; **FR** is functional redundancy; **RD** is response diversity; **Black spruce** and **White birch** are the basal area relative abundance among the corresponding functional effect group; **AIC<sub>c</sub>Wt** is the AIC<sub>c</sub> weight; **k** is the number of parameters estimated.

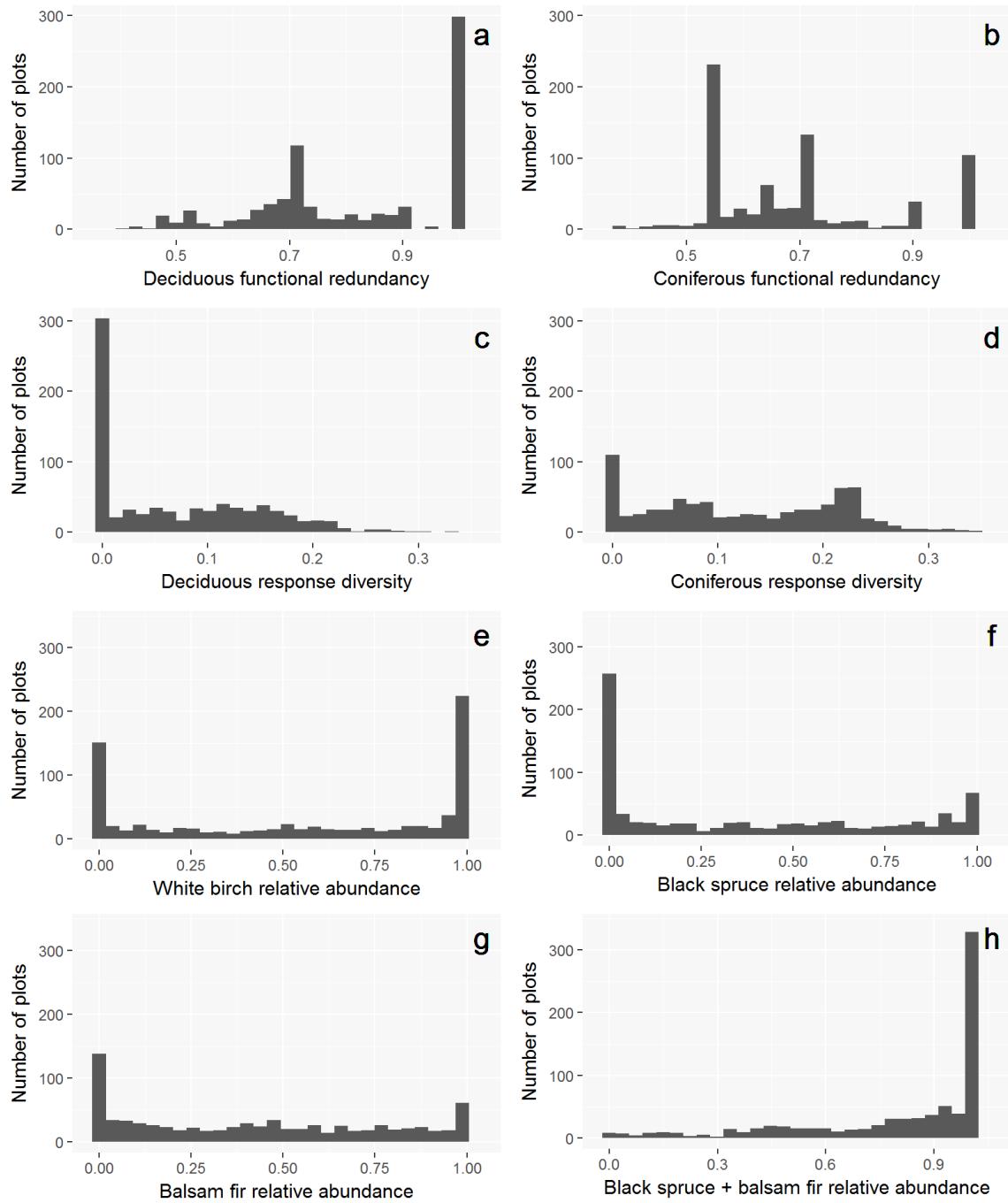
**Table 2.2.** Linear mixed effect model coefficients from the top model. Variable estimate effect sizes have been centered and standardized (Grueber et al., 2011), so they are directly comparable. PC denotes principal components. SE denotes standard error. Variable nomenclature follows the same code as Table 2.1. The reference level for the land cover variable is coniferous regeneration. \* denotes significant variables.

	<i>Estimate</i>	<i>SE</i>	<i>p-value</i>
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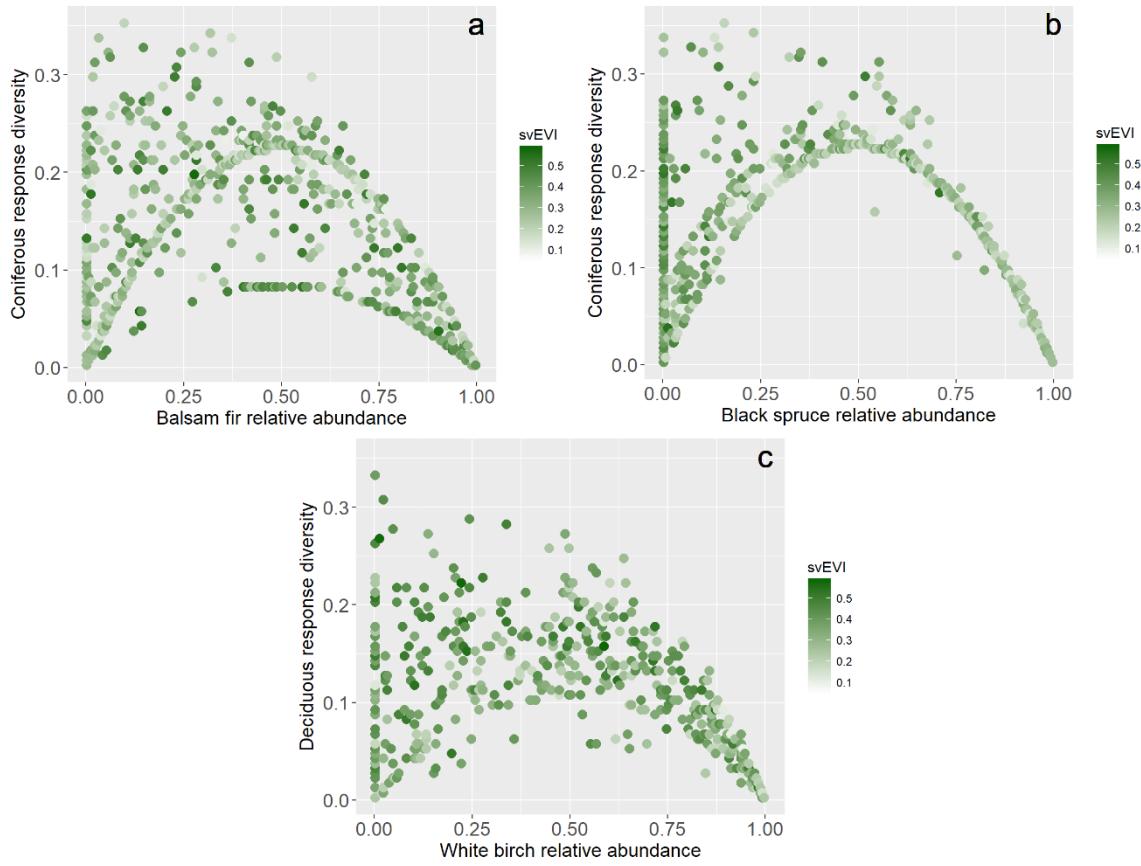
<b><i>Intercept</i></b>	0.264	0.0040	0.00000*
<b><i>Time after disturbance</i></b>	0.075	0.0018	0.00000*
<b><i>Early years</i></b>	0.041	0.0014	0.00000*
<b><i>Year of logging</i></b>	0.000	0.0041	0.97810
<b><i>Climate PC1</i></b>	0.005	0.0022	0.01690*
<b><i>Climate PC2</i></b>	0.008	0.0015	0.00000*
<b><i>Climate PC3</i></b>	-0.003	0.0011	0.00770*
<b><i>Stand Chars PC1</i></b>	0.046	0.0052	0.00000*
<b><i>Stand Chars PC2</i></b>	0.013	0.0041	0.00120*
<b><i>Stand Chars PC3</i></b>	0.020	0.0043	0.00000*
<b><i>Tree species richness</i></b>	0.040	0.0074	0.00000*
<b><i>Land cover: deciduous</i></b>	0.045	0.0052	0.00000*
<b><i>Land cover: shrub</i></b>	0.031	0.0066	0.00000*
<b><i>Coniferous RD</i></b>	-0.029	0.0047	0.00000*
<b><i>Deciduous RD</i></b>	0.013	0.0062	0.03510*
<b><i>Black spruce</i></b>	-0.027	0.0047	0.00000*



**Figure 2.1.** Map of the study area: Québec, Canada. White points represent study plots. Background shading represents bioclimatic domains.



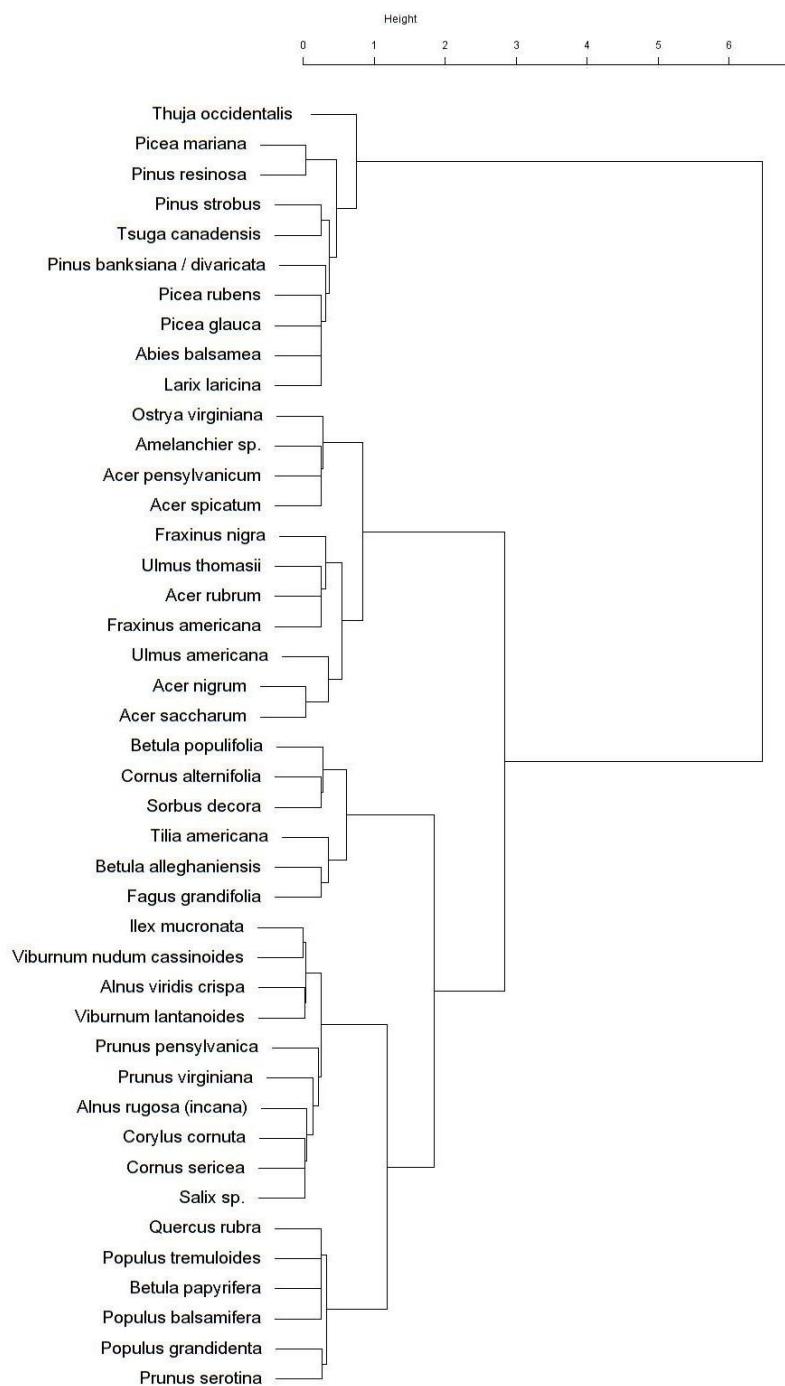
**Figure 2.2.** Histograms of plot-level species composition: (a) deciduous functional redundancy, (b) coniferous functional redundancy, (c) deciduous response diversity, (d) coniferous response diversity, (e) white birch relative abundance, (f) black spruce relative abundance, (g) balsam fir relative abundance, and (h) sum of black spruce and balsam fir relative abundance. Species relative abundance is the basal area relative abundance within the corresponding functional effect group.



**Figure 2.3.** Balsam fir (a) and black spruce (b) plotted against coniferous response diversity, and white birch relative abundance plotted against deciduous response diversity (c). Species relative abundance is the basal area relative abundance within the corresponding functional effect group. Points are coloured according to the seasonal variation of EVI (svEVI) measured 3 years after disturbance.

## Supplementary material

### Appendix 2.A. Dendrogram of functional effect groups.



**Appendix 2.B.** Functional trait data and sources.

Species name	maxH	GR	LP	WD	VR	SM	ST	LMA	NLM	NUS	SB
<i>Abies balsamea</i>	25	1	1	0,34	1	3,337780118	5	151	1,66	2	0
<i>Acer negundo</i>	20	3	0	0,44	1	1,819117288	3,5	37,04	2,5	1	0
<i>Acer nigrum</i>	30	2	0	0,52	1	1,435646158	3	70,63	1,83	1	0
<i>Acer pensylvanicum</i>	10	1	0	0,44	1	1,819117288	3,5	42,65	2,22	1	0
<i>Acer rubrum</i>	25	3	0	0,49	1	2,426501989	3,4	71,09	1,91	1	0
<i>Acer saccharinum</i>	35	3	0	0,44	1	0,556118755	3,6	36	2,36	1	0
<i>Acer saccharum</i>	35	1	0	0,56	1	1,381306804	4,8	70,63	1,83	1	1
<i>Acer spicatum</i>	10	2	0	0,44	2	2,426501989	3,3	30,6	2,49	1	1
<i>Alnus rugosa</i>	10	2	0	0,37	2	6,200145485	1	67,14	2,98	3	1
<i>Alnus viridis</i>	3	2	0	0,37	2	6,365802472	1,5	69	2	3	0
<i>Amelanchier sp.</i>	10	2	0	0,66	1	3,510796479	3,4	78,86	1,82	1	0
<i>Betula alleghaniensis</i>	25	3	0	0,55	1	5,315651639	3,2	46,08	2,2	2	1
<i>Betula papyrifera</i>	25	3	0	0,48	1	6,441478204	1,5	77,88	2,31	3	1
<i>Betula populifolia</i>	12	3	0	0,45	1	7,566052783	1,5	58,44	1,79	2	1
<i>Carpinus caroliniana</i>	10	1	0	0,58	0	2,826681929	4,6	49,05	2,15	2	0
<i>Carya cordiformis</i>	25	1	0	0,6	0	0,080997432	2,1	44,05	2,6	2	0
<i>Carya ovata</i>	25	1	0	0,64	2	0,05557906	3,4	68,39116	2,09	2	0
<i>Celtis occidentalis</i>	12	2	0	0,49	1	3,021305657	3,5	82,64463	2,8919	3	1
<i>Cornus alternifolia</i>	10	2	0	0,58	1	1,535219359	2	40	1,7	2	1
<i>Cornus sericea</i>	6	3	0	0,58	2	2,236413299	2,9	NA	NA	NA	0
<i>Corylus cornuta</i>	8	2	0	0,52	2	0,233196663	3	NA	NA	NA	0
<i>Fagus grandifolia</i>	25	1	0	0,56	2	0,553514332	4,8	61,22	2,04	2	1
<i>Fraxinus americana</i>	25	2	0	0,55	1	1,713712836	2,5	76,75	2,12	1	0
<i>Fraxinus nigra</i>	20	2	0	0,45	1	1,691397168	3	71,94	2,1	1	0
<i>Fraxinus pennsylvanica</i>	25	3	0	0,53	1	2,016108321	3,1	87,72	1,8	1	0
<i>Ilex mucronata</i>	5	NA	0	NA	2	NA	2	NA	1,62	NA	NA

<i>Juglans cinerea</i>	25	3	0	0,36	0	0,026851763	1,9	60,98	2,6	2	1
<i>Juglans nigra</i>	30	3	0	0,51	1	0,031257785	1,9	32,78689	2,96	1	0
<i>Juniperus virginiana</i>	15	1	1	0,44	1	3,034482634	1,28	333,3333	1,64	1	1
<i>Larix laricina</i>	25	3	1	0,48	0	4,895908315	1	120	1,36	2	1
<i>Ostrya virginiana</i>	12	1	0	0,63	1	2,682484004	4,6	37,04	2,2	1	0
<i>Picea abies</i>	40	1	1	0,38	0	3,40264619	4,5	235,18	1,19	2	0
<i>Picea glauca</i>	25	1	1	0,35	0	4,449254776	4,2	302,86	1,28	2	0
<i>Picea mariana</i>	20	1	1	0,41	2	5,218341091	4,1	294,12	1,12	2	1
<i>Picea rubens</i>	25	2	1	0,38	0	4,166920815	4,4	304,67	1,15	2	1
<i>Pinus banksiana</i>	20	3	1	0,42	0	4,101854681	1,4	243,9	1,24	2	1
<i>Pinus resinosa</i>	25	3	1	0,39	0	3,20570817	1,9	294,12	1,17	2	1
<i>Pinus rigida</i>	30	3	1	0,47	2	3,373229882	2	204,499	1,16	2	1
<i>Pinus strobus</i>	30	3	1	0,36	0	2,586163917	3,2	121,92	1,42	2	1
<i>Pinus sylvestris</i>	28	2	1	0,395	0	3,499280501	2	243,3905	1,304714	2	0
<i>Populus balsamifera</i>	25	3	0	0,37	1	NA	1,3	83,46	1,95	3	0
<i>Populus deltoides</i>	30	3	0	0,35	1	5,266776171	1,8	88,18	2,39	3	0
<i>Populus grandidentata</i>	20	3	0	0,39	1	7,216555002	1,2	70,45	2,5	3	0
<i>Populus tremuloides</i>	25	3	0	0,37	1	7,295925301	1,2	82,02	2,16	3	0
<i>Prunus pensylvanica</i>	12	3	0	0,36	1	2,008833191	1	50	2,4	3	0
<i>Prunus serotina</i>	22	3	0	0,47	0	1,160287138	2,5	72,3	2,48	3	0
<i>Prunus virginiana</i>	10	3	0	0,36	1	1,184304727	2,6	84,03	2,8	3	1
<i>Quercus alba</i>	35	1	0	0,6	0	0,06921588	2,9	81,21	2,39	2	0
<i>Quercus bicolor</i>	22	3	0	0,64	0	0,065824069	3	86,98	2,33	2	0
<i>Quercus macrocarpa</i>	15	1	0	0,58	0	0,046527759	2,7	92,74	2,27	2	0
<i>Quercus rubra</i>	25	2	0	0,56	1	0,067945299	2,8	84,2	2,06	3	0
<i>Salix sp.</i>	7	3	0	0,36	1	7,054167414	1,5	NA	NA	3	0
<i>Sambucus canadensis</i>	4	2	0	NA	2	4,89242591	2,2	NA	NA	NA	1
<i>Sorbus decora</i>	10	1	0	0,42	1	2,066810595	2,6	63,97	2,17	2	1
<i>Thuja occidentalis</i>	15	1	1	0,3	2	5,061169986	3,5	223	1,02	1	1

<i>Tilia americana</i>	35	2	0	0,32	1	1,15529933	4	60,81	2,94	2	0
<i>Tsuga canadensis</i>	30	1	1	0,4	0	4,453486812	4,8	122,55	0,99	2	0
<i>Ulmus americana</i>	35	3	0	0,46	1	3,501744749	3,1	79,47	2,07	1	0
<i>Ulmus rubra</i>	25	3	0	0,48	1	2,976084502	3,3	59,88	2,5	1	0
<i>Ulmus thomasii</i>	25	2	0	0,57	1	1,43240278	3,2	64,1	2,3	1	0
<i>Viburnum edule</i>	3	3	0	NA	2	1,537464112	3	NA	NA	NA	1
<i>Viburnum lantanoides</i>	4	1	0	NA	2	1,829362811	3	NA	NA	NA	1
<i>Viburnum cassinoides</i>	5	2	0	NA	2	2,605112449	3	NA	2,08	NA	0
<i>Viburnum opulus</i>	5	2	0	NA	2	1,971641798	2,7	NA	NA	NA	1

### Label codes

**maxH:** Average maximum height

**GR:** Growth rate (1: slow; 2: moderate; 3: rapid)

**LP:** Leaf phenology (1: needle/scale; 0: other)

**WD:** Wood density (g/cm3)

**VR:** Vegetative reproduction capacity (0: never; 1: possible; 2: common)

**SM:** Seed mass (mg)

**ST:** Shade tolerance (1: very intolerant, 2: intolerant, 3: medium tolerance, 4: tolerant, 5: very tolerant)

**LMA:** Leaf mass per area (g/m2)

**NLM:** Nitrogen content per leaf mass unit (%)

**NUS:** Nutrient uptake strategy (1: Arbuscular mycorrhiza; 2: Ectomycorrhiza; 3: both)

**SB:** Capacity to establish seed banks (0: seeds do not persist in seed banks over long periods of time; 1: seeds persist in seed bank)

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**Appendix 2.C.** Extended candidate model set.

Model parameters											
<i>Time after disturbance</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Early years</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Year of logging</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Climate</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Stand chars</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Land cover</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Tree species richness</i>	X	X	X		X		X	X		X	X
<i>Coniferous FR</i>		X	X			X	X	X	X		
<i>Deciduous FR</i>		X	X			X	X	X	X		
<i>Coniferous RD</i>	X	X		X	X	X					
<i>Deciduous RD</i>	X	X		X	X	X					
<i>Community FR</i>											
<i>Community RD</i>										X	
<i>Black spruce</i>	X	X	X	X		X		X	X	X	X
<i>White birch</i>											
<i>Marginal R2</i>	<b>0,48</b>	0,49	0,48	0,47	0,47	0,47	0,47	0,46	0,46	0,46	0,46
<i>Conditional R2</i>	<b>0,71</b>	0,71	0,71	0,71	0,7	0,71	0,71	0,7	0,71	0,71	0,7
<i>AIC<sub>c</sub></i>	<b>-24363,7</b>	-24355,7	-24354,6	-24344,8	-24341,4	-24336,2	-24335,2	-24334,6	-24332,7	-24332,1	-24331,7
<i>Δ AIC<sub>c</sub></i>	<b>0</b>	7,98	9,11	18,94	22,3	27,52	28,54	29,13	30,99	31,62	31,98

**Appendix 2.C.** Extended candidate model set (continued).

Model parameters											
<i>Time after disturbance</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Early years</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Year of logging</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Climate</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Stand chars</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Land cover</i>	X	X	X	X	X	X	X	X	X	X	X
<i>Tree species richness</i>	X	X	X	X	X	X	X	X			X
<i>Coniferous FR</i>				X	X		X		X		
<i>Deciduous FR</i>				X	X		X		X		
<i>Coniferous RD</i>		X			X	X		X			
<i>Deciduous RD</i>		X			X	X		X			
<i>Community FR</i>	X		X								
<i>Community RD</i>	X										X
<i>Black spruce</i>	X		X								
<i>White birch</i>		X		X	X			X			
<i>Marginal R2</i>	0,47	0,47	0,46	0,46	0,47	0,45	0,45	0,46	0,45	0,45	0,45
<i>Conditional R2</i>	0,71	0,7	0,7	0,7	0,71	0,7	0,7	0,7	0,7	0,7	0,7
<i>AIC<sub>c</sub></i>	-24331,5	-24331,2	-24331,0	-24326,1	-24325,5	-24313,8	-24312,5	-24308,6	-24307,5	-24306,2	-24305,5
<i>Δ AIC<sub>c</sub></i>	32,18	32,48	32,68	37,63	38,23	49,92	51,19	55,07	56,25	57,47	58,23

**Appendix 2.C.** Extended candidate model set (continued).

<i>Model parameters</i>										
<i>Time after disturbance</i>	X	X	X	X	X	X	X	X	X	X
<i>Early years</i>	X	X	X	X	X	X	X	X	X	X
<i>Year of logging</i>	X	X	X	X	X	X	X	X	X	X
<i>Climate</i>	X	X	X	X	X	X	X	X	X	X
<i>Stand chars</i>	X	X	X	X	X	X	X	X	X	X
<i>Land cover</i>	X	X	X	X	X	X	X	X	X	X
<i>Tree species richness</i>			X							
<i>Coniferous FR</i>		X		X						
<i>Deciduous FR</i>		X		X						
<i>Coniferous RD</i>	X			X						
<i>Deciduous RD</i>	X			X						
<i>Community FR</i>			X			X	X	X		
<i>Community RD</i>					X		X	X		
<i>Black spruce</i>										
<i>White birch</i>	X	X		X	X	X		X		
<i>Marginal R2</i>	0,45	0,45	0,45	0,46	0,45	0,45	0,45	0,45	0,45	0,42
<i>Conditional R2</i>	0,7	0,7	0,7	0,7	0,7	0,7	0,7	0,7	0,7	0,7
<i>AIC<sub>c</sub></i>	-24304,2	-24303,3	-24302,3	-24300,3	-24298,9	-24297,1	-24295,0	-24288,3	-24263,7	
<i>Δ AIC<sub>c</sub></i>	59,54	60,42	61,4	63,42	64,85	66,64	68,69	75,39	99,98	

## **Appendix 2.C.** Extended candidate model set (continued).

We tested multiple additional candidate model sets in order to address the Anonymous Reviewers initial concerns that, in this study, models using only species richness and models that did not consider two separate functional effect species (deciduous and coniferous tree species) would be more parsimonious than the main candidate model set presented in the manuscript. The following candidate model sets were tested:

- Species richness instead of functional diversity [in grey]
- Functional diversity indicators without species richness [in blue]
- Functional diversity with species richness [in green]
- Functional diversity indicators with a single functional effect group [in orange]
- No biodiversity indicators [in white]

All model parameter terms follow the same nomenclature as the one described in the main document.

Community FR and Community RD refer to functional redundancy (FR) and response diversity (RD) of the whole community (i.e. without splitting the dataset in coniferous and deciduous species).

Black spruce and white birch relate to the relative abundance of these species within their corresponding functional effect group (black spruce = coniferous; white birch = deciduous).

## **Chapitre 3: Mitigation of water loss and xylem resistance to cavitation influence the response of stand mortality to severe drought, but not productivity, in northern temperate and boreal forests**

### **Résumé**

Le changement des patrons de précipitation dans les forêts tempérées nordiques et boréales du Québec, observé dans les dernières décennies, a causé une augmentation de la mortalité des arbres et une réduction de l'accumulation de la biomasse. En principe, l'impact des extrêmes climatiques sur le fonctionnement d'une communauté forestière devrait être moindre si cette dernière est caractérisée par une grande diversité fonctionnelle. Or, les études sur la relation entre la diversité fonctionnelle des arbres et leur réponse aux extrêmes climatiques sont rares. Dans ce chapitre, j'ai voulu vérifier l'existence d'une relation entre la diversité fonctionnelle des forêts tempérées nordiques et boréales du Québec et leur réponse face à des épisodes de sécheresse extrême. J'ai testé l'influence de trois traits fonctionnels sur l'impact de la sécheresse extrême sur la mortalité et la productivité des peuplements du réseau d'inventaire forestier du Québec. Les trois traits fonctionnels testés étaient: (i) le rapport du poids sec de la feuille à la surface foliaire; (ii) la pression du xylème conduisant à une perte de 50% de sa conductivité par cavitation ( $\Psi_{50}$ ); et (iii) le rapport de la surface foliaire à la surface de l'aubier. J'ai utilisé la modélisation par équations structurelles pour comparer l'effet d'une variable latente composée de ces trois traits sur la mortalité et la productivité des peuplements ayant souffert une sécheresse extrême et sur des placettes de contrôle. J'ai trouvé qu'une variable latente composée par le rapport du poids sec de la feuille à la surface foliaire et la  $\Psi_{50}$  expliquait la mortalité causée par la sécheresse, mais n'influençait pas la réponse de la productivité à cette perturbation. Ainsi, mes résultats suggèrent que cette variable latente représente probablement la résistance du peuplement à la sécheresse, mais non sa résilience à la sécheresse. L'impact de la mortalité sur la productivité a probablement été compensé par la création d'ouvertures dans la canopée qui stimulent la croissance des individus survivants. Mes résultats suggèrent que les aménagistes forestiers peuvent utiliser la composition des peuplements pour estimer leur susceptibilité à la sécheresse et, si nécessaire, implémenter des stratégies d'aménagement qui bénéficient les espèces ou les génotypes résistants à la sécheresse.

## **Abstract**

Changing precipitation patterns have recently increased tree mortality and reduced biomass accumulation in northern temperate and boreal forests. Studies have shown that functional diversity can mitigate the impacts of climate extremes on forest ecosystem functioning, but few studies have focused on tree functional diversity. Hence, it is critical to identify functional traits that significantly reduce the impact of drought on tree mortality, and how these impact ecosystem-level aboveground productivity. We tested the influence of three functional traits on the impact of severe drought on stand mortality and productivity. The three traits tested were: (i) ratio of dry leaf mass per unit area (LMA); (ii) xylem pressure at which 50% of stem xylem conductivity is lost through cavitation ( $\Psi_{50}$ ); and (iii) leaf area to sapwood ratio. We used structural equation modelling to compare the effect of a latent variable composed of these three traits between plots that had suffered severe drought and plots that had not, on the mortality and productivity of northern temperate and boreal forests of Québec, Canada. We found that a latent variable composed of LMA and  $\Psi_{50}$  significantly explained drought-induced mortality, but did not explain stand productivity response to severe drought. Hence, even if this variable likely represents drought resistance, it did not affect stand resilience to drought. The impact of ecosystem-level tree mortality on productivity was likely compensated by the formation of canopy openings that stimulate growth of surviving species. The effect of leaf area to sapwood ratio on plant hydric stress in these forests was not significant. Mitigation of water loss and xylem resistance to cavitation contributed similarly to tree resistance to severe droughts in these forests. Our results suggest that forest managers could estimate stand drought vulnerability by using tree species composition data and, if necessary, implement forest management strategies aimed at minimizing drought-induced mortality by promoting species or genotypes with high LMA and low  $\Psi_{50}$  values.

## Introduction

Northern temperate and boreal forests provide a multitude of ecosystem services on a local and on a global scale (Gamfeldt et al., 2013). However, the capacity of these forests to reliably provide fundamental ecosystem functions and processes will likely be compromised by warming temperatures, changing precipitation patterns and increased frequency and intensity of extreme climate events (Allen et al., 2010). Given that numerous studies have demonstrated the positive effects of biodiversity on ecosystem functioning (e.g. Lefcheck et al., 2015), it is of great interest to understand how biodiversity-ecosystem functioning relationships will be affected by a changing climate, and how biodiversity can help mitigate these impacts (Hisano et al., 2017).

The effects of climate change on forested ecosystems are difficult to anticipate. While researchers initially predicted that a warmer climate should lead to increases in growth and productivity in northern forests, rising temperatures can actually limit productivity through increased costs of autotrophic respiration and reduced soil water availability (Girardin et al., 2016). Recently, changing precipitation patterns have significantly increased tree mortality and reduced biomass accumulation in Canada's northern temperate and boreal forests (Peng et al., 2011, Pan et al., 2013; but see Hartmann et al., 2015). Negative drought-related effects on tree growth are also more important than initially thought, as they can persist for several years after the return of normal precipitation conditions (Anderegg et al., 2015). Additionally, droughts can act as a trigger mechanism of other disturbances, because drought-stressed trees are more vulnerable to pests and pathogens, and extreme drought conditions generally lead to more severe forest fires (Schlesinger et al., 2016).

Drought impacts on tree mortality and productivity are highly dependent on the time of the year and on species composition. Summer droughts appear to have a more significant effect on plant communities than droughts outside this season, as they cause the premature loss of photosynthetic tissue during a key growth period (Schlesinger et al., 2016). For instance, summer drought is significantly associated with trembling aspen (*Populus tremuloides*) mortality (Anderegg et al., 2013), reduction of radial growth in white cedar (*Thuja occidentalis*) (Housset et al., 2015), and is an important factor limiting black spruce (*Picea mariana*) productivity (Girardin et al., 2016). Summer drought was also found to have unexpected negative effects on potassium availability (Houle et al., 2016), which can limit the growth of major boreal tree species, such as balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) (Ouimet & Moore, 2015). Better understanding the relationships between stand species composition, drought, mortality and productivity is essential for ensuring a reliable provisioning of forest ecosystem services in the face of climate change.

The large number of indicators available to measure different facets of biodiversity, coupled with a lack of tree-specific studies on biodiversity-ecosystem functioning relationships in the face of disturbance, greatly complicates our ability to assess how tree diversity influences the effects of climate extremes on ecosystem functioning (Mori et al., 2017). As a consequence, results can be somewhat contradictory: Isbell et al., (2015) found that species richness improved plant productivity resistance to precipitation extremes, but Craven et al., (2016) did not find such a buffering effect of species richness on the negative impacts of drought. Similarly, Paquette et al., (2017) revealed that warmer temperatures resulted in a negative relationship between functional diversity and tree growth, while Ruiz-Benito et al., (2017) found that functional diversity buffered the negative effects of climate on tree growth and recruitment. Such discrepancies are possibly due to a number of reasons. First, the underlying diversity-functioning relationships examined can vary due to spatial and species-specific differences among studies. For instance, Paquette et al., (2017) studied Canadian boreal forests while Ruiz-Benito et al., (2017) studied the main European forest types. Second, the use of species richness to evaluate community response to disturbances might be inadequate (e.g. Craven et al., 2016; Isbell et al., 2015), because unlike functional diversity, richness does not explicitly quantify species' disturbance response mechanisms (Cadotte et al., 2011). Finally, functional effect traits quantify how species influence ecosystem processes, while response traits measure how species respond to environmental changes (Mori et al., 2013). Hence, assessing ecosystem function-disturbance linkages with functional effect traits instead of disturbance-specific response traits might lead to misleading interpretations. Considering that species relative abundances might also be an integral component of these ecosystem function-disturbance relationships, the community weighted means of carefully selected functional response traits is likely to be a promising indicator in evaluating the role of biodiversity in mitigating the effect of climate extremes (Hisano et al., 2017).

The aim of this study was to identify which functional response traits play an important role in buffering the impact of drought on stand-level tree mortality and aboveground productivity of northern temperate and boreal forest. We identified permanent sample plots of Québec, Canada, where severe drought occurred between sampling years in order to analyse these relationships. We employed structural equation modelling and used drought response traits to measure tree drought response as a latent variable; i.e. a theoretical variable that cannot be directly measured, but whose presence may be revealed by associations among observed variables (Grace et al., 2012). Structural equation models were built separately for each bioclimatic domain in order to explicitly consider significant environmental and species compositional differences among bioclimatic domains. Depending on the effect of the latent variable on stand-level responses to drought, we hypothesized

that it might represent drought tolerance (defined as the ability of species to survive drought and persist in their current location; Aubin et al., 2016) or drought resistance (characterized as the maintenance of plant productivity during drought events; Volaire, 2018).

## **Methodology**

### **Study area**

We analysed data from permanent forest sample plots located in Quebec, Canada (Figure 3.1). These plots are spread across a latitudinal gradient that encompasses multiple northern temperate and boreal bioclimatic domains (sugar maple-bitternut hickory, sugar maple-basswood, sugar maple-yellow birch, balsam fir-yellow birch, balsam fir-white birch and black spruce-feathermoss), affected by a variety of natural disturbance and forest management regimes. Plots have a 400 m<sup>2</sup> circular area and, on average, were sampled once every 10 years. Within this area, each tree with a diameter at breast height (DBH) greater than 9 cm was measured, and its status (living/dead, DBH) was followed during each successive remeasurement of the plot. New recruits are monitored once they pass the 9 cm DBH threshold (MFFP, 2016). Partial and severe disturbance codes are assigned to each plot when they occur. Some stand-level variables, such as the organic soil depth, are also measured.

With the purpose of decreasing noise introduced by disturbances other than drought, forest plots from this sampling program were selected according to four criteria: (i) only the measurements taken after the year 1990 were used, in order to avoid the confounding effect of the spruce budworm outbreak that significantly affected most forest stands in our study area between the early 1970s and the late 1980s (Pothier et al., 2012); (ii) there is no record of partial or stand-replacing disturbances other than drought having occurred after the year 1970; (iii) biomass did not decrease more than 25% between sampling periods; and (iv) less than half the trees died between sampling periods. The last two criteria were established with the objective of removing any residual plots that suffered disturbances that were not registered by the measurers. Plots were measured between 1990 and 2012, and only one pair of consecutive sampling periods was used per sampling plot.

### **Identification of drought conditions**

Our dataset was split into two groups (drought and non-drought) according to the occurrence of severe droughts between sampling periods. These rare climate events were identified with the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010). This climatic drought index uses a dataset of site-level measurements of water balance accumulated over an adjustable time period to fit a log-logistic probability distribution. SPEI was measured over the growing season (May

to September) across a 100-year dataset of plot-level water balance estimates. Plot-level water balance between 1915 and 2014 was calculated using BioSIM (version 10; Régnière et al., 2014), a software tool that uses geographic coordinates, elevation, slope and aspect to interpolate climate data from nearby weather stations. Hence, calculated SPEI values are plot-specific and are relative to the 100 year calibration period used. For instance, a  $\text{SPEI}_5$  value of -1.28 corresponds to a level of drought during the growing season that has historically occurred once every 10 years in a given plot. Plots were classified as “drought plots” when  $\text{SPEI}_5$  was equal to or smaller than -1.28 in at least 20% of the years between sampling periods (i.e. when an extreme drought event that usually occurred once every ten years between 1915 and 2014 happened once every five). Plots were classified as “non-drought plots” when the percentage of plots with  $\text{SPEI}_5$  equal to or lower than -1.28 was 0 (i.e. when no severe drought events occurred). Plots where this percentage was greater than 0 and smaller than 20 were not included in the analysis in order to remove noise introduced by mild droughts. Mean annual temperature of each sampling period was also estimated with BioSIM.

### **Productivity and mortality**

Plot-level productivity, specifically mean annual aboveground biomass increment, was calculated according to the equation (3.1):

$$Y = \frac{\sum_{i=1}^{n_2} b_{i2} - \sum_{i=1}^{n_1} b_{i1}}{t_2 - t_1}$$

where  $Y$  is the mean annual aboveground biomass increment between measurement pairs at time  $t_1$  and time  $t_2$ ,  $n_1$  ( $n_2$ ) is the number of living trees with a DBH greater than 9 cm found in the plot at  $t_1$  ( $t_2$ ), and  $b_{i1}$  ( $b_{i2}$ ) is the biomass of tree  $i$  at  $t_1$  ( $t_2$ ). Trees that reached a DBH greater than 9 cm between sampling periods were not included (e.g. Paquette & Messier, 2011). Plot-level mortality was calculated as the mean increment of dead aboveground biomass, following the equation (3.2):

$$M = \frac{\sum_{i=1}^d b_{i1}}{t_2 - t_1}$$

where  $M$  is the mean increment of dead aboveground biomass between sampling periods  $t_1$  and  $t_2$ ,  $d$  is the number of trees that died between time  $t_1$  and  $t_2$ , and  $b_{i1}$  is the biomass of tree  $i$  at  $t_1$ . Tree biomass was computed using the DBH-based aboveground biomass allometric equations published in Lambert et al., (2005).

## **Functional traits**

Three drought functional response traits suggested in Aubin et al., (2016) were selected according to their availability and to the type of drought response mechanisms they were associated with: (i) dry leaf mass per unit area (LMA), which is positively associated with drought tolerance via mitigation of water loss (Poorter et al., 2009); (ii)  $\Psi_{50}$  (i.e. xylem pressure at which 50% of xylem conductivity in the stem is lost through cavitation), which is negatively associated with drought tolerance via xylem resistance to cavitation (Choat et al., 2012); and (iii) leaf area to sapwood ratio, which is negatively related to drought tolerance via the economy of water (McDowell et al., 2008). Plant functional trait data was obtained from the TOPIC database (Traits Of Plants In Canada; Aubin et al., 2015). When  $\Psi_{50}$  and leaf area to sapwood ratio measurements were unavailable, genus-level means of  $\Psi_{50}$  and leaf area to sapwood ratio of species native to the study area were used instead. LMA trait values were available for all tree species.

Plot-level community weighted means (CWMs) for each trait were calculated at time 1 and 2 with the FD R package (v1.0-12; Laliberté & Legendre 2010). As recommended by Villéger et al., (2008), trait data were standardized (mean of 0 and unit variance) before CWMs were calculated in order to give the same weight to each trait. The means of LMA,  $\Psi_{50}$  and leaf area to sapwood ratio CWMs at time 1 and 2 were then calculated.

Drought and non-drought stand CWMs, initial biomass, productivity and mortality were compared within each bioclimatic domain using non-parametric Mann-Whitney *U*-tests from the R *stats* package. Non-parametric tests were used because data distribution was not always normal across all plots. All analyses were done with the R open-source software, version 3.4.2 (R Core Team, 2017).

## **Structural equation modelling**

Structural equation models (SEM's) are probabilistic models that permit the specification of multiple causal pathways (Grace et al., 2012). This framework is particularly useful in ecology for two main reasons. First, it gives researchers the ability to explicitly study the impacts of direct and indirect pathways within a given system, which are otherwise challenging to disentangle. Second, it allows us to measure latent variables such as drought tolerance, which are “hypothesized variables for which we have no direct measurements, but whose existence may be revealed by associations among measured variables” (Grace et al., 2012). To assess the goodness of fit of the SEM's, we used a chi-square to compare the observed covariance matrix against the predicted covariance matrix, where a  $P > 0.05$  indicated that the model did not significantly lack fit (Shipley, 2016).

Endogenous variables (biomass at time 1, mortality and productivity) are those that are predicted by another variable in the model, whereas exogenous variables are those whose variations are not explained in the model (Grace et al., 2012). In order to prevent data normality-related errors, endogenous variables were log-transformed, plots where mortality was 0 were removed from the analysis, and the Satorra-Bentler robust maximum likelihood estimator was used in the chi-square test (Satorra & Bentler, 1994). Six SEM's were built using the *lavaan* R package (v0.5-22; Rosseel 2012) for each combination of bioclimatic domains (balsam fir-yellow birch: BF-YB; balsam fir-white birch: BF-WB; and black spruce-feathermoss: BS-FM) and drought conditions (drought and non-drought; Figure 3.1). No SEM's were built for the southernmost bioclimatic domains due to a lack of sufficient data. In order to minimise the influence of spatial autocorrelation in the analysis, we only included plots located in ecological sub-regions where both drought and non-drought plots were present.

Models were built according to the guidelines proposed by Grace et al., (2012). We built a causal diagram where mean annual temperature and mean organic soil depth influenced biomass at time 1, which directly influenced mortality and productivity. Mortality also directly affected productivity. Considering that temperature and organic soil depth can both influence stand conditions, we introduced additional causal pathways when mortality and productivity were not d-separated from these stand-level variables (i.e. when these variables were not causally independent; Grace et al., 2012). Finally, we specified a latent variable that directly influenced biomass at time 1, mortality and productivity. For each subset of data (combinations of bioclimatic domains and drought conditions), we tried to fit the hypothesized latent variable with all 2 and 3 way combinations of the three drought response traits considered (LMA,  $\Psi_{50}$  and leaf area to sapwood ratio). If more than one valid model was obtained for a given group, the SEM with the lowest AIC<sub>c</sub> was kept (Burnham & Anderson, 2002).

## Results

### Permanent sample plot dataset

No major differences were found inside bioclimatic domains among the initial biomass estimates of drought and non-drought plots (Mann Whitney *U*-test BF-YB p-value = 0.9765; BF-WB p-value = 0.3776; BS-FM p-value = 0.7736; Figure 3.2a). The impact of drought on stand mortality and productivity appeared to be greater in the BF-YB domain than in the other two bioclimatic domains. Stand mortality was markedly greater in drought plots of the BF-YB domain (*U*-test p-value = 0.0002), and differences between drought and non-drought plots were non-significant in the BF-WB

( $U$ -test p-value = 0.0894) and BS-FM domains ( $U$ -test p-value = 0.2792; Figure 3.2b). At the genus level, aspen appeared to be more vulnerable to drought in the BF-YB than in the BF-WB domain, whereas birch vulnerability to water stress appears to increase along the latitudinal gradient (Appendix 3.A). Maple species were affected by drought in the BF-YB domain, the only bioclimatic domain where the presence of this genus was significant because it delimits the northern limit of the distribution of most maple species (Appendix 3.A). The effect of hydric stress on balsam fir (*Abies balsamea*) mortality was substantial in the BF-YB and the BS-FM domains, while spruce mortality did not appear to be significantly affected by drought (Appendix 3.A).

Productivity was noticeably smaller in the drought plots of the BF-YB domain ( $U$ -test p-value < 0), but was comparable among drought and non-drought plots of the remaining two bioclimatic domains (BF-WB  $U$ -test p-value = 0.203; BS-FM  $U$ -test p-value = 0.264; Figure 3.2c). The overall influence of drought on stand conditions (positive effect on mortality and negative effect on productivity) was considerably greater when plots where no trees died between sampling periods was taken into account, as the proportion of plots with zero mortality was always substantially greater when no severe droughts occurred (Appendices 3.B & 3.C). These plots ( $n = 166$ ) were removed from the main SEM analyses because including them would result in a zero-inflated endogenous variable, which would violate a key SEM data normality assumption.

Overall, community weighted means (CWMs) of standardized traits were similar between drought and non-drought plots of the BF-YB and BS-FM domains, but varied substantially among plots from the BF-WB domain: LMA CWMs were greater ( $U$ -test p-value < 0) and  $\Psi_{50}$  CWMs were smaller in drought plots than in non-drought plots within this domain ( $U$ -test p-value < 0; Figures 3.2d & e). Minor differences between drought and non-drought plots were also present in the BF-YB domain:  $\Psi_{50}$  CWMs were somewhat greater in drought plots ( $U$ -test p-value = 0.0226), while leaf area to sapwood ratio CWMs were marginally smaller ( $U$ -test p-value = 0.0001; Figures 3.2e & f). Such differences in CWMs of drought functional response traits likely reflect the spatial nature of severe droughts, as such events are quite rare and are unlikely to occur in the same area within the 23 year time period considered. While some differences in trait composition remain among drought and non-drought plots, such divergences have been minimized by removing plots located in ecological sub-regions where one of the groups was absent.

### **Structural equation models**

Overall, results were consistent across bioclimatic domains and drought events: for drought plots, the latent variable was composed of LMA and  $\Psi_{50}$ , while for non-drought plots a valid latent variable

model was either impossible to fit (BF-YB), or the latent variable fitted was composed of a large proportion of LMA and a smaller proportion of leaf area to sapwood ratio (BF-WB and BS-FM; Table 3.1; Figure 3.3). More than one valid model was specified for two groups: BF-YB drought plots and BF-WB non-drought plots. For the former, the LMA- $\Psi_{50}$  latent variable model was substantially more parsimonious than the LMA-leaf area to sapwood ratio SEM according to the Akaike Information Criteria ( $\Delta AIC_c = 187.5$ ; Table 3.1). For the latter, the LMA-leaf area to sapwood ratio SEM had a lower  $AIC_c$  than the  $\Psi_{50}$ -leaf area to sapwood ratio latent variable model ( $\Delta AIC_c = 2.7$ ; Table 3.1). While the  $AIC_c$  difference between these two SEM's is small, the latent variable in both models is not significantly associated with stand mortality and productivity (Figure 3.3c; Appendix 3D). Hence, the interpretation of our results is not affected by this model selection procedure. Other attempts at specifying SEM's with alternative latent variable structures resulted in models that were either misspecified (i.e. negative estimated variances) or failed to pass the chi-square goodness of fit test (i.e. p-value smaller than 0.05; Grace et al., (2012); Table 3.1). Valid SEM's for non-drought plots were also considerably less adequate than corresponding SEM's for drought plots, since in the BF-WB domain the latent variable was not significantly associated with stand conditions, while in the BS-FM domain the large number of covariances confounds the relationships between variables (Figures 3.3c & e). Since no valid SEM was defined for the non-drought plots of the BF-YB domain, parameter estimates for these plots are not presented.

Stand mortality and productivity were adequately explained by the SEM's, with  $R^2$  estimates ranging from 0.32 to 0.69 for mortality and 0.26 to 0.47 for productivity (Figure 3.3). Across all plots and bioclimatic domains, initial biomass had a significant positive effect on mortality (Figures 3.4a, c & e), while mortality had a significant negative effect on productivity (Figures 3.4b, d & f). The total effect of initial biomass on productivity was consistent among plots, but varied between bioclimatic domains: while this variable had a marginally negative impact on productivity in BS-FM domain due to its direct influence on mortality and to the lack of significant direct effects on productivity (Figures 3.3d & e; Figure 3.4f), it was non-significant in the remaining bioclimatic domains (Figures 3.4b, d). The effects of the two control variables used (mean annual temperature and mean organic soil depth) on mortality and productivity were similar among plots of each bioclimatic domain (Figure 3.4). There was a single exception for the impact of mean annual temperature on productivity of the BS-FM domain plots: this variable had a marginally positive significant effect on drought plots, but had a non-significant effect on non-drought plots (Figure 3.4f).

The effects of the latent variable defined in the drought plots (LMA- $\Psi_{50}$ ) were consistent across domains: this variable had a significant negative effect on mortality due to a combination of both

direct and biomass-mediated indirect effects (Figures 3.3a, b & d; Figures 3.4a, c & e). The total impact of this latent variable on productivity was non-significant across all bioclimatic domains (Figures 3.4b, d & f). The latent variable defined in the non-drought plots ( $\Psi_{50}$ -leaf area to sapwood ratio) had a non-significant total effect on productivity in both BF-WB and BS-FM domains (Figures 3.4d & f), while its total effect on mortality varied across domains: it had a non-significant impact in the BF-WB domain but a significant negative impact in the BS-FM domain (Figures 3.4c & e).

## Discussion

Out of the three functional response traits tested, dry leaf mass per unit area (LMA) and xylem pressure at which 50% of xylem conductivity in the stem is lost through cavitation ( $\Psi_{50}$ ) were consistently associated with reduced drought-induced mortality across all bioclimatic domains. These effects agree with those hypothesized and reported in the literature: LMA is positively associated with drought resistance, while increased values of  $\Psi_{50}$  decrease resistance to hydric stress (Aubin et al., 2016). Recent meta-analyses have reached similar conclusions: Greenwood et al., (2017) reported that wood density and specific leaf area (the inverse of LMA) significantly reduced mortality induced by severe droughts, and O'Brien et al., (2017) reported that wood density correlated well with vessel architecture traits, such as  $\Psi_{50}$ , and that both traits were significantly associated with drought-induced mortality.

Leaf area to sapwood ratio, the third functional trait examined in this study, did not appear to contribute to reduced mortality in northern temperate and boreal forests. Although this trait is theoretically associated with drought resistance via the economy of water (McDowell et al., 2008), O'Brien et al., (2017) also failed to find any evidence of its importance in northern temperate and boreal forests. Hence, our results suggest that drought avoidance via mitigation of water loss and drought resistance through xylem resistance to cavitation contribute similarly to tree resistance to severe droughts in these forests. However, considering that LMA is also associated with the broader plant economic spectrum (Brodribb, 2017), some care must be taken when interpreting the importance of mitigation of water loss as a drought tolerance mechanism. Root-related water acquisition traits are also likely to play an important role in mitigating the effects of severe droughts, but these traits remain difficult to characterize at the species-level due to high spatial and intraspecific variability (Anderegg et al., 2016).

The latent variable significantly reduced stand mortality during periods of severe water stress. However, this influence did not result in a significant effect on overall stand productivity. This result

suggests that the combination of response traits tested influences stand tolerance to drought, but is inadequately associated with stand resistance to drought, i.e. the capacity of forest stands to maintain productivity during drought events (Volaire, 2018). Three main reasons might explain this non-significant effect on stand productivity. First, traits related to the ability of trees to react positively to the creation of canopy openings might significantly influence stand productivity response to drought. Canopy openings caused by tree mortality lead to an increased growth of surviving trees (Vepakomma et al., 2011), which might offset the negative effects of a drier climate on productivity. Second,  $\Psi_{50}$  is significantly associated with drought-induced mortality mechanisms, but is not directly associated with productivity (Urli et al., 2013). Third, other traits not examined in this study might better measure the relationship between stand productivity and severe drought. Particularly, intrinsic water use efficiency, i.e. the ratio between net CO<sub>2</sub> assimilation rate and stomatal conductance (Monclús et al., 2006), is a promising trait that explicitly quantifies the relationship between photosynthetic rate and water consumption. However, since this trait has only been documented for a few species, its use in large-scale studies remains unfeasible.

Intraspecific trait plasticity is likely one of the drivers of such conflicting results. Even though ontogeny and local environmental conditions influence intraspecific variation of frequently used traits (Aubin et al., 2016), most functional diversity studies tend to collate data from online data sources in order to expand their amplitude at little additional cost (e.g. Paquette & Messier, 2011; Correia et al., 2017). While the use of species-level trait means has allowed researchers to study important functional diversity-ecosystem functioning relationships, such an approach fails to incorporate species adaptations to local conditions. For instance, forest communities can adapt to long-term drought by shifting trait composition towards a greater proportion of drought-tolerant functional traits (Fauset et al., 2012). Such an adaptation potential might explain why O'Brien et al., (2017) found that trees in the wettest sites are the ones most vulnerable to drought-induced mortality across biomes, and why Grossiord et al., (2014) found that increased stand diversity only improved drought resistance in drier sites: frequent mild droughts should favor the selection of drought-tolerant individuals, whereas sharp increases in drought severity and intensity in historically wet regions might cause mortality of maladapted individuals (Schlesinger et al., 2016).

The LMA and  $\Psi_{50}$  trait group was associated with decreased mortality in drought plots across all bioclimatic domains, whereas the composition of the latent variable was different and its effect was not strongly expressed in non-drought situations. These differences in latent variable composition and significance among drought and non-drought plots likely reflect the distinct ecological meaning behind these variables: while the drought latent variable that significantly reduces mortality

represents drought resistance, the non-drought latent variable whose effect on mortality depends on the bioclimatic domain likely represents functional identity. During non-drought conditions, traits associated with reduced mortality can distinguish deciduous species from coniferous ones (Appendix 3.E). As climatic and site-level conditions are less favourable for deciduous species within the black spruce-feathermoss domain than in the balsam fir-white birch domain (Messaoud et al., 2007), deciduous species in the northern bioclimatic domain tend to be more stressed and more vulnerable to mortality than their dominant coniferous counterparts. Hence, lower values of dry leaf mass per unit area (i.e. deciduous species) are more likely to be associated with increased mortality than higher values of this trait (i.e. coniferous species) in the northern bioclimatic domain. The spatial distribution of our dataset might also have influenced our results, as drought and non-drought plots seldom overlapped due to the spatial nature of drought events. Nevertheless, the effect of such spatial autocorrelation was reduced by using only plots located in ecological sub-regions where both drought and non-drought plots were present.

## Conclusion

Considering that severe droughts are likely to increase in frequency in the near future due to climate change, and that trees might be more vulnerable to drought-induced mortality than initially thought (Allen et al., 2015), forest managers should take action to monitor and manage drought-associated risks. As mounting evidence suggests that LMA and  $\Psi_{50}$  significantly influence tree response to hydric stress (e.g. this study; Anderegg et al., 2016; Greenwood et al., 2017), using the community weighted means of these traits as indicators of vulnerability to drought-induced mortality should be an efficient way of monitoring drought vulnerability. Alternatively, wood density can be measured instead of  $\Psi_{50}$  because both traits are highly correlated and wood density is easier and less expensive to estimate (Aubin et al., 2016).

Overall, our results support that classic adaptation measures, such as favoring the presence of mixed-species forests through passive (natural regeneration) or active (plantation) silvicultural measures, are likely to reduce the risk of ecosystem-level losses of productivity in the face of climate extremes (Millar et al., 2007). In order to further reduce the impact of drought on stand mortality, multiple pro-active and targeted management strategies could also be implemented. Prioritizing economically-important drought-resistant species could reduce the impact of severe drought on stand mortality and productivity (Bréda et al., 2006). Such prioritization could be done either through the planting of drought-tolerant species or through the selective logging of individuals or species more vulnerable to drought. However, care must be taken to implement measures that reduce stand vulnerability to

drought without compromising vulnerability to other disturbances. Further, more intensive management interventions are also available, such as the breeding and planting of drought-tolerant genotypes (e.g. genotypes with higher LMA) and the assisted colonization of tree species (Gray et al., 2011). Alternative management strategies designed to reduce stand vulnerability to drought have also been proposed in the literature, namely the reduction of stand density (Bottero et al., 2017), the development of multi-aged stands (Bennett et al., 2015) and the planting of mixed stands that capitalize on niche complementarity effects (Lebourgeois et al., 2013). Employing such proactive solutions should help ensure the sustainability of forest management and prevent the late introduction of costly reactive management strategies.

## Acknowledgments

This work was funded by the Fonds de recherche du Québec, Nature et technologies (FRQ-NT). We would like to thank the Forest Complexity Modelling program, which is funded by NSERC through its CREATE program, and the Fonds Produits forestiers Résolu for supporting this project. We would also like to thank the Canadian Forest Service for developing and funding the TOPIC database, as well as everyone that has contributed to this project. Finally, we would like to thank Morgane Urli and Frédéric Doyon for their useful comments and suggestions.

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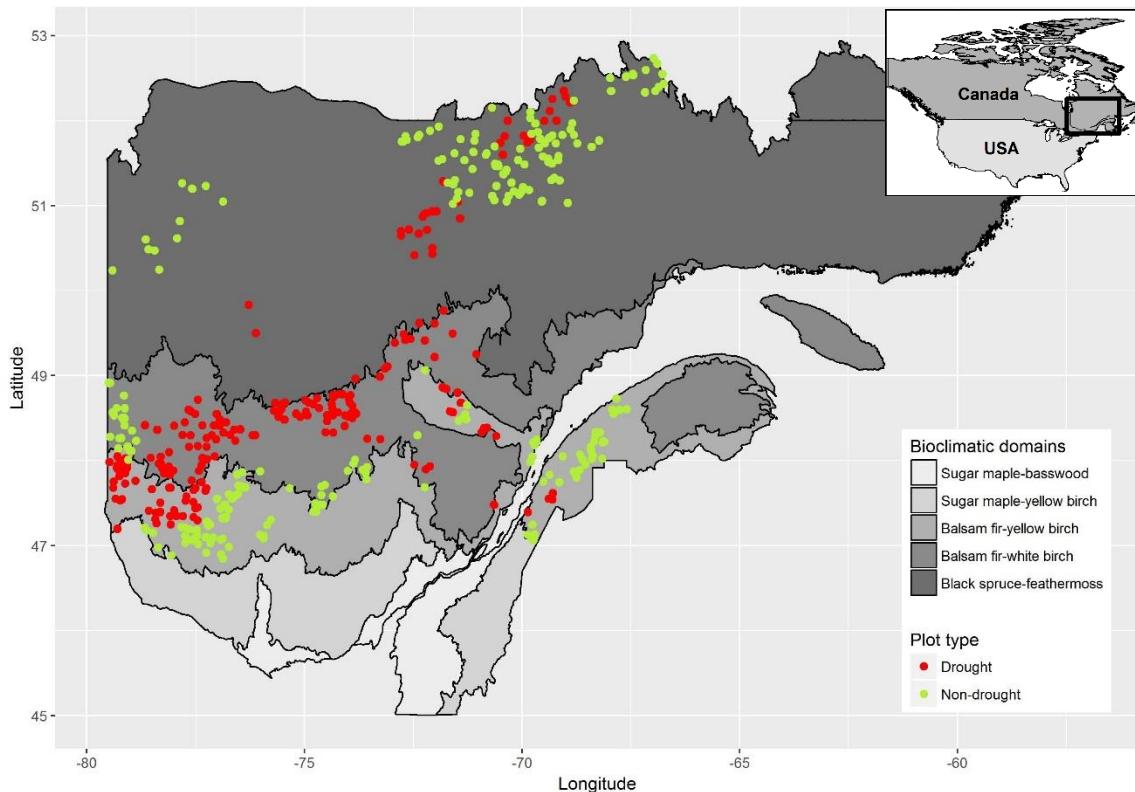
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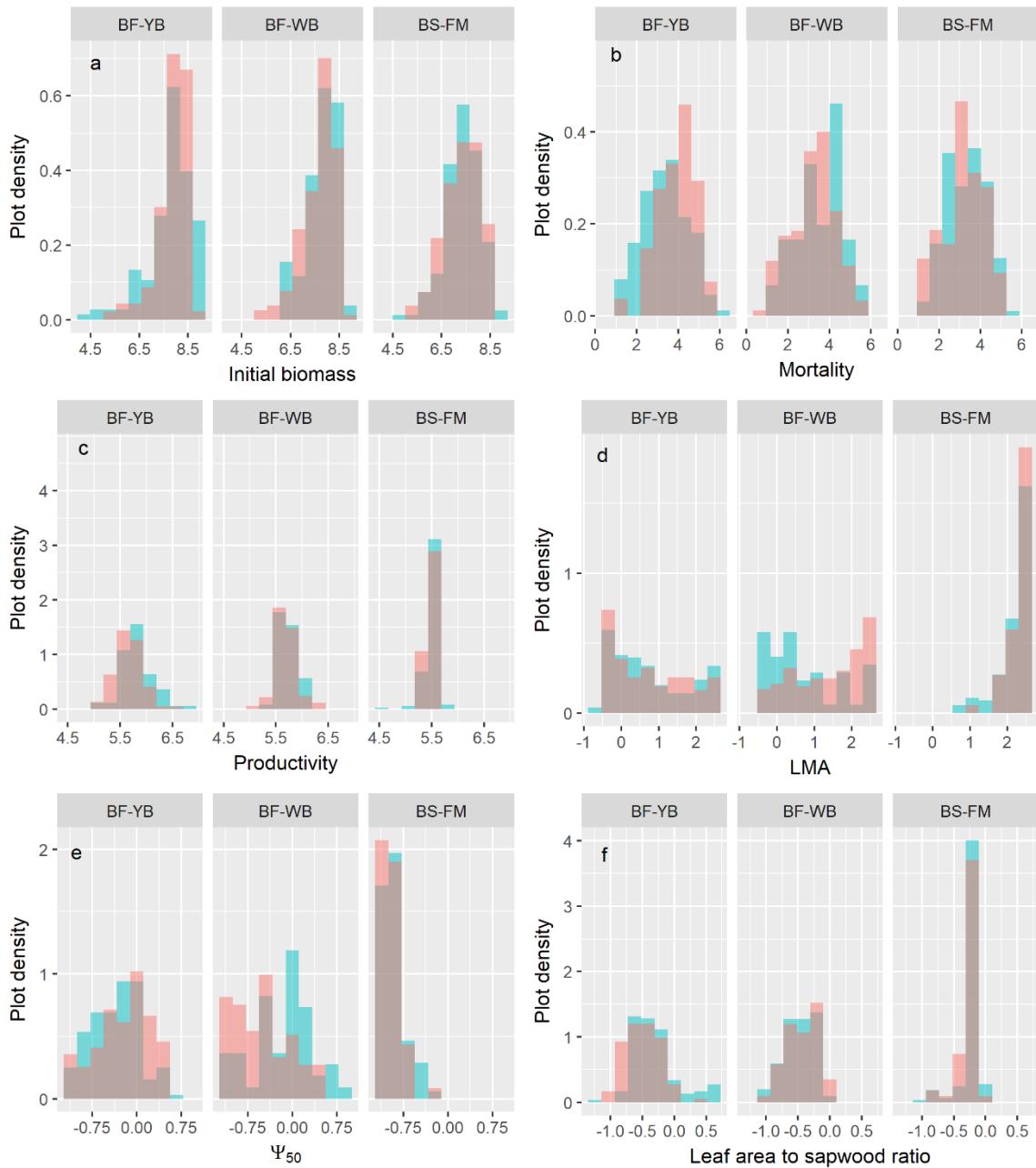
## Tables and figures

**Table 3.1.** AIC<sub>c</sub> and p-values of chi-square goodness of fit tests for SEM models per bioclimatic domain and plot type with varying latent variable compositions. *Leaf-sap* represents the leaf area to sapwood ratio functional trait. Models are valid if p-value is greater than 0.05. X corresponds to misspecified models (i.e. some estimated variances were negative). Valid models are shown in bold.

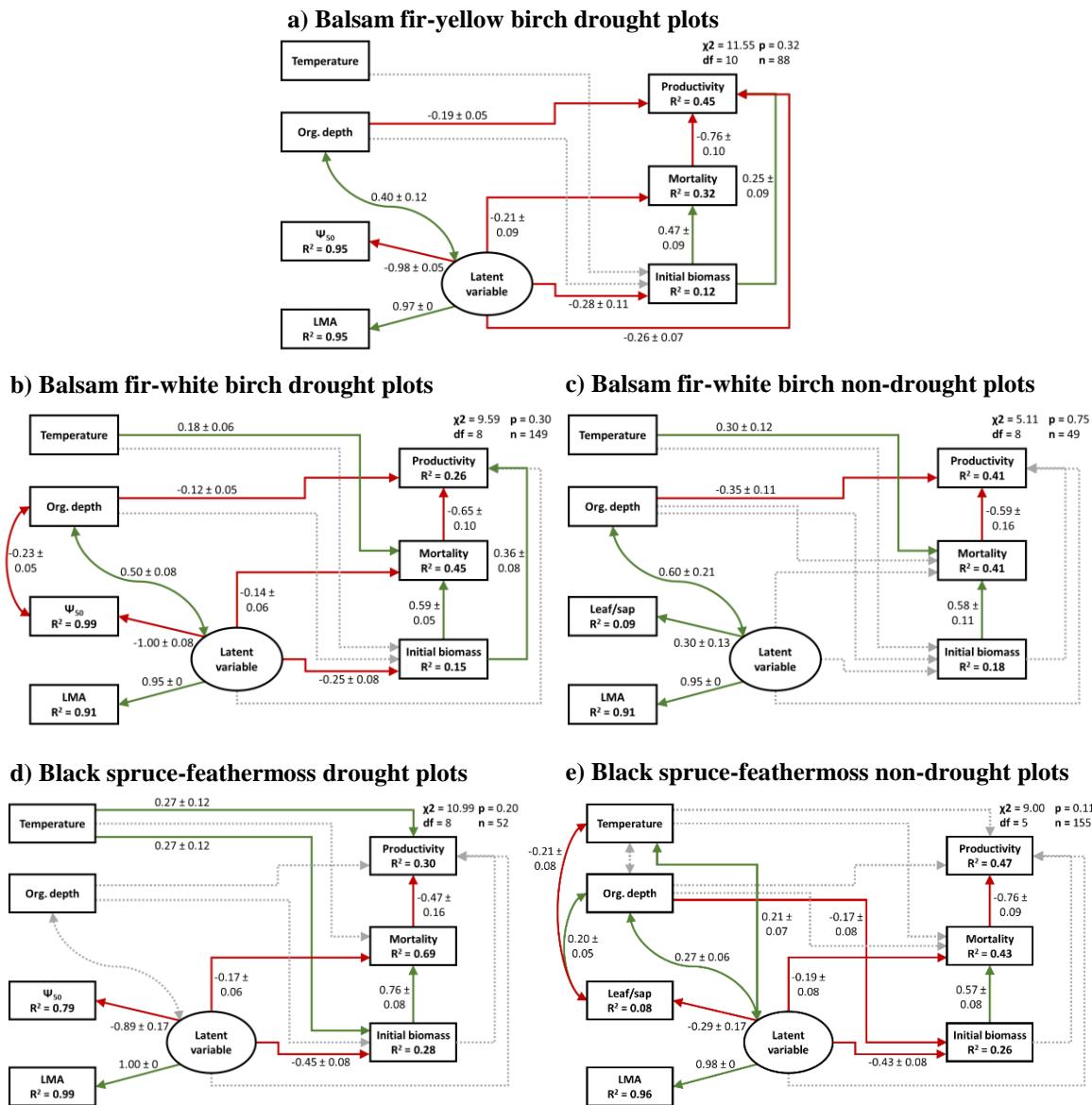
Latent variable structure	Parameters	BF-YB		BF-WB		BS-FM	
		Drought	Non- drought	Drought	Non- drought	Drought	Non- drought
LMA + $\Psi_{50}$ + Leaf-sap	p-value	X	X	X	X	X	X
	AIC <sub>c</sub>						
LMA + $\Psi_{50}$	p-value	<b>0.316</b>	X	<b>0.295</b>	X	<b>0.202</b>	X
	AIC <sub>c</sub>	<b>1504.6</b>		<b>2494.1</b>		<b>966.7</b>	
LMA + Leaf-sap	p-value	<b>0.258</b>	0.001	0.012	<b>0.745</b>	X	<b>0.109</b>
	AIC <sub>c</sub>	<b>1692.1</b>	2709.3	2821.1	<b>1011.6</b>		<b>2873.1</b>
$\Psi_{50}$ + Leaf-sap	p-value	0.001	X	0	<b>0.666</b>	X	X
	AIC <sub>c</sub>	1699.5		2825.0	<b>1014.3</b>		



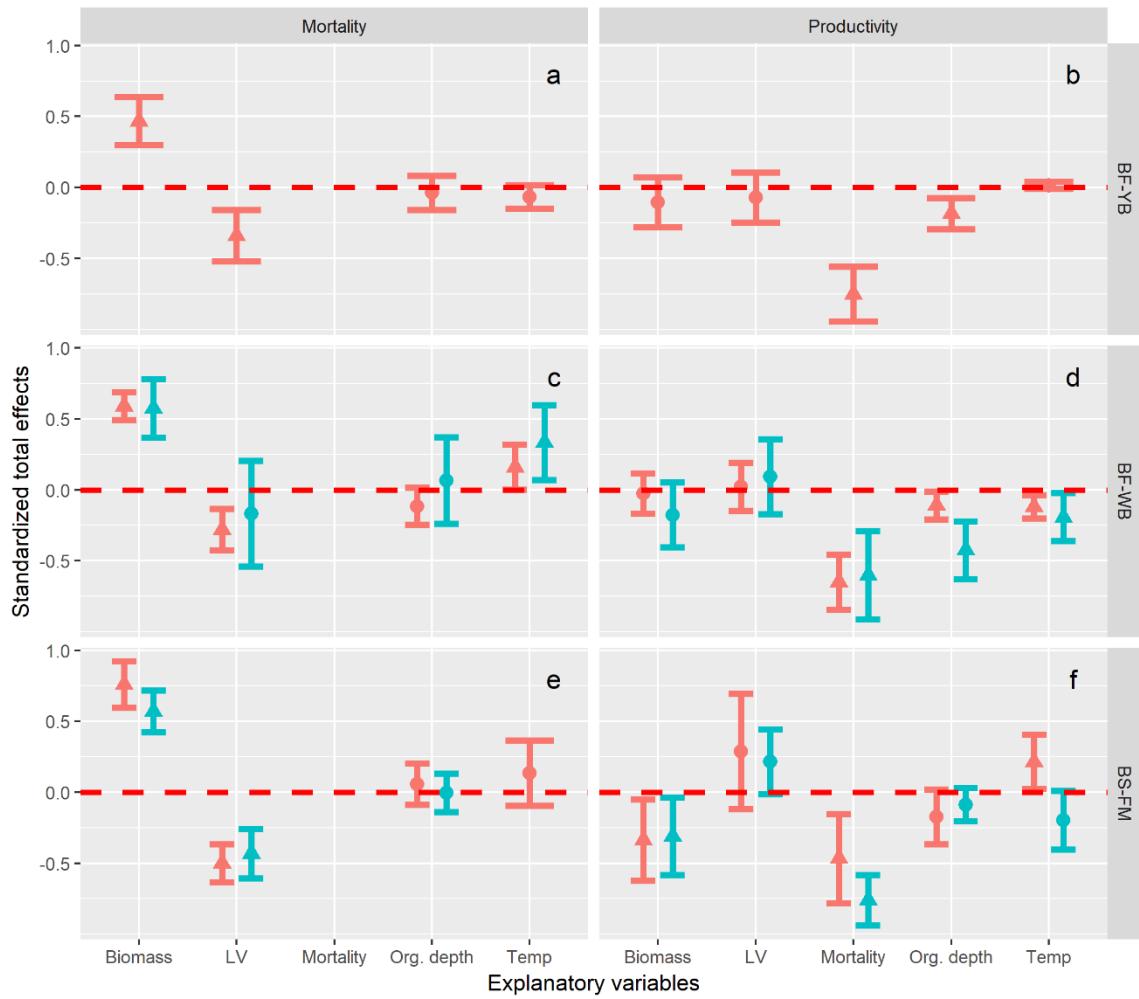
**Figure 3.1.** Map of the study area. Red points represent sampling plots where severe droughts occurred between sampling periods (balsam fir-yellow birch = 88; balsam fir-white birch = 149; black spruce-feathermoss = 52), and green points represent plots where no severe droughts occurred (balsam fir-yellow birch = 143; balsam fir-white birch = 49; black spruce-feathermoss = 155). Shading represents bioclimatic domains.



**Figure 3.2.** Histograms of plot-level data: biomass at time 1 (a), mortality (b), productivity (c), dry leaf mass per unit area (d), xylem pressure at which 50% of xylem conductivity in the stem is lost through cavitation (e), and leaf area to sapwood ratio (f). Drought plots are shown in red and non-drought plots are shown in blue. The natural logarithm of biomass, mortality and productivity is shown. Trait values correspond to community weighted means of standardized traits. Each bin represents the density of points scaled to integrate to 1 in order to make groups directly comparable despite differences in sample size.



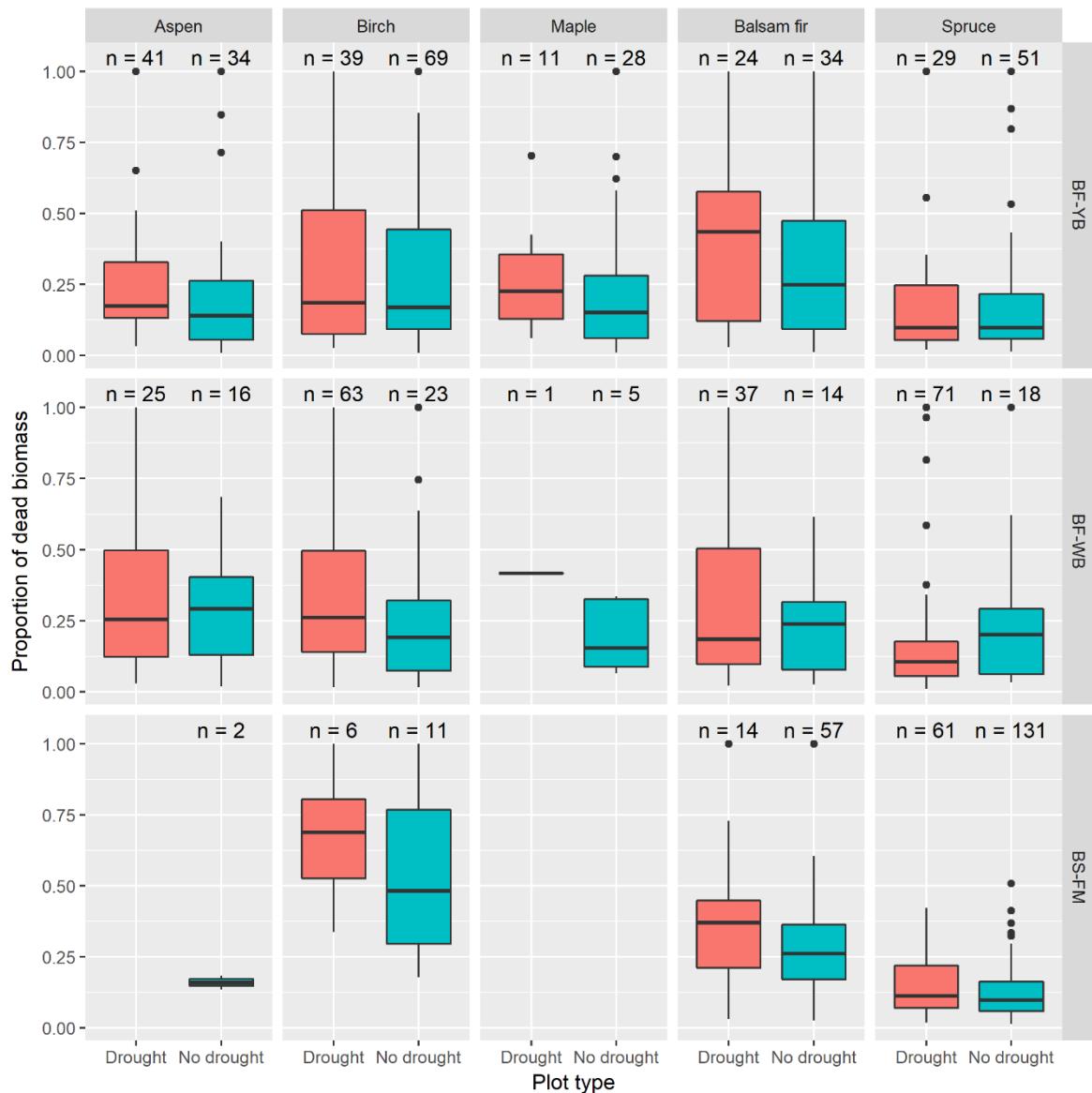
**Figure 3.3.** Results of the structural equation models of each bioclimatic domain and plot type. Each SEM's robust chi-square statistic, degrees of freedom, p-value and number of plots is shown. Presented path coefficients and standard errors have been standardized. Observed variables are represented by squares and latent variables are represented by circles. Arrow type is dependent on path coefficient effect and significance (green: positive and significant; red: negative and significant; grey and dotted: non-significant). The proportion of the variation explained for each dependent variable is shown in the corresponding boxes.



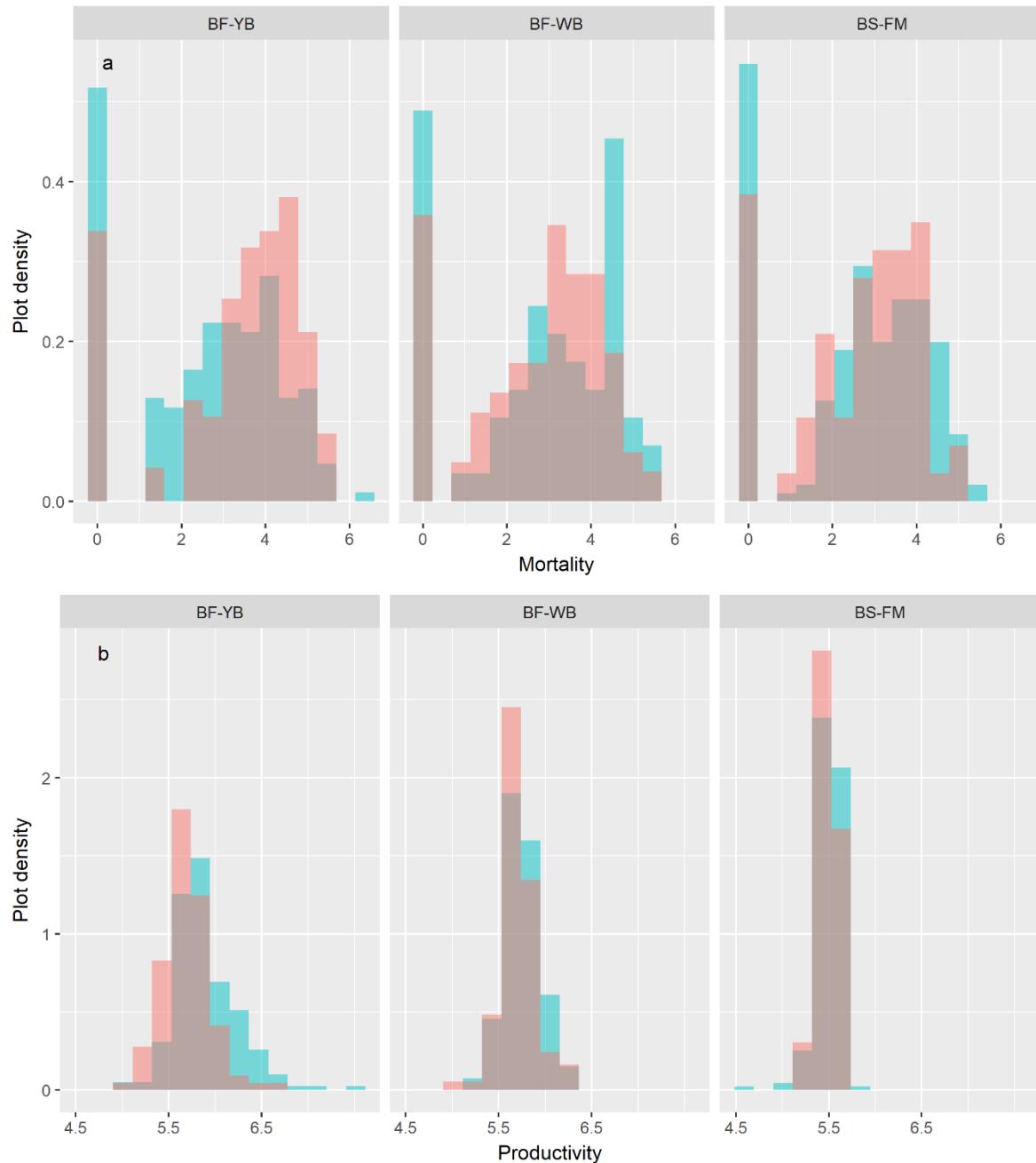
**Figure 3.4.** Total effects of observed variables on mortality and productivity across bioclimatic domains and plot types: BF-YB mortality (a) and productivity (b); BF-WB mortality (c) and productivity (d); and BS-FM mortality (e) and productivity (f). Drought plots are shown in red and non-drought plots are shown in blue. Significant effects are represented by triangles and non-significant effects are represented by circles. Error bars depict 95% confidence intervals. LV stands for latent variable and *Org. depth* stands for organic soil depth. Effects have been standardized in order to facilitate comparisons among different variables. A horizontal red dashed line is shown at an effect size of 0.

## Supplementary material

**Appendix 3.A.** Boxplot of the proportion of dead biomass of the main taxonomic groups found within our study area per plot type and per bioclimatic domain. Bioclimatic domains represented are balsam fir-yellow birch (BF-YB), balsam fir-white birch (BF-WB) and black spruce-feathermoss (BS-FM). N denote the number of plots per group.



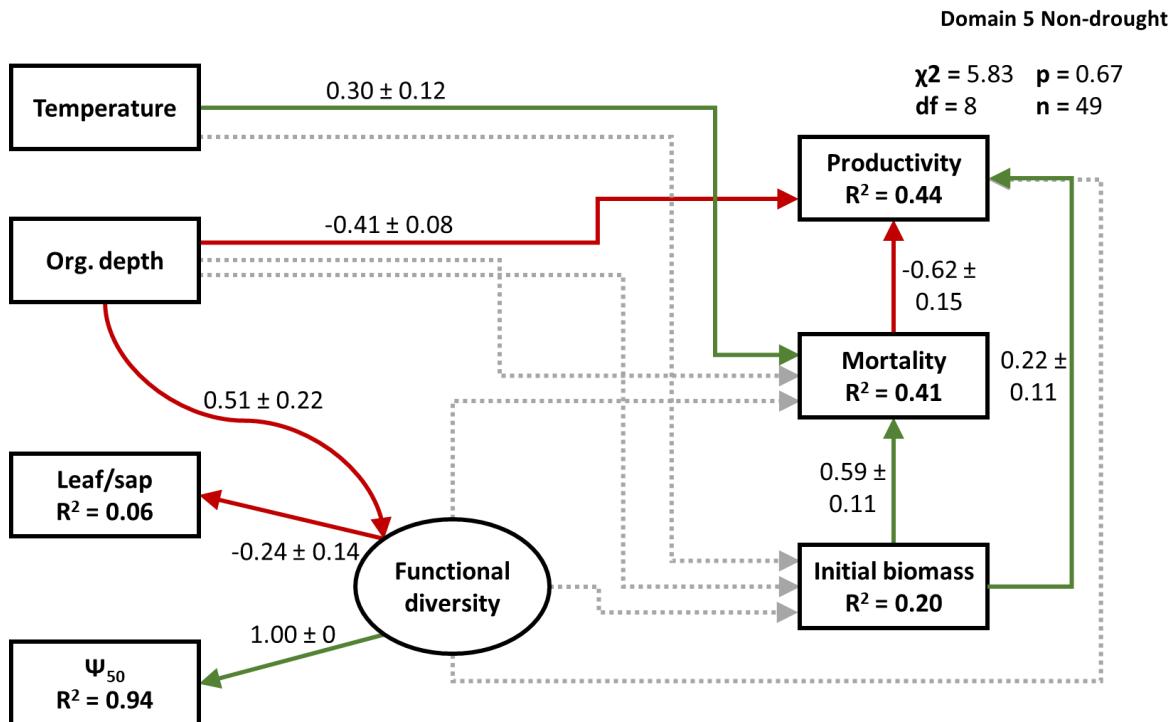
**Appendix 3.B.** Histograms of stand mortality (a) and productivity (b) per bioclimatic domain. Drought plots are shown in red and non-drought plots are shown in blue. The natural logarithm of mortality and productivity is shown. Each bin represents the density of points scaled to integrate to 1 in order to make groups directly comparable despite differences in sample size. Bioclimatic domains follow the same nomenclature as in Appendix 3.A.



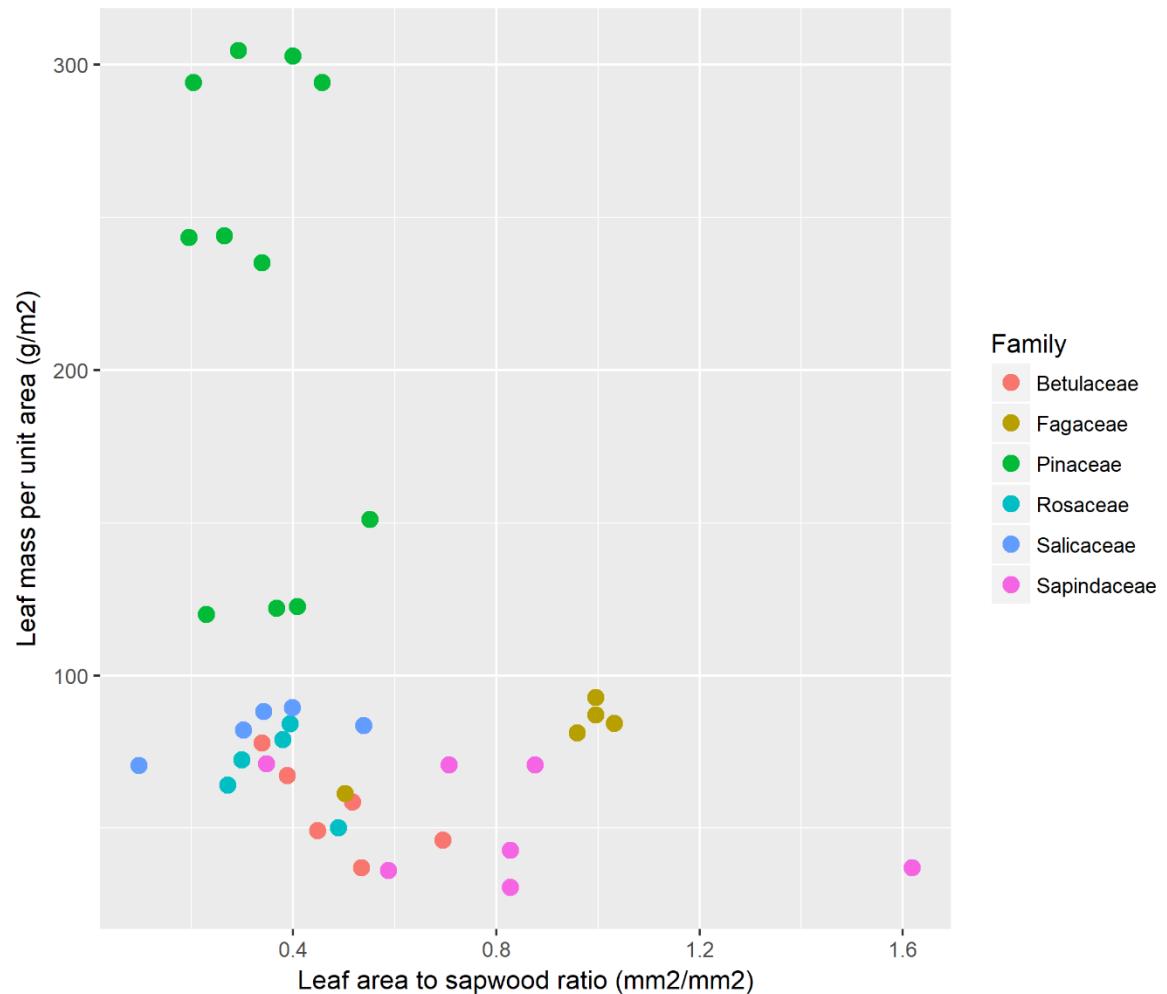
**Appendix 3.C.** Number and percentage of plots where mortality did not occur and number of plots where mortality was greater than 0 per bioclimatic domain and plot type. Bioclimatic domains follow the same nomenclature as in Appendix 3.A.

Bioclimatic domain	Plot type	No mortality	Mortality greater than 0	Percentage of plots with 0 mortality
<b>BF-YB</b>	Drought	16	88	15.4
	No-drought	44	143	23.5
<b>BF-WB</b>	Drought	29	149	16.3
	No-drought	14	49	22.2
<b>BS-FM</b>	Drought	11	52	17.5
	No-drought	52	155	25.1

**Appendix 3.D.** Alternative structural equation model of the non-drought Balsam fir-White birch bioclimatic domain. The difference in AICc was 2.7. Robust chi-square statistic, degrees of freedom, p-value and number of plots is shown. Presented path coefficients and standard errors have been standardized. Observed variables are represented by squares and latent variables are represented by circles. Arrow type is dependent on path coefficient effect and significance (green: positive and significant; red: negative and significant; grey and dotted: non-significant). The proportion of the variation explained for each dependent variable is shown in the corresponding boxes.



**Appendix 3.E.** Tree species leaf mass per unit area plotted against leaf area to sapwood ratio coloured according to taxonomical family.



## Conclusion générale

La diversité fonctionnelle est de plus en plus perçue comme un concept prometteur pour le développement d'un aménagement forestier visant à la fois la multifonctionnalité des forêts et leur pérennité face aux perturbations (Mori, Lertzman, et Gustafsson, 2017). Par contre, le manque de connaissances sur le rôle de la diversité fonctionnelle dans la dynamique des écosystèmes forestiers (Aubin et al., 2016) et l'incompatibilité entre les mesures de diversité fonctionnelle et les données disponibles (Mori, Lertzman, et Gustafsson, 2017) freine son utilisation dans un contexte d'aménagement forestier. L'objectif de ma thèse était d'analyser le potentiel et le rôle de la diversité fonctionnelle des arbres dans l'aménagement durable des forêts tempérées nordiques et boréales, de façon à faciliter l'utilisation du concept de la diversité fonctionnelle en aménagement forestier.

Dans le premier chapitre j'ai utilisé des tests non-paramétriques de Mann-Whitney et du bootstrapping pour analyser l'impact de l'âge, de la hauteur et du type de couvert sur trois composantes de la diversité des arbres (compositionnelle, structurelle et fonctionnelle) dans près de 100 000 placettes d'inventaire forestier. Ces analyses suggèrent que l'âge des peuplements, l'un des indicateurs de biodiversité les plus utilisés à une échelle globale (Montréal Process Working Group, 2015), ne devrait probablement pas être utilisé comme le seul indicateur de biodiversité dans l'aménagement des forêts tempérées nordiques et boréales. Suivant cette analyse, il appert que la biodiversité des peuplements forestiers pourrait être évaluée de manière plus exhaustive par l'utilisation d'indicateurs de diversité fonctionnelle. Les deux chapitres suivants ont été dédiés à l'utilisation d'indicateurs de diversité fonctionnelle afin de mesurer les liens entre la biodiversité du peuplement, son fonctionnement et sa réponse aux perturbations.

Dans le deuxième chapitre, j'ai analysé le rapport entre deux indicateurs de diversité fonctionnelle des arbres avant-coupe (la redondance fonctionnelle et la diversité des réponses), et la productivité après coupe du peuplement, afin de vérifier si les peuplements plus diversifiés sont plus résilients à cette perturbation. Bien que les deux métriques utilisées offrent un potentiel intéressant pour évaluer l'impact des perturbations sur le fonctionnement des écosystèmes forestiers, les études empiriques qui valident ces liens théoriques dans les forêts tempérées nordiques et boréales demeurent rares (Mori, Furukawa, et Sasaki, 2013). Pour ce chapitre, le réseau de placettes temporaires du MFFP a été utilisé pour quantifier la biodiversité des peuplements avant-coupe, et des séries temporelles provenant de capteurs satellitaires ont été utilisées pour quantifier la productivité après coupe. Les résultats mettent en évidence la valeur ajoutée de l'utilisation de la diversité des réponses lors de l'analyse de la productivité après coupe, de même que l'avantage de considérer des groupes

fonctionnels distincts (les feuillus et les conifères) dans ce genre d'études. Mes résultats suggèrent que la diversité des réponses est un meilleur prédicteur de la productivité de l'écosystème après des perturbations totales que la redondance fonctionnelle. Étant donné que le calcul de la diversité des réponses s'appuie directement sur des traits fonctionnels reliés aux stratégies des arbres face aux perturbations (ex. le rapport du poids sec de la feuille à la surface foliaire, la densité du bois; Elmquist et al., 2003), cet indicateur est plus efficace que la redondance fonctionnelle pour prévoir l'effet de ces stratégies de réponse suivant une coupe totale. L'utilisation de l'abondance relative des espèces dominantes comme co-variables dans les modèles statistiques nous a également permis de détecter un effet négatif de l'abondance de l'épinette noire sur la productivité après coupe. Cet effet semble refléter une plus grande susceptibilité des peuplements dominés par cette espèce à des facteurs menant à une réduction de la productivité après coupe, comme la paludification et l'invasion par des éricacées (Thiffault et al., 2013).

Dans le troisième chapitre, j'ai examiné la relation entre trois traits fonctionnels associés à la résistance à la sécheresse et la réponse des arbres de peuplements tempérés nordiques et boréaux à la sécheresse. J'ai utilisé la modélisation par équations structurelles pour identifier lesquels parmi ces traits fonctionnels sont les plus fortement corrélés à la réponse des arbres à la sécheresse, et pour identifier si ces effets étaient directs ou indirects. Étant donné que les relations entre les traits fonctionnels et la tolérance à la sécheresse des arbres changent selon les zones climatiques (O'Brien et al., 2017), des données empiriques locales doivent être utilisées pour vérifier l'importance des traits fonctionnels pour chaque écosystème. Mes résultats suggèrent que dans ces forêts, un rapport plus fort du poids sec de la feuille à la surface foliaire et une plus faible valeur de pression du xylème conduisant à une perte de 50% de sa conductivité par cavitation ( $\Psi_{50}$ ) réduisent d'une façon significative la mortalité causée par la sécheresse. Par contre, l'impact de ces traits fonctionnels sur la mortalité ne mènent pas à un effet significatif sur la réponse de la productivité du peuplement à la sécheresse. Aucune relation significative n'a été trouvée entre le troisième trait fonctionnel considéré (le rapport de la surface foliaire à la surface de l'aubier) et la réponse des peuplements forestiers à la sécheresse.

## **Implication des résultats**

Mes résultats mettent l'emphase sur l'importance de considérer la diversité fonctionnelle pour mieux comprendre l'impact des perturbations sur les écosystèmes. La diversité fonctionnelle permet de quantifier les liens mécanistiques entre les espèces et leurs réponses aux changements environnementaux (Suding et al., 2008), alors que la richesse spécifique, l'indicateur de biodiversité

le plus commun dans ce genre d'études (p. ex. Isbell et al., 2015), ne le permet pas. En plus, les résultats suggèrent que la diversité des réponses est un indicateur plus efficace que la redondance fonctionnelle lors de l'analyse de la réponse de la productivité des peuplements forestiers aux perturbations totales. Par ailleurs, les résultats du second chapitre suggèrent que la réponse de la productivité après coupe dans les forêts tempérées nordiques et boréales est conforme à la « mass ratio hypothesis » (Grime, 1998). Selon cette hypothèse, les traits des espèces dominantes, c'est à dire l'épinette noire, influencent fortement le fonctionnement de l'écosystème. Finalement, j'ai identifié deux traits fonctionnels (le rapport du poids sec de la feuille à la surface foliaire et la  $\Psi_{50}$ ) qui influencent d'une façon significative la mortalité causée par la sécheresse des arbres dans les forêts tempérées nordiques et boréales.

Ces découvertes scientifiques ont des conséquences potentiellement importantes pour l'aménagement forestier. Mes résultats suggèrent que le maintien de peuplements plus âgés dans les forêts aménagées n'est pas suffisant pour protéger toutes les composantes de la biodiversité. Historiquement, l'âge des peuplements a été proposé comme un indicateur de biodiversité avec le but de protéger des espèces rares associées aux vieilles forêts. Cet indicateur n'a pas été développé comme indicateur de toutes les composantes de la biodiversité, mais il est souvent utilisé dans ce but (Hunter et Malcolm, 1990). En effet, les communautés d'espèces associées aux vieilles forêts ne sont pas fortement corrélés à la diversité fonctionnelle, soit la composante de la diversité la plus liée au fonctionnement de l'écosystème (Cadotte, Carscadden, et Mirochnick, 2011) et à sa réponse aux perturbations (Elmqvist et al., 2003). En fait, mes résultats mettent en évidence l'influence de la diversité fonctionnelle sur la réponse de la productivité des peuplements aux perturbations totales (les coupes forestières dans le deuxième chapitre) et partielles (la sécheresse dans le troisième chapitre).

Malgré les progrès effectués lors des dernières années (Mori, Lertzman, et Gustafsson, 2017), l'intégration directe de la diversité fonctionnelle dans les plans d'aménagement forestier demeure compliquée. Mes études sur la diversité fonctionnelle des forêts tempérées nordiques et boréales m'ont toutefois amené à proposer quelques stratégies d'aménagement. D'abord, inclure le type de couvert et la hauteur du peuplement est une façon efficace d'améliorer la performance de l'âge des peuplements en tant qu'indicateur holistique de la biodiversité. Deuxièmement, afin de maximiser la productivité après coupe, les aménagistes doivent accorder une attention particulière aux peuplements dominés par l'épinette noire, puisqu'ils sont plus vulnérables à une perte de productivité par le biais de la paludification et de l'invasion par des éricacées (Thiffault et al., 2013). Finalement, l'utilisation de la moyenne pondérée du rapport du poids sec de la feuille à la surface foliaire et de la  $\Psi_{50}$  des peuplements peut renseigner les aménagistes sur la vulnérabilité des peuplements à la sécheresse,

tandis que la priorisation des espèces (Bréda et al., 2006) ou des génotypes (Gray et al., 2011) tolérants à la sécheresse peuvent réduire cette vulnérabilité.

## **Limites**

Une étape essentielle de toute étude scientifique est de poser une réflexion critique sur la portée des résultats. Dans cette perspective, il m'apparaît important de déterminer et d'examiner de façon explicite les faiblesses de mon étude dans le but d'éviter une mauvaise interprétation de mes résultats et de prévenir le développement de stratégies d'aménagement inadéquates. De plus, cette réflexion vise à inspirer la poursuite de nouvelles avenues de recherche ayant pour objectif de répondre aux limites soulevées.

D'abord, dans cette thèse j'ai étudié la réponse d'une seule fonction de l'écosystème, c'est-à-dire la productivité, aux perturbations. Or, l'aménagement durable des forêts doit gérer plusieurs services écosystémiques en même temps (Fürstenau et al., 2007). Bien que la performance de la production primaire des forêts influence fortement celle de plusieurs services écosystémiques (p. ex. séquestration du carbone; Hulvey et al., 2013), une relation significative entre la diversité des arbres et la production primaire n'assurent pas une relation significative avec la performance d'autres services. De plus, mon analyse a porté seulement sur la diversité des arbres. Alors que les arbres jouent évidemment un rôle très important dans le fonctionnement des forêts, la diversité de ce groupe taxonomique n'est pas forcément corrélée à celle d'autres groupes. En outre, je n'ai pas considéré la variabilité intra-spécifique des traits fonctionnels et je n'ai pas examiné l'importance de plusieurs autres traits fonctionnels qui peuvent éventuellement être informatifs pour prédire certaines fonctions comme la résistance aux sécheresses (p. ex. l'efficacité intrinsèque de l'utilisation de l'eau; Monclús et al., 2006).

Malgré l'étendue de l'aire d'étude analysée, mon analyse du rapport diversité-productivité a été réalisée à l'échelle locale des placettes d'inventaires. Les unités d'aménagement forestier au Québec sont toutefois aménagées à une échelle plus grande, à laquelle opèrent des processus environnementaux et écologiques (flux de nutriments, dispersion d'espèces, etc.) qui peuvent influencer d'une façon significative les relations analysées (Brose et Hillebrand, 2016). Par exemple, Barnes et al., (2016) ont montré que la richesse spécifique et la biomasse totale des macroinvertébrés de la litière sont plus fortement corrélées avec le fonctionnement d'un écosystème tempéré à l'échelle du paysage que la dispersion fonctionnelle. Finalement, l'influence du temps sur les rapports diversité-productivité peut également être importante. Le deuxième chapitre a étudié une série

temporelle après coupe relativement courte (10 ans) par rapport à la longévité des espèces d'arbres étudiées, tout comme le fait que les périodes d'échantillonnage des placettes dans le troisième chapitre s'échelonnaient sur une vingtaine d'années. La plupart de ces limitations sont donc liées en bonne partie à la grande longévité des arbres par rapport à d'autres types d'organismes, et à l'étendue de leurs aires de distribution, et sont ainsi propres à l'ensemble des études empiriques sur les relations entre la biodiversité des arbres et le fonctionnement de l'écosystème.

## Perspectives

Les arbres sont incontestablement un groupe taxonomique qui joue un rôle majeur dans la productivité primaire des forêts. Toutefois, d'autres groupes taxonomiques influencent la productivité (p. ex. les lichens et les mousses; Nilsson et Wardle, 2005), mais leur impact n'a pas été intégré directement dans mes analyses. Explorer comment les interactions entre plusieurs groupes taxonomiques affectent la réponse de la productivité primaire aux perturbations pourrait dévoiler des résultats très intéressants. En outre, il existe une forte différence entre l'échelle à laquelle mes analyses ont été effectuées et l'échelle à laquelle les forêts sont aménagées. Étant donné que les processus importants à une échelle locale ne sont pas nécessairement significatifs à une échelle plus grande, analyser l'effet des échelles spatiales et temporelles sur les interactions entre la diversité des arbres, la productivité primaire et les perturbations, serait important pour valider l'importance de ces relations. Au Québec, l'estimation des relations espèce-superficie avec les placettes d'inventaire forestier et le calcul de la productivité au niveau provincial à plusieurs résolutions provenant de capteurs satellitaires pourrait nous permettre de faire ce saut d'échelle. Finalement, l'utilisation des bases de données de traits fonctionnels ne tient pas compte de l'importance de la plasticité intra-spécifique des traits fonctionnels. Puisque les valeurs des traits fonctionnels peuvent varier considérablement entre individus de la même espèce, intégrer cette variabilité dans des futures études est fortement recommandé.

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