UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DÉVELOPPMENT DES PEUPLEMENTS ET DYNAMIQUE TEMPORELLE DES EFFETS DE LA DIVERSITÉ SUR LA PRODUCTIVITÉ DES ARBRES

THÈSE
PRÉSENTÉE
COMME EXIGENCE PARTIELLE
DU DOCTORAT EN BIOLOGIE

PAR
JON URGOITI OTAZUA

OCTOBRE 2023

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

THE ROLE OF STAND DEVELOPMENT IN DRIVING THE TEMPORAL DYNAMICS OF THE DIVERSITY EFFECTS ON PRODUCTIVITY

DISSERTATION
PRESENTED
AS PARTIAL FULFILLMENT
OF THE DOCTORATE IN BIOLOGY

BY
JON URGOITI OTAZUA

OCTOBER 2023

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to my research director Alain Paquette, and co-directors, Christian Messier and William Keeton, for their mentoring and support. I want to particularly highlight the figure of my director for his patience, understanding, enthusiasm, and guidance. He has always been willing to help at all times. This gave me the courage and confidence to face all the doubts and difficulties that could arise during my Ph.D. I am very grateful to have had him as my director.

In addition to my supervisors, many people have helped me through my studies. The following paragraphs are intended to offer my deepest gratitude to each and every one of the people who have helped me in one way or another in the achievement of this dissertation.

In the first two years of my studies, I spent a considerable amount of time in the IDENT-MAC experiment collecting data. The field seasons would not have been possible without the esteemed help of many interns – Francis Giard, Pilar Orejas, Claudia Masso, Manon Monfort, Theotime Fily, Luis Andres Morelo, Maribel Carol, Kaila Langile, Takele Birhanu, Sohail Akram, Juan Cordoba, Meggy Legault. Thank you all for your dedication and effort. I will never forget the discussions, laughs, and funny stories we shared during our lunch breaks at the Morgan Arboretum that lightened up the strenuous work in the field.

The lab groups of Alain Paquette and Christian Messier have been a tremendous source of inspiration and support. Special thanks to Eric Searle and Daniel Schoning for helping me immensely with the data analyses, Michael Belluau for great theoretical discussions about diversity and its effects, and also for your immense work collecting traits data that I ultimately benefited from, and Bastian Lecigne for giving a hand with R software every time I needed it, and for inviting me to be part of the football team. Also, heartfelt thanks to Elyssa Cameron who provided essential administrative support at the university. And the last but not least, my most sincere thanks to Rita Sousa-Silva who, despite joining the lab in the late years of my Ph.D., she has had a tremendous impact on my studies. Rita, thank you for the endless help, and support. I am sure that without your friendship, this Ph.D. would have been much more difficult to carry, and certainly less fun.

Out of the university environment, there are also people I would like to thank for supporting my journey and goal. Utku Karakaya and Cana Dai, we met thanks to our dogs. And from there, we built a beautiful friendship in which I always found the energy and motivation I needed to pursue my studies. In a similar way Lino Tremblay, Luis Aledo, and Daniel Haché, your friendship helped me cope with moments of stress and doubts related to my studies in a better way. Thank you for welcoming me and Misha into your ‘family’ and making us feel so at home.

Naturally, across the ocean, I have had the unconditional support of my family that goes beyond these studies. Both my parents and my siblings have always believed in me, even when I doubted myself. Your unwavering support and endless encouragement have been my backbone throughout my academic journey. I cannot forget to also mention, of course, my lifelong friends, my "cuadrilla". Spending time with you and feeling you close has helped me greatly to face all the challenges of my Ph.D. My family’s and friends’ love and support, even at a distance, have made a world of a difference.

And by last, none of this would be possible without the constant support and encouragement of my partner. Thank you, Misha, for everything. You are the person who has not stopped encouraging me and supporting me in the most difficult moments of my Ph.D., but also the person with whom I have shared the good moments of it. I feel very lucky and proud to have you by my side.

DEDICATION

To my family and friends,
as well as all the people who supported
and helped me in the realization of this work.
My deepest gratitude for your
support and encouragement.
And above all, to my partner and wife-to-be,
for being my greatest support during these years.

TABLE OF CONTENTS

Acknowledgements iii
Dedication v
Table of Contents vi
List of Figures vii
List of Tables ix
Résumé x
Abstract xii
Introduction 1
Chapter 1 No complementarity no gain – Net diversity effects on tree productivity occur once complementarity emerges during early stand development 11
Chapter 2 Functional diversity and identity influence the self-thinning process in young forest communities 43
Chapter 3 Early tree community overyielding is explained by asymmetric species-specific response to diversity 72
Conclusions 103
References 116

LIST OF FIGURES

Chapter 1

Figure 1.1 Principal Component Analysis of the species traits values 31
Figure 1.2 Net diversity effects on *G* (m^2/ha) over time driven by complementarity and selection 32
Figure 1.3 Net diversity effects on *G* (m^2/ha) over time for high and low diversity mixtures grouped by PC1 33
Figure 1.4 Net diversity effects on *G* (m^2/ha) over time for plots with high, medium, and low CWM values group by PC1....................................... 34
Figure 1.5 Net diversity effects on *G* (m^2/ha) over time for plots with high, medium, and low CWM values group by PC2 35
Figure S1.1 Cumulative stand basal area as a proxy of competition intensity over time in IDENT-MTL 39
Figure S1.2 Stand basal area by monocultures and mixtures for the final year of the experiment (i.e., year 11) 40
Figure S1.3 Cumulative stand basal area and cumulative mortality through time for each monoculture and mixture 41

Chapter 2

Figure 2.1 Estimated self-thinning trajectories for each tree community 62
Figure 2.2 Predicted self-thinning knee point against functional identity of PC2 63
Figure 2.3 Predicted self-thinning slope against functional diversity and identity of PC1 64
Figure 2.4 Predicted quadratic mean diameter against functional diversity and identity of PC1 over time 65
Figure 2.5 Predicted mortality against functional diversity and identity of PC1 over time 66

Figure S2.1 The approach followed to estimate the knee point and slope of the $lnN \sim ln\overline{d}_q$ trajectory for each plot 67
Figure S2.2 Correlation between tree community self-thinning slope and productivity in the last year of the study 68

Chapter 3

Figure 3.1 Species specific *G* (m^2/ha) against species richness over time 92
Figure 3.2 Species RY over time against the gradient of the first principal component (i.e., $PC1_{target}$) 93
Figure 3.3 Mixtures' RYT and constituent species' RY over time 94
Figure S3.1 Species' RY against the heterospecific neighbors mean basal area (m^2) 99
Figure S3.2 Estimates of the effect of functional identity of the target species on species' RY over time 100
Figure S3.3 RYT of each mixture that contains deciduous and evergreen species for the last year of the study 101
Figure S3.4 Species' mean RY across blocks and plots over time 102

Conclusion

Figure 4.1 Overview of the main findings of each of the three chapters 105
Figure 4.2 Outline of mechanisms proposed in BEF literature to diversity effects on productivity 114

LIST OF TABLES

Chapter 1

Table 1.1 Summary of the generalized additive model of significant diversity indices on net diversity effects over time 30
Table S1.1 Species' trait values used in analyses 36
Table S1.2 Correlation of each functional trait and the both Principal Components extracted from the PCA analysis 37
Table S1.3 Summary of the data from IDENT-MTL tree diversity experiment 38

Chapter 2

Table 2.1 Summary of the linear mixed-effects model of significant diversity indices on the "knee" point of the self-thinning 60
Table 2.2 Summary of the linear mixed-effects model of significant diversity indices on self-thinning slopes 61
Table S2.1 Parameter estimates and fit statistics for self-thinning models for each tree community 69
Table S2.2 Summary of the linear mixed-effects model of significant diversity effects on QMD over time 70
Table S2.3 Summary of the generalized linear mixed-effects model of significant diversity effects on mortality over time 71

Chapter 3

Table 3.1 Summary of the linear mixed model testing the effects of species identity, and species richness on species' productivity over time 96
Table 3.2 Summary of the linear mixed model the effects of the target species' and heterospecific neighbors' functional identity on RY over time 97
Table 3.3 Summary of the repeated measures ANOVA testing whether mixtures' RYT changed over time 98

RÉSUMÉ

Au cours des dernières décennies, l'étude de la relation entre la diversité et la productivité dans les écosystèmes forestiers a fait l'objet d'une grande attention. Bien qu'il existe maintenant des preuves irréfutables que la diversité des arbres affecte positivement la productivité des forêts, les études présentent une variation considérable de la force de ces effets, et leur apparition au long du développement de la forêt. Ma thèse, alimentée par ces résultats divergents, cherche à comprendre le rôle du développement de la forêt sur la dynamique temporelle des relations diversité-productivité. En utilisant les enregistrements annuels de croissance et de mortalité de l'expérience de biodiversité IDENT-MTL, j'étudie si et comment les relations diversité-productivité changent au cours des étapes initiales du développement du peuplement (c'est-à-dire l'établissement, la fermeture de la canopée et le début de l'auto-éclaircie). Je montre d'abord que la force des effets de la diversité sur la productivité augmente de façon non linéaire au cours du développement de la forêt et que cela est principalement dû à une augmentation graduelle de la complémentarité. Ensuite, je démontre que l'émergence de ces effets positifs de la diversité s'explique par les différences entre les communautés d'arbres dans la façon dont elles se développent au cours de la phase d'auto-éclaircie, lorsque la concurrence pour la lumière est la plus intense. Je souligne que ces différences dans les trajectoires d'auto-éclaircie sont fortement influencées par la diversité fonctionnelle et l'identité des communautés d'arbres. Troisièmement, au niveau des espèces, j'illustre comment, tout au long du développement de la forêt, les réponses asymétriques des espèces à la diversité, basées sur leur identité fonctionnelle et celle de leurs voisins hétérospécifiques, expliquent le surrendement des mélanges au fil du temps. Dans l'ensemble, cette thèse illustre, à partir de différentes perspectives et dimensions, les mécanismes et processus qui conduisent à la dynamique temporelle des relations diversité-productivité au cours du développement des peuplements forestiers et à l'optimisation des mélanges à long terme. Ce travail a des implications majeures pour la gestion et la conservation des forêts, car il fournit des informations cruciales pour guider des aménagements plus performants.

Mots clés: IDENT; biodiversité-fonctionnement des écosystèmes; productivité; long-terme effets de diversité; diversité fonctionnelle; identité fonctionnelle

ABSTRACT

During the last decades, investigating the relationship between diversity and productivity in forest ecosystems has received much attention. As a result, there is now compelling evidence that tree diversity, in general, positively affects forest productivity. Yet there is considerable variation among studies on the strength of such effects and their timing during stand development. My research, fueled by these divergent results, seeks to understand the role of stand development on the temporal dynamics of diversity-productivity relationships. Using the annual growth and mortality records from the IDENT-MTL biodiversity experiment, I investigate whether and how diversity-productivity relationships change through the initial stages of stand development (i.e., stand establishment, canopy closure, and beginning of self-thinning). Toward a more complete picture, I first show that the strength of diversity effects on productivity increases non-linearly and that this is driven primarily by gradual increases in complementarity among species (niche-partitioning that leads to reduced competition). Second, I demonstrate that the emergence of these positive diversity effects is explained by differences among tree communities in how they develop through the self-thinning phase of stand development when competition for light is most intense. I highlight that these differences in the self-thinning trajectories are strongly influenced by tree communities' functional identity and diversity. And third, at the species level, I illustrate how, along stand development, asymmetric species-specific responses to diversity based on their functional identity and that of their heterospecific neighbors, ultimately explain mixtures overyielding over time. Overall, this thesis illustrates from different perspectives the mechanisms and processes leading to the temporal dynamics of the diversity-productivity relationships along stand development and mixtures' overyielding in the long term. This work has major implications for forest management and conservation, as it provides crucial information to guide more effective management in the long term.

Key words: IDENT; biodiversity-ecosystem functioning; productivity; long-term diversity effects; functional diversity; functional identity

INTRODUCTION

Forests are the major terrestrial ecosystems. From the northern boreal forests to lush tropical rainforests, forests cover nearly one-third of the earth's land and contain more than 75% of terrestrial biodiversity (FAO, 2020). However, pressures from human activities leading to forest loss, fragmentation and degradation, have caused much biodiversity decline and homogenization in these ecosystems (Lindenmayer & Franklin, 2002; Newbold et al., 2015; Plas et al., 2016). The area of natural forests has been steadily reduced over time and replaced, in many cases, by simplified, less diverse tree plantations (Bremer & Farley, 2010; Newbold et al., 2015; Spiecker, 2003). Moreover, the vast majority of these plantations have been established as monocultures under the premise that they facilitate and maximize the harvesting of a few desirable tree species (FAO, 2020). Collectively, these trends in forest cover are a major concern because they may alter the functioning of these ecosystems (i.e., ecosystem functioning), and ultimately the services they provide to human societies, including climate regulation, water and air quality, timber, or biodiversity preservation (i.e., ecosystem services) (Bauhus et al., 2010; Liang et al., 2016; Mori et al., 2017). Therefore, understanding the ecological consequences of changing forest diversity is imperative for managing these ecological systems in a sustainable way. My thesis research aims to contribute to improving the existing knowledge in this field by focusing on understanding the role of stand development on the temporal dynamics of diversity effects on productivity.

Biodiversity – Ecosystem Functioning

The notion that the functioning of ecosystems may be impaired by declines in biodiversity has been argued at least since the 19th century. In 1828, the German forester von Cotta already stated that "since not all tree species utilize resources in the same manner, growth is more lively in mixed stands…" (in Pretzsch, 2005). Also, Darwin in his seminal work *On the origin of species* (1859) wrote "It has been

experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, [in the latter] a greater number of plants and a greater weight of dry herbage can thus be raised".
However, despite this early emphasis, the current era of biodiversity-ecosystem functioning (hereafter BEF) research did not consolidate until the late 20th century when, fueled by the accelerating loss of global biodiversity, the conference in Bayreuth (1991) and the Earth Summit in Rio (1992) increased the interest on the topic (Schulze & Mooney, 1994; Tilman, 1994). Soon after, the first experiments testing the relationship between biodiversity and ecosystem functioning emerged (e.g. Cardinale et al., 2006; Hector et al., 1999; Tilman et al., 1996). These experiments were carried out under controlled, standardized conditions, where variation in other factors than biodiversity was minimized, thus allowing to focus on the causal effects of biodiversity on ecosystem functioning, typically measured through productivity (Cardinale et al., 2012; Hooper et al., 2012). These foundational BEF experiments were dominated by grassland ecosystems, and soon they provided the first evidence that biodiversity loss can negatively affect the productivity of ecosystems (Hector et al., 1999; Hooper et al., 2012; Naeem, 2002; Tilman et al., 1996). Stimulated by these findings, as well as by some criticism (e.g. Aarssen, 1997; Huston, 1997; Wardle, 1999), BEF research has since expanded into other ecosystems, including forests, to test whether or not these findings are generalizable to other ecosystem types.

The effect of tree diversity on forest productivity: Causes, concepts and mechanisms

Historically, the relationship between tree diversity and productivity has been studied using observational data (i.e., forest inventories) (e.g. Liang et al., 2016; Paquette & Messier, 2011). However, isolating diversity effects are more difficult in this type of studies due to the many potential confounding factors and the lack of appropriate control (e.g. monoculture plots or replication). In response to the need for a deeper knowledge about the tree diversity-productivity relationship, and also influenced by the findings in grassland experiments, tree diversity experiments have been planted worldwide over the last two decades (Paquette et al., 2018; Verheyen et al., 2015). As a result, a large number of experimental studies – but also observational – investigating the diversity-productivity relationship in forest ecosystems have been published, all leading to the general consensus that diverse tree communities are generally more productive than species-poor ones (Grossman et al., 2018; Jactel et al., 2018; Liang et al., 2016; Paquette & Messier, 2011; Zhang et al., 2012).

As species diversity had a repeatable and consistent effect on productivity across studies (Grossman et al., 2018; Jactel et al., 2018) - and on ecosystem functioning in general - the BEF community pointed out the necessity of addressing the underlying mechanisms that explain such relationships. The mechanisms proposed tended to be reductionist descriptions of complex biophysical processes between organisms and their environment (soil nutrients, water, light, etc.) that lead to variations in the functioning of ecosystems over a gradient of biodiversity. In general, nutrients, water, and light are the three main classes of resources that limit plant performance (i.e., growth, survival, reproduction) (Craine & Dybzinski, 2013). Therefore, they are considered to be the resources for which individual plants compete. Plant species possess specific attributes or traits – any measurable feature of an individual that potentially affects performance or fitness – that define how they capture, use, and conserve limiting resources in a given environment (Lavorel & Garnier, 2002; Violle et al., 2007). Ultimately, these patterns of resource-use determine plants' performance relative to others (i.e., reduce or increase competition, or positive interactions) with consequences for which species will grow and which species will perish, and for ecosystem functions such as productivity (Kunstler et al., 2015; Reich, 2014). Such particularities of the species at capturing and using the limiting resources are the cornerstone of the underlying mechanisms explaining BEF relationships. These mechanisms are often grouped in terms of complementarity and selection effects (Loreau & Hector, 2001).

First, ***Complementarity effects*** are those that arise from *niche partitioning* (i.e., reduction of competition) or interspecific *facilitation* (i.e., positive interaction among species).

Niche partitioning is one of the most commonly proposed mechanisms for explaining the positive diversity effects on productivity (Cardinale et al., 2011; Hooper et al., 2005). It predicts that mixing species with contrasting characteristics or traits results in niche or resource partitioning, alleviating competition for the limiting resources (Kinzig et al., 2001). This, in turn, leads to more efficient resource exploitation at the community level, thus increasing productivity. For example, in forests, combining tree species with contrasting crown architectures and light requirements promotes better use of canopy space (Jucker et al., 2015; Williams et al., 2017). This reduces competition for light among neighboring trees and allows diverse communities to intercept a greater proportion of incoming light and grow faster compared to their respective monocultures (Kunz et al., 2019; Sapijanskas et al., 2014; Searle & Chen, 2020; Williams et al., 2017).

Facilitation describes species interactions that benefit at least one of the species pin the mixture, providing advantages over solitary growth (Bertness & Callaway, 1994). For example, neighbouring species may increase the availability of resources, such as soil nutrients and water, or ameliorate microclimatic conditions, such as air temperature and soil moisture, thus improving the conditions to grow and thrive (Dawson, 1993; Forrester & Bauhus, 2016). Consequently, facilitation may favor the growth and survival of trees in mixtures over the negative effects caused by their competition for limiting resources (Callaway et al., 2002). Distinguishing between the effects of *niche partitioning* and *facilitation* is, however, difficult in practice. Therefore, we usually refer to them collectively as complementarity effects (Loreau & Hector, 2001).

Second, ***Selection effects*** on productivity arise through selective processes, such as interspecific competition, which cause dominance of species with particular traits (Loreau & Hector, 2001; Roscher et al., 2012). In the context of biodiversity experiments, these effects are interpreted to result from differences in the productivity of species in monoculture, and from the greater likelihood that a more productive species would be present (i.e., stronger competitor randomly "selected" from a pool of species) at more diverse stands (Loreau & Hector, 2001; Tilman et al., 2014). Therefore, selection effects are positive when the most productive species in monoculture performs better in the mixture and negative when the less productive species in monoculture overyield in the mixture.

Such mechanistic explanations and concepts are central in BEF literature and essential to our understanding of how and why biodiversity affects forest productivity (Huang et al., 2018; Paquette & Messier, 2011). Importantly, both complementarity and selection effects are not necessarily mutually exclusive. They have been shown to operate simultaneously in a variety of tree systems, with variations in their relative importance driving the net diversity effects. For example, whereas Tobner et al. (2016) showed that mixtures overyielding were driven mostly by selection effects, Huang et al. (2018) highlighted that complementarity effects (i.e., *niche partitioning* or *facilitation*) were, overall, more important.

BEF relationships vary across space and time

Despite BEF literature showing an overall positive relationship between tree diversity and productivity, the strength of diversity effects varies considerably among individual studies (Jactel et al., 2018; Jucker et al., 2016; Zhang et al., 2012). Given that the BEF relationships arise from interactions among constituent tree species and their environments, it is reasonable to expect that both effects of diversity on productivity and its underlying mechanisms will vary across space and time. Recent studies have demonstrated how complex interactions between abiotic factors and stand structure explain some of these divergences across space in different forest types (Forrester, 2014; Hulvey et al., 2013; Jactel et al., 2018; Jucker et al., 2016). For example, diversity-productivity relationships have been shown to become progressively stronger under harsher environmental conditions where beneficial complementarity interactions among species become more important (Bertness & Callaway, 1994; Jucker et al., 2016; Paquette & Messier, 2011; but see Belluau et al., 2021). Whereas, in more stable and productive sites, competitive exclusion is the most probable outcome of species interactions, thus favoring few dominant, highly productive species (i.e., selection effects) (Bertness & Callaway, 1994; Paquette & Messier, 2011).

Thesis objectives

While variations in the strength of diversity effects on productivity across space along environmental gradients are well established, there are significant knowledge gaps about how and why diversity-productivity relationships change over time during forest development (Grossman et al., 2018; Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020).

Throughout forest development, both the availability of resources and the competition for them undergo rapid changes over time as trees grow and occupy space (Chesson et al., 2001; Fichtner et al., 2018; Jucker et al., 2014; Morin et al., 2011). For example, in the early years following stand establishment, essential resources such as light and nutrients are normally abundant (relative to demand), fulfilling trees requirements to grow and survive. Consequently, competition among trees for resources is expected to be minimal during these early years. However, as trees grow, competition for light and growing space gradually intensifies until canopy closure is achieved and stands begin to suffer tree mortality in direct relation to the growth of trees (i.e., self-thinning process) (Zeide, 1987). When this relationship is fitted, it provides a self-thinning line that represents a barrier such that any further increase in mean tree size is only possible if the density of trees declines along this line (Reineke, 1933). This dynamism in the physical environment of trees provides challenges and opportunities for species relative to others with consequences for how they interact and, ultimately, for ecosystem productivity.

My thesis aims to address persisting knowledge gaps in BEF science throughout three different chapters that, together, may provide a complete picture of the processes and mechanisms that help explain the changes in diversity-productivity relationships over the course of stand development.

First, at the community level, recent studies have shown that the strength of tree diversity effects on productivity may vary considerably over time along stand development (Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020). However, empirical evidence of it and how the underlying mechanisms (i.e., complementarity and selection) drive this relationship through succession is poorly understood (Huang et al., 2018).

Second, evidence points to canopy closure and the subsequent self-thinning as key phases of stand development during which positive diversity effects emerge (Jucker et al., 2020; Taylor et al., 2020). A number of studies have shown that self-thinning can differ among species (Pretzsch, 2006; Pretzsch & Del Río, 2020; Puettmann et al., 1993), and also in mixtures compared to monocultures (Ducey & Knapp, 2010; Pretzsch et al., 2015; Reyes-Hernandez et al., 2013). Yet, how diversity influences the process of canopy closure and self-thinning remains elusive.

Third, diversity effects at the community level are the net outcome of multiple interactions among species over time and, thus, do not inform about individual species' responses to diversity. While studies have shown that species may respond differently to community diversity (Grossman et al., 2017; Jucker et al., 2020), the species-level mechanisms leading to overyielding at the community level through time over the course of stand development are far less clear.

Through the three chapters of my thesis, I have used a trait-based approach to address these knowledge gaps. This approach views trees in terms of their functional traits – any measurable feature of an individual that potentially affects performance or fitness – rather than their botanical identity (Violle et al., 2007). Furthermore, since functional traits capture the inherent differences in resource-based niches of species, they can better determine competitive interactions between species and predict community productivity than species richness (Kunstler et al., 2015; McGill et al., 2006; Reich, 2014). Two different approaches to measuring functional aspects of the community provide mechanistic insights into the diversity effects on productivity as well as the underlying effects (i.e., complementarity and selection) at play. The first is functional diversity (related to complementarity effects) which quantifies the effect of the variability in functional trait values on productivity. Whereas the second is functional identity (related to selection effects) which allows the evaluation of the effect of dominant traits on productivity (Grime, 1998; Morin et al., 2011; Roscher et al., 2012; Shipley et al., 2006).

The three studies presented in this thesis were conducted in a tree diversity experiment located on the island of Montreal, which is part of the International Diversity Experiment Network with Trees (IDENT) (Tobner et al., 2014). This experiment contains 12 native temperate-boreal tree species planted in a wide range of mixtures, among which underlying environmental gradients are minimized. One of the main characteristics of this experiment is its high-density design which favors a fast development of competition among neighboring trees as stands develop. These conditions make this experiment ideally suited for addressing my study aims.

Thesis Plan

The thesis is divided into three chapters, each addressing a series of hypotheses with specific aims directly related to the above-mentioned knowledge gaps.

Chapter 1 sets the baseline for subsequent chapters by analyzing how diversity effects on productivity change through time over the course of stand development at the community level. I also seek to investigate what type of species interactions (i.e., complementarity and selection) drive the temporal dynamics of these effects. I hypothesize that the strength of diversity effects increases with stand development, driven primarily by co-varying complementarity effects as competition for light and growing space increases. To test this, I used annual growth data over 11 years from the IDENT-MTL experiment that allows separating the net diversity effects into complementarity and selection. This study further explores the functional significance of the diversity effects on productivity throughout stand development.

In **chapter 2**, I change the focus to how tree diversity impacts community structure and function through changes in self-thinning. More specifically, I examine how the functional diversity and identity of tree communities affect the self-thinning process that ultimately helps explain mixtures' overyielding in the long term. Using 11 years of growth and mortality data records from the IDENT-MTL experiment, I fit self-thinning trajectories for each tree community of the experiment, and then I analyze how tree communities’ functional diversity and identity may affect these trajectories. The study also analyzes if these effects on self-thinning trajectories are due to differences in growth or in mortality.

By last, in **chapter 3**, I seek to better understand the underlying species-level mechanisms leading to overyielding at the community level by looking at each species' performance in mixtures relative to the neighboring composition. Trees are able to adjust their form and size in response to changes in their local competitive environment directly influencing their productivity (Jucker et al., 2015; Pretzsch & Dieler, 2012; Vieilledent et al., 2010; Williams et al., 2017). Also, trees' competitive ability and fitness to a given environment are strongly related to their functional traits (Reich, 2014; Violle et al., 2007). In this study, I estimate temporal dynamics of species-specific performances in mixtures related to their functional traits and those of their heterospecific neighbors. Then I analyze how these results at the species level scale up and explain mixtures' overyielding along stand development. To test this, I used growth data of each species within each mixture and monoculture over 11 years from the IDENT-MTL experiment.

Chapter 1

No complementarity no gain – Net diversity effects on tree productivity occur once complementarity emerges during early stand development

Originally published as: Urgoiti J, Messier C, Keeton WS, Reich PB, Gravel D, Paquette A. No complementarity no gain – Net diversity effects on tree productivity occur once complementarity emerges during early stand development (2022). *Ecology Letters*. https://doi.org/10.1111/ele.13959

ABSTRACT

Although there is compelling evidence that tree diversity has an overall positive effect on forest productivity, there are important divergences among studies on the nature and strength of these diversity effects and their timing during forest stand development. To clarify conflicting results related to stand developmental stage, we explored how diversity effects on productivity change through time in a diversity experiment spanning 11 years. We show that the strength of diversity effects on productivity progressively increases through time, becoming significantly positive after 9 years. Moreover, we demonstrate that the strengthening of diversity effects is driven primarily by gradual increases in complementarity. We also show that mixing species with contrasting resource-acquisition strategies, and the dominance of deciduous, fast-developing species, promote positive diversity effects on productivity. Our results suggest that the canopy closure and the subsequent stem exclusion phase are key for promoting niche complementarity in diverse tree communities.

Key words*:* biodiversity- ecosystem functioning, functional diversity, functional identity, functional traits, IDENT, life- history strategy, long- term diversity effects, productivity, resource partitioning, tree diversity experiment

INTRODUCTION

Recent decades have seen a large number of studies, both observational and experimental, investigating the diversity-productivity relationship (hereafter DPR) in forest ecosystems. As a result, there is now a general consensus that diverse tree communities, on average, promote higher biomass production than their species-poor counterparts (Liang et al., 2016; Paquette & Messier, 2011; Zhang et al., 2012). However, within this body of research there are important divergences in the magnitude of diversity effects, with some studies reporting negligible or only marginal effects (e.g. Li et al., 2014; Tobner et al., 2016). While recent studies have demonstrated how complex interactions between abiotic factors and stand structure explain some of these divergences across different forest types (Forrester, 2014; Hulvey et al., 2013; Jucker et al., 2016), much less is known about the mechanisms driving the temporal dynamics of the strength of DPR over time during forest development (Grossman et al., 2018; Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020). In particular, diversity effects are thought to be especially important during the early phases of forest development (i.e. stand establishment, canopy closure, and stem exclusion), when competition for limited resources is the major driver determining the future forest structure and functioning (Fichtner et al., 2018).

Two main mechanisms have been proposed to explain positive diversity effects on productivity. The first is complementarity effects, which include niche partitioning and interspecific facilitation; and the second is selection effects, which are caused by the dominance of one or few species driving community's productivity (Loreau & Hector 2001; Roscher et al. 2012). These depend, in turn, on species-specific functional traits. Functional traits define species' life-history strategies, thus determining their capacity to grow, survive, and use resources in competitive environments (Violle et al. 2007). Two different approaches to measuring functional aspects of the community can provide mechanistic insights into DPRs as well as the underlying mechanisms at play. The first is functional identity (FI; selection effects) which allows the evaluation of the effect of dominant traits on productivity, whereas the second is functional diversity (FD; complementarity effects) which quantifies the effect of the variability in functional trait values on productivity (Grime, 1998; Morin et al., 2011; Roscher et al., 2012; Shipley et al., 2006). Long-term studies in grassland biodiversity experiments have already shown that the strength of diversity effects and the relative importance of complementarity over selection tend to increase over time (Reich et al. 2012). This observation explains the ability of functionally diverse communities to progressively optimize the use of limiting resources over time and to enhance soil fertility and nutrient availability (Reich et al. 2012).

A similar observation of the increasing importance of complementarity effects over time is expected in forest ecosystems (Huang et al., 2018). However, as community dynamics in forests are relatively slow compared to those in grassland ecosystems, complementarity effects driving mixtures' overyielding (i.e. when mixtures' productivity is higher than their components' respective monocultures) might take many years (e.g. a decade or more) to manifest following tree establishment (Jucker et al. 2020; Huang et al., 2018). This is because essential resources such as light and nutrients are normally abundant (relative to demand) in the early years following stand establishment, fulfilling trees' requirements to grow and survive. Consequently, competition among trees for resources are minimal during these early years. This reduces the likelihood of complementarity effects and increases the probability of sampling a dominant, high productive species with a specific set of functional traits driving community productivity (i.e. selection effects) as found by Tobner et al. (2016). However, as stands develop, trees progressively expand their crowns (i.e. canopy closure), gradually intensifying competition for light and growing space. This, in turn, might increase the importance of complementarity effects driving DPR, as is expected under harsher conditions (Callaway et al., 2002; Paquette & Messier, 2011; Searle & Chen, 2020; but see Belluau et al., 2021). For example, mixing species with contrasting life strategies promotes a better use of canopy space (Jucker et al., 2015). This, in turn, reduces competition for light and allows diverse communities to intercept a greater proportion of incoming light and grow faster compared to their respective monocultures (Jucker et al., 2015; Kunz et al., 2019; Pretzsch, 2014b; Sapijanskas et al., 2014). This helps explain why, in contrast to studies carried out in the early years of tree diversity experiments where negligible or only marginal positive DPRs were found (Healy et al., 2008; Li et al., 2014; Tobner et al., 2016; Verheyen et al., 2015), recent studies conducted many years after stand establishment highlighted strong positive diversity effects on productivity (Huang et al., 2018; Schnabel et al., 2019; Van de Peer et al., 2017).

Few studies have analyzed the temporal dynamics of diversity effects on productivity during stand development (e.g. Jucker et al. 2020; Taylor et al. 2020; Huang et al., 2018). Furthermore, much less is known about how underlying mechanisms (Complementarity and Selection) drive this relationship through succession (Huang et al. 2018). Testing these relationships is challenging, as it requires long-term, repeated growth data from a tree diversity experiment that allows separating net diversity effects into complementarity and selection. Only few experiments to date allow conducting such a study as most of them are still in the stand establishment phase where competition for resources is minimal. One of these experiments is IDENT-MTL in Montreal, Canada, which was planted in spring 2009 (Tobner et al. 2014). This experiment is ideally suited to test the temporal dynamics of diversity effects because its high-density design favors development of competition and therefore expression of complementarity.

In this study, we analyze how diversity at initial stage affects stand-level development of productivity. Our analysis focuses on basal area because it cumulates annual increments and subsequent mortality, and therefore best indicates the trajectory of stand development. We focus on the early stages of stand development covering the stand establishment, canopy closure and the beginning of the self-thinning stages. We hypothesize that the strength of the DPR increases with stand development, driven primarily by co-varying complementarity effects as competition for resources increases. To complement this analysis, we further explored how the functional composition of tree communities (i.e., functional diversity and identity) contributed to DPR over time. We expect that functional diversity and identity both explain net diversity effects on productivity, with the former being a stronger relative predictor.

MATERIALS AND METHODS

Site description

The study was conducted in IDENT-MTL tree diversity experiment that was established in Ste-Anne-de-Bellevue (near Montreal, Quebec, Canada, 45°25’30.1”N, Long 73°56’19.9”W, 39 m.a.s.l.) in the spring of 2009. Mean annual temperature is 6.2°C and mean annual precipitation totals 963 mm (climate.weatheroffice.gc.ca). The experiment was planted on a former agricultural field that was intensively managed for decades. The soil consists of a 20-70 cm deep sandy layer overtopping clay (Tobner et al. 2016).

In the spring of 2009, an area of 0.6 ha was planted with 1- or 2-years old tree seedlings (Tobner et al. 2014). The experiment includes 12 North American temperate forest species - five broad-leaf species and seven conifers (Table S1.3). This experiment is part of the ‘International Diversity Experiment Network with Trees’ (IDENT) that includes several sites in North America, Europe and Africa (Verheyen et al. 2015).

Experimental Design

Two orthogonal gradients were established: 1) a species richness gradient, and 2) a functional diversity gradient (Table S1.3). This design allows separating the two different diversity effects. The functional diversity gradient consists of plots with species combinations of equal species richness but increasing functional diversity. The functional diversity levels are repeated using different species combinations and are pooled in groups of similar FD value (Table S1.3).

Trees were planted in square plots of 8 x 8 individuals (i.e. 64 trees), with 50 cm spacing among trees and 1.25 m between plots to allow movement and minimise inter plot interactions (Tobner al. 2014). The experiment includes monocultures of all 12 species, 14 combinations of two-species mixtures, 10 combinations of four-species mixtures and one mixture including all 12 species (Tobner et al. 2014) for a total of 37 different tree communities (i.e., unique species composition). Each community was replicated four times in a randomised block design for a total of 148 plots and 9,472 trees (note that the site includes more plots addressing other questions that were not used in this experiment) (Tobner et al. 2014). The proportion of species within plots was equal and their distribution randomised with restrictions to prevent monospecific patches (see Tobner et al. 2014 for details). The distribution of trees within the plots remained constant in all the blocks; however, the distribution of plots within blocks was randomised.

Around the outermost rows of the experiment, three rows of trees at 50 cm distance were planted to minimise edge effects. A fence to protect against herbivory by large vertebrates was constructed around the experiment and all plots were regularly weeded manually during the first years to eliminate herbaceous competition.

Cumulative productivity as measured by tree basal area

We used basal area (G; m^2/ha) as a proxy for cumulative aboveground productivity at the plot level from 2009 to 2019. Only the inner 6 x 6 trees of each plot were used to minimize edge effects from neighbouring plots. The basal diameter (at 15 cm aboveground) of every live tree was measured at the end of each growing season from 2009 to 2019, hereafter years 1 to 11, from which species G were computed for each year and plot. Note that mortality was, therefore, taken into account when computing species G. We attributed tree mortality solely to competition for resources as any visible damage by biotic (pathogens or insect herbivores) or abiotic factors were negligible over the first 11 years. Total *G* of a plot was simply the sum of species *G*. Net diversity effects (NE), complementarity effects (CE) and selection effects (SE) were calculated according to Loreau and Hector (2001, details below) using the estimated *G* values for each year and plot.

DATA ANALYSIS

Quantification of the diversity effects and its underlying mechanisms

We followed Loreau and Hector's (2001) approach to calculate the net diversity effects (NE) as well as complementarity (CE) and selection (SE). This approach is based on the calculation of a general deviation of yield in mixture (observed yield, Y_O) from that in monoculture (expected yield, Y_E, eqn 1). A NE = 0 indicates that the performance of the mixture is equal to the weighted average of respective component monocultures (i.e., no diversity effect; the mixture performs as expected from monocultures). A NE > 0 indicates a positive diversity effect and when NE < 0, a negative diversity effect. This approach also allows for partitioning the net diversity effects (NE) into complementarity (CE) and selection effects (SE) (Loreau & Hector 2001).

$$\begin{aligned} NE &= YO - YE = CE + SE \\ &= N\overline{\Delta RYM} + N\mathrm{cov}(\Delta RY, M) \end{aligned} \tag{1}$$

Both mechanisms of diversity effects (CE and SE) hinge on the calculation of the relative yield of each species (RY, De Wit 1960), expressed in this equation as ΔRY (eqn 2).

$$\Delta RY = \frac{yieldA(Mixture)}{yieldA(Monoculture)} - P_A \qquad (2)$$

Where P is the proportion of the species at the initial stage in mixture.

CE is the mean of the deviation from the expected relative yield of each species in the mixture ($\overline{\Delta RY}$) multiplied by the mean of each species' yields in monoculture $(\overline{M})$ and by the number of species (N). Therefore, CE averages positive and negative diversity effects of all species in the mixture. On the other hand, SE is the covariance between species' relative (ΔRY) and monoculture yields (M) multiplied by the number of species in the mixture (N). SE is positive when the most productive species in monoculture performs better in the mixture. Alternatively, SE is negative when the less productive species in monoculture overyield in the mixture. In case of both high and low productive species in monocultures overyielding in the mixture, SE can be positive or negative depending on the stronger effect.

Trait data collection and calculation of functional composition

We computed functional diversity and identity at the initial stage of the experiment. We considered seven above- and belowground traits that are linked to plant resource-use strategies and competition capacities. They include specific leaf area (SLA), leaf nitrogen content by mass (LNmass), leaf nitrogen content by area (LNarea), net maximum photosynthesis by unit leaf mass (Amass), wood density (WD), specific root length (SRL) and seed mass (seedmass). All trait data were collected from the literature (Belluau 2020; Table S1.1). We included seed mass because it is a trait associated with differing functional strategies that might influence productivity, rather than due to any direct link between seed size and production. Then, we performed a Principal Component Analysis (PCA) of the trait values at the species level in order to avoid collinearity among traits and identify species main axes of life-history strategies (Figure 1.1). Seed mass values were log-transformed prior to analysis.

The first two principal components explained 80% of the variance in traits. The first principal component (PC1) was correlated to wood density (WD), leaf nitrogen content by unit mass (LNmass), specific leaf area (SLA) and specific root length (SRL), clearly separating gymnosperms from angiosperms (Table S1.2). These functional traits are involved in the acquisition, processing and conservation of resources and, hence, define species' life history strategy largely by influencing growth vs survival trade-offs (Reich 2014). It is worth noting that WD is a highly phylogenetically conserved trait (i.e. less variable within phylogenetic groups than expected by chance) with angiosperms typically having significantly denser wood than gymnosperms (Zhang et al., 2017), as evidenced in our PCA, with that factor overwhelming the typical within-group association of high WD with slow growth (Swenson & Enquist, 2007). As a result of this strong phylogenetic conservatism, high WD - a 'slow' trait - is positively correlated with high values of 'fast' leaf traits among the studied species, which is different than the general pattern observed in nature (Reich 2014). The second principal component (PC2) was related only to seed mass (Table S1.2). Seed mass is considered as an indicator of the trade-off between colonization (early vs late successional species) and competitive capacity (Turnbull et al., 2004). For example, small-seeded species are typically better colonizers but less shade tolerant and thus, lesser competitors. Using the species scores over these two life-history axes (i.e. principal components), we calculated the communities' FD and FI using functional dispersion (Fdis, Laliberté & Legendre 2010) and community weighted means (CWMs, Lavorel et al. 2008) respectively (i.e. $Fdis_{PC1}$, $Fdis_{PC2}$, CWM_{PC1} and CWM_{PC2}). Functional dispersion is the mean distance in a multidimensional trait space of each species to the center of mass of all species, weighted by their relative abundances (Laliberté & Legendre 2010). We calculated the Fdis for all possible species combinations of two, four and twelve species. CWM values were computed for the two principal components collecting the variance of functional traits following Lavorel et al. (2008). CWMs are, thus, the mean value of each principal component of all species present in a community weighted by their relative abundance. We used the R package FD to calculate CWM and Fdis (Laliberté & Legendre 2010).

Statistical Analysis

We performed a Generalized Additive Model (GAM) with REML estimation to test the effects of time (Year), functional diversity (Fdis) and functional identity (CWM) on net diversity effects (NE). Block and plot (i.e., the different tree communities) were set as random factors (noted *R*), yielding the following model:

$$\begin{gathered} NE = Year + Fdis_{PC1} + Fdis_{PC2} + CWM_{PC1} + CWM_{PC2} + \\ Year \ X \ Fdis_{PC1} + Year \ X \ Fdis_{PC2} + \\ Year \ X \ CWM_{PC1} + Year \ X \ CWM_{PC2} + \\ Plot \ (R) + Block \ (R) + \varepsilon \end{gathered} \tag{3}$$

where ‘Fdis’ is functional dispersion, and ‘CWM’ community weighed means. The subscripts ‘PC1’ and ‘PC2’ refer to the principal components obtained from the PCA previously done on the functional trait values that represent two axes of life-history strategies. The best model was selected based on AIC. We ran a variance-based sensitivity analysis from the best model to estimate the deviance explained by each predictor of the model.

We subsequently explored the effects of FD and FI on NE over time. We performed independent cluster analyses for each of the diversity parameters of the best model (i.e., $\mathrm{Fdis}_{\mathrm{PC1}}$, $\mathrm{CWM}_{\mathrm{PC1}}$ and $\mathrm{CWM}_{\mathrm{PC2}}$). The cluster analysis classifies the different mixtures of the experiment into similarity groups (i.e., clusters) according to a defined distance measure based on their Fdis and CWM values. The cluster analyses performed on the diversity components grouped the different mixtures of the experiment into 1) plots with high (no. of plots 16) and low (9) functional diversity on the resource-use strategy axis (i.e., Fdis_{PC1}); 2) plots with high (5), medium (16) and low (4) mean values on the resource-use strategy axis (i.e., CWM_{PC1}); and 3) plots with high (9), medium (12) and low (4) mean values on the colonization strategy axis (i.e., CWM_{PC2}). We then extracted the fitted NE values from the model (eqn 3) and plotted them 1) against the measured CE and SE over time to observe the temporal dynamics of the forces driving the NE, and 2) against the different Fdis and CWM groups generated by the cluster analyses.

Finally, we tested whether mixtures performed better than expected compared to their respective monocultures over the duration of the experiment (after 11 years). We applied two-tailed t-tests (n = 4 blocks) to determine when net diversity effects were significantly different from zero. We then applied one-tailed t-tests to determine whether some mixtures performed significantly better than even the best monoculture (i.e., transgressive overyielding).

RESULTS

Our results show a non-linear increase in net diversity effects (NE) over time (Table 1.1). Net diversity effects were negative from year 3 to 6 after the establishment of the experiment, became positive after year 8, and then significantly so from year 9 onward (Figure 1.2). This strengthening of the net diversity effect was primarily driven by gradual increases in complementarity effects as stands developed (notably > year 5), while during the first years, negative selection effects (which peaked in year 6) were more common in driving the net diversity effects (Figure 1.2). In the last year of the experiment (year 11), net diversity effects had accumulated enough through time to be easily detected looking at plot total G, with six mixtures overyielding their component monocultures, and four even showing transgressive overyielding (Figure S1.2).

Further analysis of the effect of tree communities' functional trait-based composition on productivity shows that net diversity effects vary substantially among mixtures during the early stages of stand development (Table 1.1). We observed that mixtures characterized by species with contrasting resource-use strategies (i.e., high Fdis_PC1) performed similarly to their constituent monocultures during the first years of the experiment. However, starting in year 6, these tree communities progressively increased their productivity compared to their respective monocultures, increasingly overyielding from year 9 onwards (Figure 1.3). Mixtures characterized by species with similar resource-use strategies (i.e., low Fdis_PC1) showed similar productivity to their monoculture counterparts during the whole experiment except for the last year when, in general, they slightly overyielded (Figure 1.3).

In addition, we also observed that the functional identity of tree communities (i.e., CWM_PC1 and CWM_PC2) had a substantial effect on mixtures' productivity over time. For instance, mixtures with highly acquisitive resource economic traits (other than WD) (i.e., medium and high CWM_PC1) showed, in general, an increasing trend of diversity effects since year 6 that started to overyield from year 9 onwards (Figure 1.4). Conversely, mixtures in the "slow" end (again, other than WD) of the resource economic spectrum (i.e., low CWM_PC1) showed, in general, negative diversity effects from year 8 onwards (i.e., negative NE; Figure 1.4). Seed mass CWM had a negative relationship with overyielding. In mixtures with low and medium values of seed mass, diversity effects tended to increase progressively over time, overyielding their constituent monocultures in the last three years (Figure 1.5). In contrast, mixtures dominated by late-successional species (i.e., high CWM values of seed mass) showed negligible or even negative diversity effects during the early stages of stand development except for the last year, where, in general, they slightly overyielded (Figure 1.5).

DISCUSSION

Here we present the results of what is, to the best of our knowledge, the first study with trees to test the temporal dynamics of both net diversity effects and its component mechanisms, complementarity and selection, on cumulative productivity during the first decade of stand development. Our results support the widespread evidence from prior studies that mixtures are, on average, more productive than monocultures of their constituent species. Our study brings new insight into the temporal changes of such effects; showing that the strength of net diversity effects on cumulative productivity is non-linear during the first phases of stand development, taking many years to manifest itself (Figure 1.2). While an earlier study of the same experiment found, on average, a negligible net diversity effect on cumulative productivity by year 4 (i.e., Tobner et al., 2016), these updated results over a longer temporal scale show i) that the strength of the net diversity effects on cumulative productivity increases throughout stand development (Jucker et al. 2020; Taylor et al. 2020), and that ii) this is driven by gradual increases of complementarity (Huang et al. 2018; Sapijanskas et al. 2014). Previous studies have shown how complex interactions between resource availability, climatic conditions and stand structures can explain some of the variation in the strength of net diversity effects on productivity across different forest ecosystems (Forrester 2014; Jucker et al. 2014; Jucker et al. 2016; Mori 2017). Our results mirror the long-term studies in grasslands (Guerrero-Ramírez et al., 2017; Reich et al., 2012) and forest ecosystems (Huang et al. 2018). They show that changes in the relative importance of complementarity and selection effects during the first stages of stand development strongly influence net diversity effects on productivity over time.

The emergence of complementarity's larger role under increased competition is the key driver of the positive diversity-productivity relationships during stand development

During the first years following stand establishment we found that, on average, net diversity effects were driven by opposing forces of complementarity and selection (i.e., negligible net diversity effects; Figure 1.2). This is consistent with our expectations that in years immediately following stand establishment, high resource availability eliminates or reduces the opportunity for complementarity to have much of an impact on productivity (Forrester 2014; Paquette & Messier 2011; Taylor et al. 2020; Zhang et al. 2012). Instead during this phase, selection effects have more impact on productivity (Tobner et al. 2016).

Net diversity effects were negligible at first due to negative selection effects being larger than initially weak (but positive) complementarity effects. This means that, overall, the species with relatively high monoculture productivity had lower performances in mixtures. The opposite was true for species with relatively low monoculture productivity. Selection effects have been hypothesized to be more important in more stable and productive environments, whereas in more stressful environments complementarity effects are expected to be more important (the stress gradient hypothesis, Bertness & Callaway 1994; but see Belluau et al. 2021). In this study, the intense agricultural activity at the study site prior to the experiment establishment, and the complete removal of herbaceous competition during the first years, resulted in resource-abundant conditions for trees, possibly favoring selection effects initially (Tobner et al. 2016). However, as stands underwent canopy closure and entered the stem exclusion phase, resource competition among trees intensified (c. year 5 or 6; Figure S1.1). In diverse stands, the impact of competition may have been reduced since the likelihood of two individuals competing for the same niche decreases; this then allows for the emergence of complementarity, and consequently, positive net diversity effects. These strong positive effects must have been driven by the faster growth of surviving trees within mixtures because tree survival rates remained similar between monocultures and mixtures (Figure S1.3). Numerous studies have shown that different mechanisms can explain positive diversity effects on productivity, including reduced pest and pathogen loads, or improved resource uptake belowground (Ammer, 2019). However, arguably the most important one is the ability of diverse communities to fill canopy space more efficiently than their species-poor counterparts (Jucker et al. 2015; Pretzsch 2014). This reduces competition for light and allows these communities to grow faster overall, compared to their respective monocultures (Jucker et al. 2015; Sapijanskas et al. 2014). Therefore, the increase of competition associated with the canopy closure and stem exclusion phases seems to be a key factor in allowing conditions for mixtures to overyield through niche partitioning or facilitation (Jucker et al. 2020).

Although our results show a clear strengthening of complementarity through time that determines the positive net diversity effects on productivity, this experiment covered only the early stages of stand establishment, canopy closure and stem exclusion. How long will positive net diversity effects due to complementarity last is unknown, but we suspect they might continue until a later stage of stand development when some tree species will come to dominate again. For example, late-successional species could progressively increase in relative dominance, allowing selection effects to take over again in determining the net diversity effects on productivity. Future research should focus, therefore, on understanding how DPR and its underlying mechanisms are likely to change in the more advanced stages of stand development.

Functional significance of the Net Diversity effects on productivity throughout stand development

Our analysis of the effects of tree communities' functional composition on productivity shows that mixing fast-growing deciduous species with slow-growing evergreen species (i.e., high Fdis_PC1) progressively increased productivity as competition intensified during stand development (Figure 1.3). This seemed to be related to the canopy closure where trees begin to compete for light and where contrasting architectural and physiological traits allow mixtures to benefit from light partitioning (Jucker et al., 2020; Taylor et al., 2020; Williams et al., 2017). Indeed, in a previous study conducted in the same experiment, Williams et al. (2017) observed that in year 4 (coinciding with the emergence of competition; Figure S1.1), there was a substantial neighbourhood-driven variation in crown size and shape, indicating that stands had reached the canopy closure and started to compete for light and space, and optimize resource-use to avoid or reduce competition. Increasing diversity effects by mixing species with contrasting life strategies has been related to the vertical canopy stratification and intraspecific crown plasticity throughout stand development (Jucker et al., 2015; Morin et al., 2011; Williams et al., 2020). Through differences in their crown architectures, contrasting species can use different canopy positions (i.e., crown complementarity), reducing competition and allowing for the capture of more light at the community level. Moreover, as competition for light lessens, trees also might invest a greater proportion of fixed carbon towards the development of lateral branches increasing their crown size (i.e., crown plasticity; Forrester 2014; Jucker et al. 2015; Williams et al. 2017). In this regard, vertical stratification and crown plasticity might be the mechanisms driving the net diversity effects observed in this study.

In addition, we show that, functional identity also plays an important role in driving diversity effects over time. We found that the dominance by slow-developing conifers reduced mixture productivity, compared to more mixed stands and stands dominated by fast-developing deciduous species. Therefore, our study suggests that complementarity effects are also driven by functional identity of specific species (i.e., life-history strategies) that are able to take advantage of diverse conditions, thus leading to overyielding at the community level (Grossman et al., 2018; Zheng et al., 2021). Specifically, our results suggest that effective light acquisition of tree communities dominated by deciduous "fast" developing early-successional species allow these communities to grow faster (Hisano & Chen, 2020; Zheng et al., 2021). Fast growth (and consequently better access to light) has been linked to a reduced ability to tolerate competitive pressures such as shading from others (Kunstler et al. 2016). Indeed, all the mixtures that overyielded were mixtures of deciduous and evergreen species (except for one) and all but one contained *B.papyrifera* (Figure S1.2). In other words, this light-demanding pioneer species (the most productive monoculture) probably benefited from reduced competition when growing in mixtures, ultimately dominating them and overyielding at the community level. This could promote niche partitioning through the development of multilayered canopies over time, where shade-tolerant species grow under taller, light-demanding pioneers (Jucker et al., 2015; Niinemets, 2010). Therefore, these results show that both functional diversity and identity of tree communities play important roles in driving positive complementarity effects, thus promoting net diversity effects on productivity in the mid-term (Grossman et al. 2018; Van de Peer et al. 2017; Zheng et al. 2021) – whether complementarity among initially slower growing species would catch up over time is unknown.

CONCLUSION

Analyzing 11 years of growth records from a tree diversity experiment, we show that diversity effects on productivity strengthen progressively during the early stages of stand development driven by gradual increases of complementarity. While previous studies have shown how abiotic factors and forest structure can explain a considerable amount of variation in the strength of DPR across space, this study highlights that changes in the relative importance of complementarity and selection effects during stand development also play an important role in determining the strength of these relationships over time. This pattern seems to be related to the progression into the canopy closure and stem exclusion phase of stand development, where increasing competition for resources allows positive complementarity effects to develop, and ultimately determines more diverse communities' success in the long-term. Moreover, our study highlights that diversity effects on productivity are affected by both functional diversity and identity. We show that mixing species with contrasting resource-acquisition strategies, and the dominance of deciduous, fast-developing species promote positive diversity effects on productivity during the initial phases of stand development.

Our results are important from a management and conservation perspective, as this study shows when and how positive diversity effects should manifest along stand development. Tree diversity experiments are essential to further research on biodiversity and ecosystem functioning in forests. However, existing experiments should be allowed to mature to track the many trajectories that diversity effects could take through more advanced stages of forest succession.

ACKNOWLEDGEMENTS

This research would not have been possible without the dedication of the many grad students, postdocs and interns who worked on the IDENT-MTL experiment over the last 11 years. We also thank M. Belluau for collecting and providing functional traits, E. Searle and D. Schönig for welcomed suggestions in data analysis, and R. Sousa-Silva for helpful discussions and comments on earlier versions of the manuscript. The research leading to these results was financially supported by grants from the National Research Council Canada (NSERC) to CM, DG and AP. The contribution of PR was supported by the U.S. NSF Biological Integration Institutes grant DBI-2021898.

Table 1.1 Summary of the generalized additive model (REML estimation) of significant diversity indices on net diversity effects (NE; *N* = 1100) over time (fixed effects). Summary includes estimated degrees of freedom (edf), deviance explained (DevExp), and p-values. When edf is close to 1, the effect on NE is linear. And when edf is 2 or greater it is considered non-linear. The model includes Block and Plot as random effects. The "s" and "ti" are GAM-specific terms that mean smooth term (main effects) and tensor product (interactions) respectively. The coefficient of determination (R^2) for the whole model was 0.506.

Effect	**edf**	**DevExp**	**p-value**
s(Year)	4.112	0.080	<.001
s(Fdis_PC1)	2.698	0.012	<.001
s(CWM_PC1)	1.111	0.016	<.001
s(CWM_PC2)	1.102	0.019	<.001
ti(Year, Fdis_PC1)	5.461	0.066	<.001
ti(Year, CWM_PC1)	8.510	0.064	<.001
ti(Year, CWM_PC2)	5.291	0.067	<.001

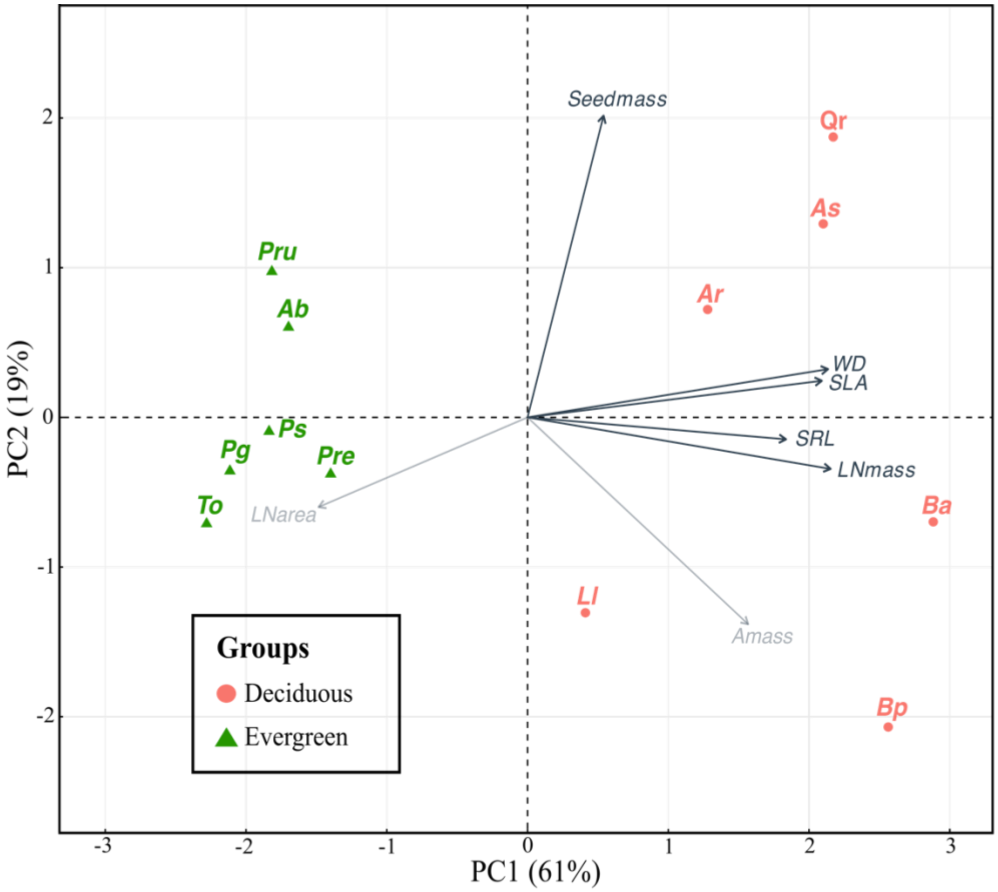


Figure 1.1 Principal Component Analysis of the functional trait values used to characterize the species of the experiment. The first Principal Component (i.e., PC1) is explained mostly by Wood Density (i.e., WD), Specific Leaf Area (i.e., SLA), Specific Root Length (i.e., SRL), and Leaf Nitrogen Mass (i.e., LNmass). And the second Principal Component (i.e., PC2) is explained primarily by Seed Mass (i.e., Seedmass). Leaf Nitrogen Area (i.e., LNarea) and net maximum photosynthesis by unit leaf mass (i.e., Amass) were not correlated with any of the two principal components. Species codes are: Ab, *Abies balsamea*; Ar, *Acer rubrum*; As, *Acer saccharum*; Ba, *Betula alleghaniensis*; Bp, *Betula papyrifera*; Ll, *Larix laricina*; Pg, *Picea glauca*; Pru, *Picea rubens*; Pre, *Pinus resinosa*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; To, *Thuja occidentalis.*

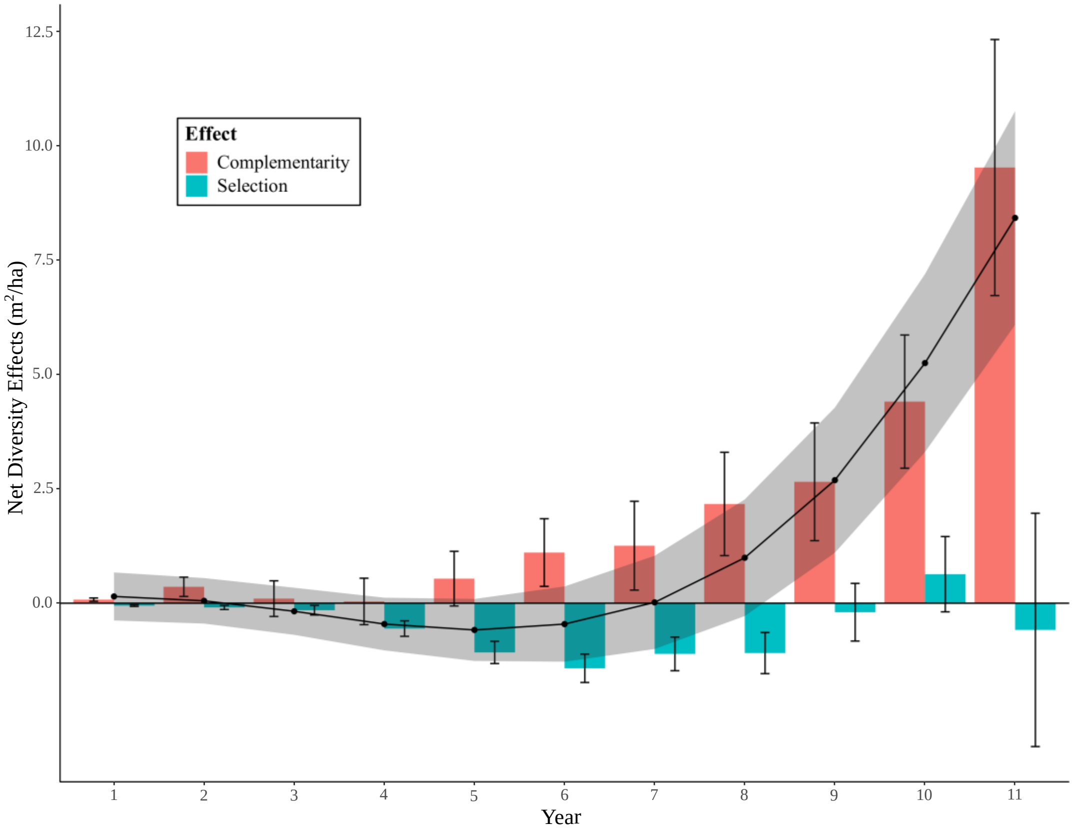


Figure 1.2 Fitted (eqn 3) Net Diversity Effects (NE; Black line ± confidence interval 95% across mixtures and blocks; $N = 1100$) on G (m^2/ha) over time driven by complementarity and selection effects (red and blue bars respectively ± standard error).

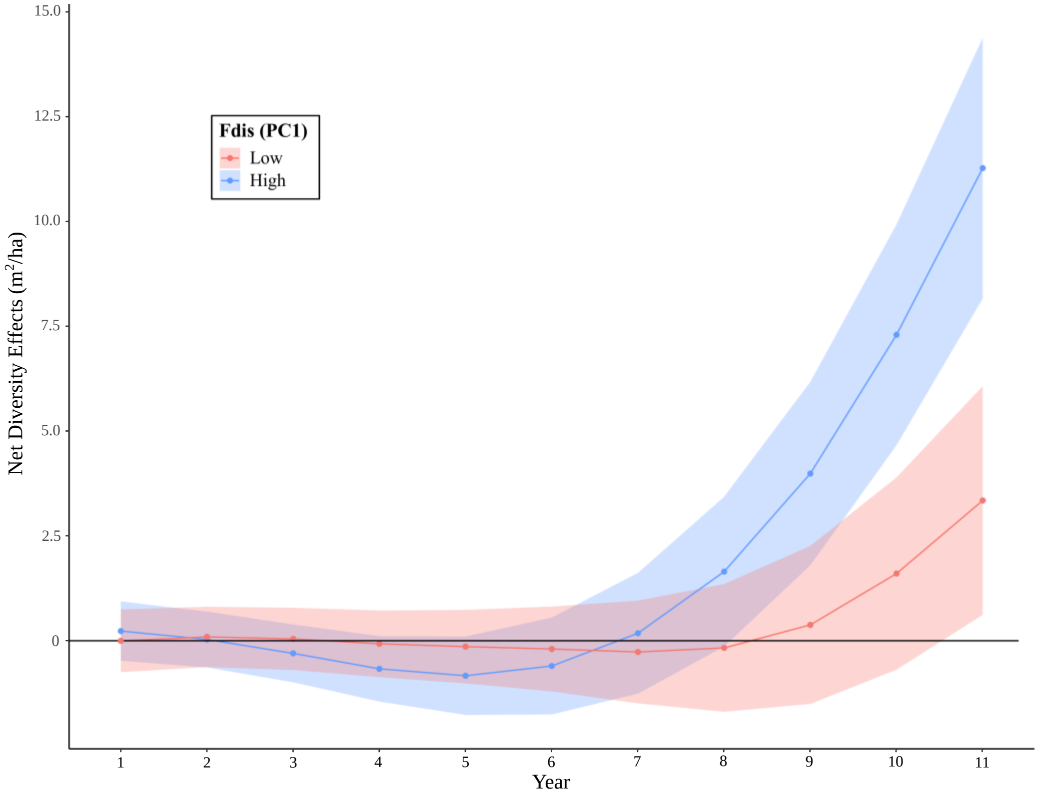


Figure 1.3 Fitted (eqn 3) Net Diversity Effects (NE) on G (m^2/ha) over time for high and low diversity mixtures grouped by the first principal component (i.e., resource-use strategy, PC1). The graph shows that plots with high diversity in resource-use strategy (blue line ± confident interval 95%, $N = 704$) overyielded as stands developed. In contrast, plots with low diversity in resource-use strategy (red line ± confident interval 95%, $N = 396$) showed negligible diversity effects over time, except the last year, where they slightly overyielded.

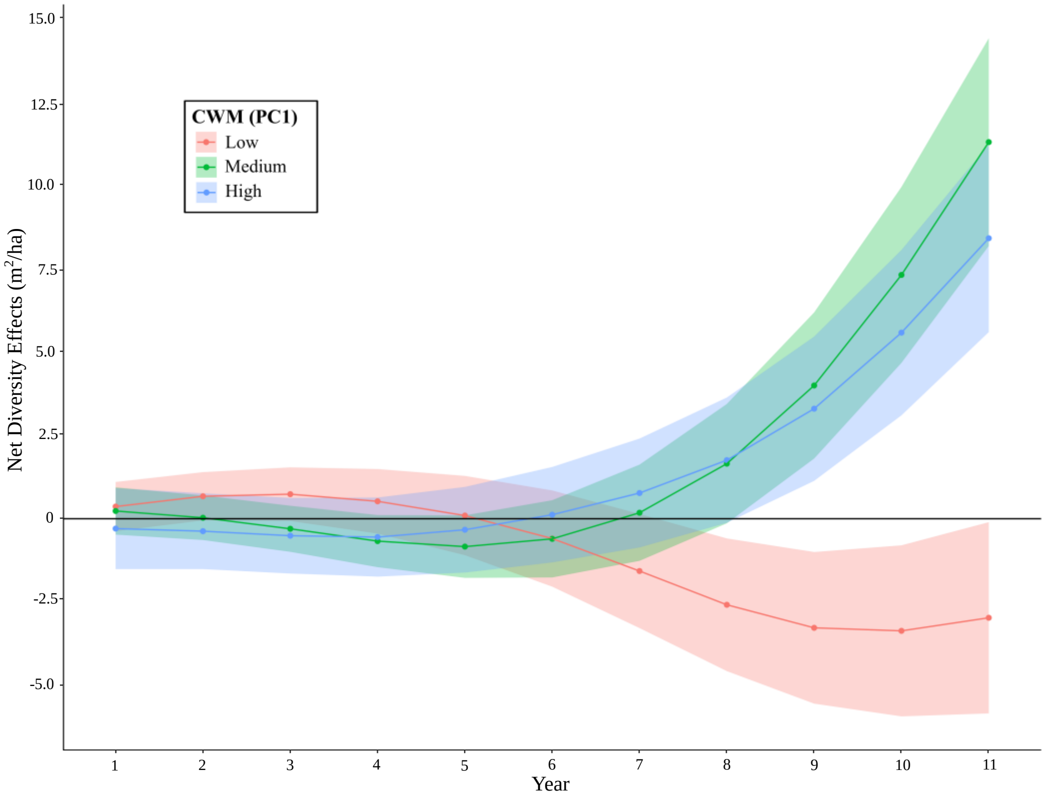


Figure 1.4 Fitted Net Diversity Effects (NE) on *G* (m^2/ha) over time for mixtures with high, medium, and low CWM values group by the first principal component (i.e. resource-use strategy, PC1). The graph shows that mixtures with high and medium values in the resource-use strategy (blue and green line respectively ± confidence interval 95%, *N* = 220 and 704 respectively) overyielded over time. Conversely, mixtures with low values (red line ± confidence interval 95%, *N* = 176) showed negative diversity effects over time.

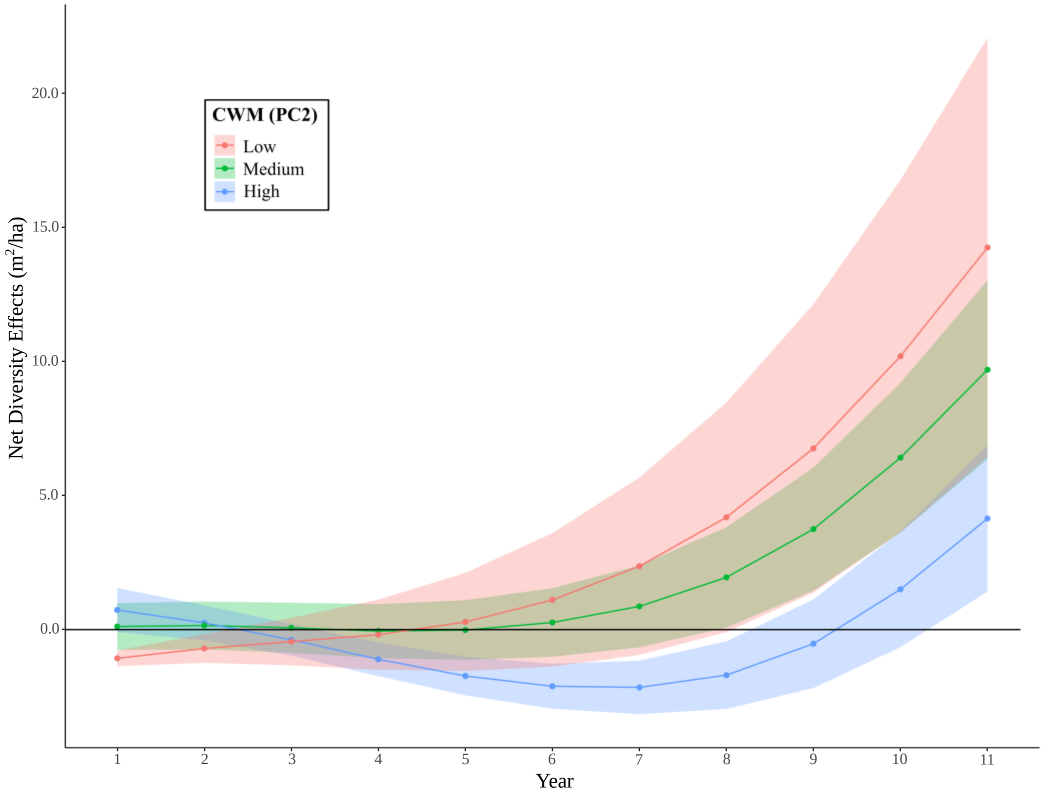


Figure 1.5 Fitted Net Diversity Effects (NE) on *G* (m^2/ha) over time for plots with high, medium, and low CWM values of the second principal component (i.e. colonization strategy, PC2). The graph shows that mixtures with low and medium values in the colonization strategy (red and green lines ± confidence interval 95%, *N* = 176 and 528 respectively) progressively overyielded as stands developed. However, mixtures with high values (blue line ± confidence interval 95%, *N* = 396) showed negative diversity effects, except the last year where they also overyielded.

SUPPORTING INFORMATION

Table S1.1 Species present in the experiment and their respective trait values used in analyses. Traits included: leaf nitrogen content per mass (Leaf Nmass, mg g-1), leaf nitrogen content per area (Leaf Narea, g m-2), specific leaf area (SLA, mm2 mg-1), specific root length (SRL, m g-1), net maximum photosynthesis by leaf mass (A_mass, µmol g-1 s-1), seed mass (log transformed values; Seed Mass), and wood density (WD, g cm-3).

Species	Code	Leaf Nmass	Leaf Narea	SLA	A mass	SRL	Seed Mass	WD
Abies balsamea	Ab	12.23	1.60	7.57	0.06	23.98	0.88	0.37
Acer rubrum	Ar	16.81	1.12	16.52	0.12	64.45	1.35	0.52
Acer saccharum	As	18.69	1.06	19.95	0.11	57.78	1.80	0.62
Betula alleghaniensis	Ba	20.01	0.84	17.52	0.21	90.34	0.34	0.61
Betula papyrifera	Bp	23.14	1.42	16.33	0.26	73.98	-0.47	0.54
Larix laricina	Ll	16.26	1.89	8.67	0.23	41.32	0.20	0.53
Picea glauca	Pg	12.08	3.00	4.51	0.06	48.28	0.35	0.38
Picea rubens	Pru	11.03	1.05	4.24	0.03	68.25	0.52	0.39
Pinus resinosa	Pre	12.46	3.04	3.49	0.08	27.89	0.95	0.46
Pinus strobus	Ps	14.48	2.90	7.67	0.12	16.10	1.18	0.36
Quercus rubra	Qr	20.18	1.50	13.35	0.15	71.94	3.44	0.61
Thuja occidentalis	To	11.85	2.025	4.92	0.12	13.88	0.12	0.31

Trait data source: IDENT TRAIT DATABASE (Belluau, 2020)

Table S1.2 Correlation table of each functional trait and the both Principal Components (i.e. PC1 and PC2) extracted from the PCA analysis.

Functional Trait	**PC1**	**PC2**
Amass	0.6904798	-0.60880949
LNarea	-0.6537786	-0.263928172
LNmass	0.9485813	-0.151553488
SLA	0.9209959	0.107663377
WD	0.9404454	0.141932394
SRL	0.8088467	-0.064570846
Seed mass	0.2378572	0.887808339

Table S1.3 Summary of the data from IDENT-MTL tree diversity experiment used in this study.

	IDENT-MTL
Location	45°25’30.1”N, 73°56’19.9”W
No. of plots	148 plots (100 mixtures, 48 monocultures) arranged in four blocks
No. of species	12 native species – 6 x deciduous 6 x evergreen (Table S1 to see the species)
Plot size	4 x 4 m (16 m^2)
Trees per plot	64 (40000 trees ha^{-1})
Stand age	11 years (2009-2019)
Study design	12 x monocultures 14 x 2-species mixtures 10 x 4-species mixtures 1 x 12-species mixtures
Sampling design	Annual basal diameter measurement of every alive tree
No. of observations	1100 observations (100 mixtures x 11 years) - Deviation of yield in mixture against the respective monocultures

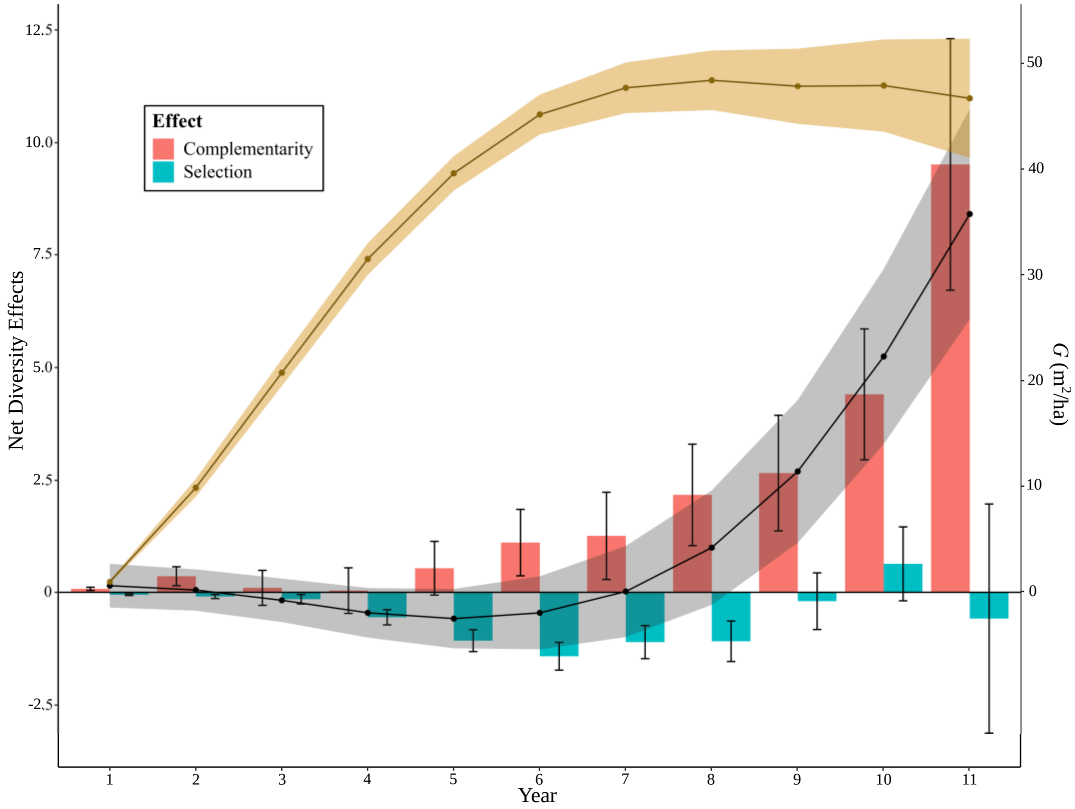


Figure S1.1 Cumulative stand basal area (*G* ± 95 % confidence interval of the means across mixtures and blocks) as a proxy of competition intensity over time in IDENT-MTL. The graph shows that the stand basal area increases steadily during the first years until around years 5 or 6 when competition intensity among trees begins to regulate growth. The moment when stand basal area saturates matches with the moment when complementarity effects begin to increase progressively over time (Figure 1.2), suggesting that resource partitioning or facilitation (*sensu* Loreau & Hector 2001) are key mechanisms promoting positive diversity effects under harsher conditions due to competition for resources.

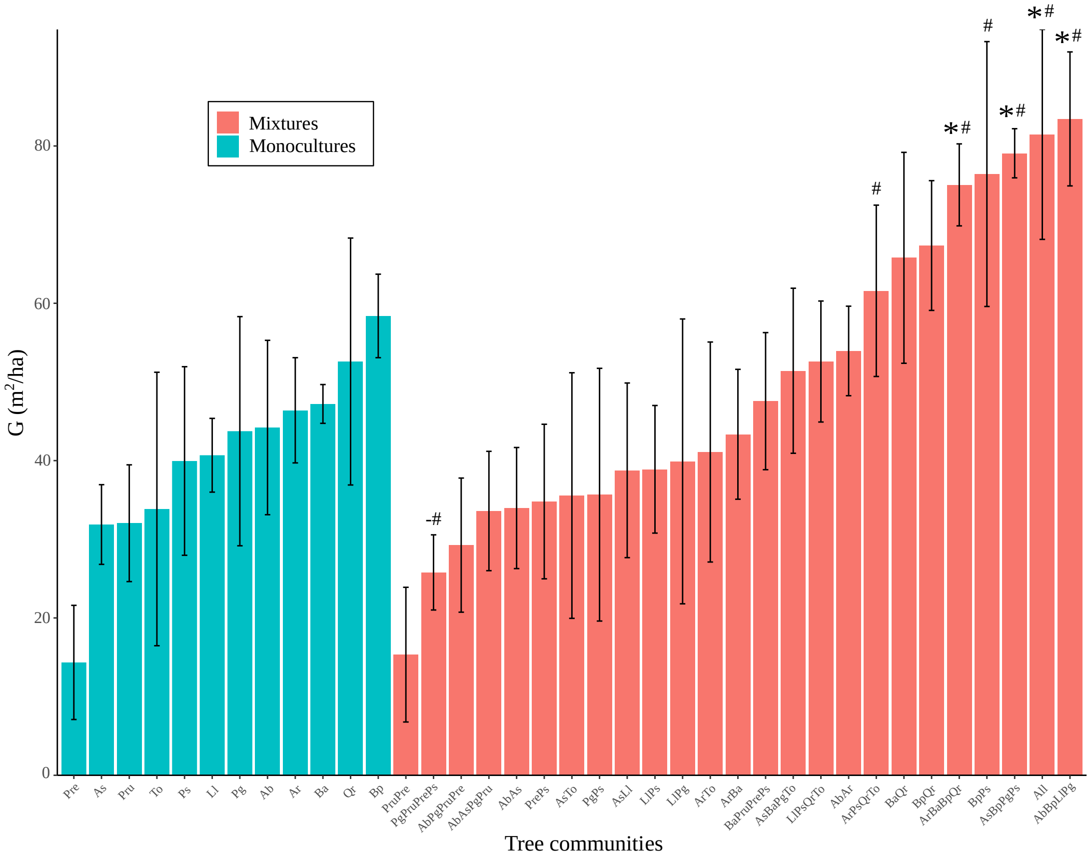


Figure S1.2 Stand basal area (G ± standard deviation across blocks) by monocultures (blue bars) and mixtures (red bars) for the final year of the experiment (i.e. year 11). Mixtures with significant net diversity effects are annotated with # (positive effect) or - # (negative effect), whereas significant transgressive overyielding is noted using * ($P < 0.05$).

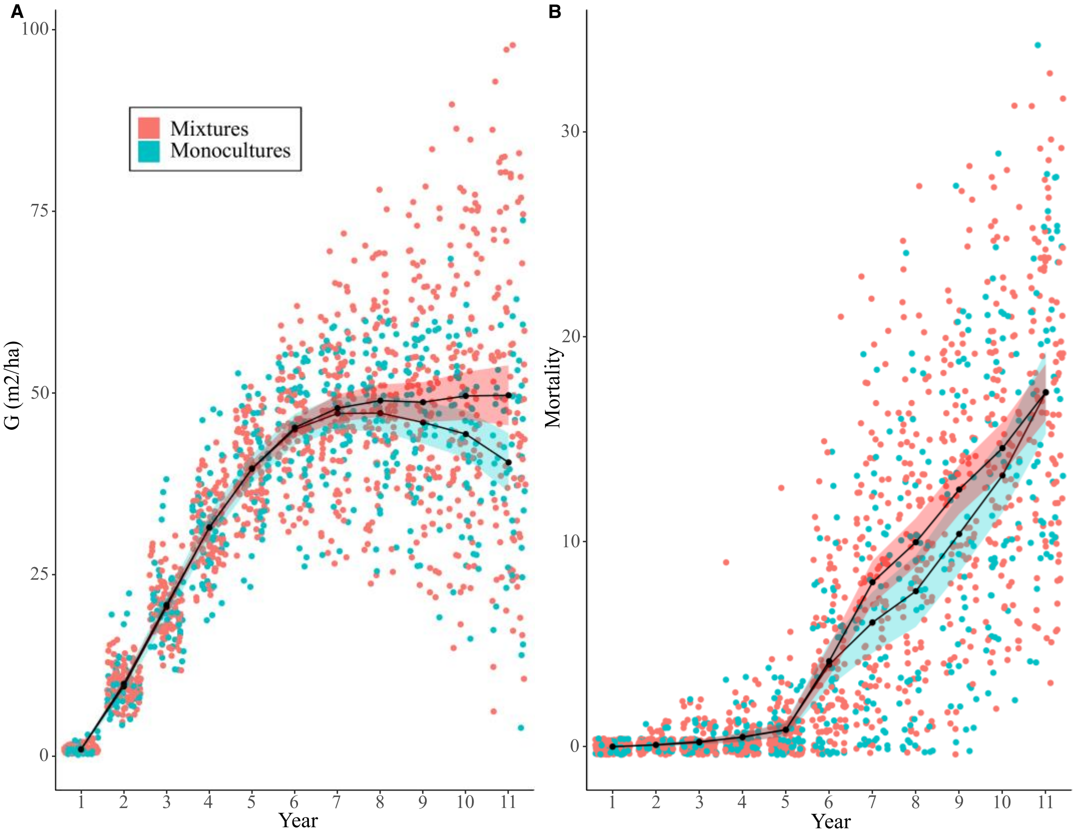


Figure S1.3 (A) Cumulative stand basal area (*G*) and (B) cumulative mortality through time for each monoculture (blue) and mixture (red). The black lines and the colored area surrounding them represent the mean values ± 95 % confidence intervals.

Appendix S1.1 – Correction for diameters measured at different heights

From years 1 to 8, tree diameters were measured at 5 cm from ground, and 15 cm onwards. In year 9 we measured diameters of every tree still alive (9274) at both heights. To ensure the change in measurement height did not bias estimates of tree growth, we modelled the difference in diameter measured at 15cm and 5cm using year 9 data through a mixed effect model with species nested in diameter values at 5cm as random factor (noted *R*).

$$D_{15} = D_5 + D_5[Species](R) \tag{1}$$

Chapter 2

Functional diversity and identity influence the self-thinning process in young forest communities

This chapter was submitted initially to Journal of Ecology (December 2022) as: Urgoiti J, Messier C, Keeton WS, Belluau M, Paquette A. Functional diversity and identity influence the self-thinning process in young forest communities - JEcol-2022-1068. It is now under revision following an initial decision (January 2023) and invitation to submit a revised version.

ABSTRACT

1- There is increasing evidence that the strength of tree diversity effects on productivity varies considerably over the course of forest development. Evidence points to canopy closure and the subsequent self-thinning as key phases of forest development during which positive diversity effects emerge. A number of studies have shown that self-thinning can differ among species, and also in mixtures compared to monocultures. Yet, how diversity influences the process of canopy closure and self-thinning remains poorly understood.

2- In this study, using 11 years of growth and mortality records from a large diversity experiment, we fitted self-thinning trajectories for 37 tree communities with equal initial densities and explored whether and how functional diversity and identity may affect these trajectories. We then examined whether the diversity effects on self-thinning were influenced by differences in growth or in mortality.

3- We found that tree communities' functional diversity and identity strongly influence the self-thinning process. First, we observed that tree communities dominated by early successional species begin self-thinning at a larger mean tree size. Second, we found that mixing species with contrasting resource-use strategies, and the dominance of deciduous, fast-growing species, reduce tree mortality rate in relation to mean tree size during self-thinning (i.e., shallower self-thinning slope). The lower rates of self-thinning in these functionally diverse communities seem to be explained by both an increase in tree growth and a reduction in density-related mortality simultaneously over time.

4- *Synthesis*. Overall, this study highlights that increasing tree diversity has the potential to enhance forest productivity in the long term through a better performance during the self-thinning process when competition for resources is most intense.

Key words: Plant population and community dynamics; IDENT; biodiversity-ecosystem functioning; tree diversity experiment; self-thinning; stand development; functional traits; life-history strategy.

INTRODUCTION

There is compelling evidence that tree diversity generally increases forest productivity (Liang et al., 2016; Paquette & Messier, 2011; Zhang et al., 2012). However, there are important divergences in the strength of diversity effects on productivity (e.g. Schnabel et al. 2019; Tobner et al. 2016). A number of factors account for this variation, including the role of stand development in driving the temporal dynamics of this relationship (Jucker et al., 2020; Taylor et al., 2020; Urgoiti et al., 2022). Recent studies have shown that diversity effects vary considerably as stands develop and take many years to manifest after seedling establishment (Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020; Urgoiti et al., 2022). The results point to canopy closure and the subsequent self-thinning (i.e., density-dependent mortality) as key phases of stand development during which positive diversity effects on productivity emerge. Yet, the mechanisms by which diversity influences forest development processes, and ultimately diversity-productivity relationships, remain poorly understood.

Competition for light and growing space is considered to be the major driver determining forest structure and functioning in young, densely regenerated stands (Fichtner et al., 2018; Jucker et al., 2014; Morin et al., 2011). Following stand establishment, the relatively abundant light and resources allow trees to rapidly grow and expand their crowns. However, as trees grow, competition for light and growing space gradually intensifies until canopy closure is achieved. Canopy closure induces high levels of inter-tree competition (Zeide, 1987), leading to mortality (i.e. self-thinning) with rates dependent on living tree density and size. In self-thinning communities, the relationship between tree density (N) and mean size of living trees (w) can be described by the following equation:

$$\mathit{ln}\ (\mathrm{N}) = \mathit{intercept} + \mathit{slope} \times \mathit{ln}\ (w)$$

Seminal studies on the topic assumed that the slope of the self-thinning relationship, when plotted as a curve, is -2/3 when *w* is volume (Yoda et al.,1963) or -1.605 when *w* is the quadratic mean diameter (Reineke, 1933) for all species in monospecific even-aged stands. Although these stand-level allometric equations have been intensively used in forest growth models to predict density-dependent mortality, increasing evidence supports that both the intercept and slope are not, in fact, constant. Regardless of environmental conditions (Forrester et al., 2021; Morris, 2003; Zeide, 1987) both parameters can differ among species (Pretzsch, 2006; Pretzsch & Biber, 2005; Pretzsch & Del Río, 2020; Puettmann et al., 1993), and also in mixtures compared to monocultures (Ducey & Knapp, 2010; Pretzsch et al., 2015; Reyes-Hernandez et al., 2013). This suggests that species-specific characteristics and competition among trees for resources are essential for understanding how communities develop in young, crowded stands.

Functional traits capture the inherent differences in species' resource-based niches and life-history strategies and, therefore, can determine the competitive interactions within tree communities (Kunstler et al., 2015; McGill et al., 2006). Thus, a trait-based approach might be a useful framework to link the competitive interactions among species and their consequences at the community level through the self-thinning process. A long-standing hypothesis is that the intensity of competition decreases as species diverge in trait values (i.e., functional diversity; FD), since the likelihood of two individuals competing for the same niche decreases (i.e., intraspecific vs interspecific competition; Clark, 2010). For example, mixing species with contrasting life strategies promotes more efficient use of canopy space (Jucker et al., 2015; Williams et al., 2017). This, in turn, alleviates competition for light and allows diverse communities to capture a greater proportion of incoming light and grow faster compared to less diverse communities (Jucker et al., 2015; Kunz et al., 2019; Pretzsch, 2014; Sapijanskas et al., 2014). However, a logical consequence of this higher productivity is that it should speed up the self-thinning process. This stands to reason because as productivity increases, competition for light increases, and ultimately density-dependent mortality should accelerate through a positive feedback loop. It remains uncertain, however, whether more diverse stands simply grow faster or maintain higher tree densities during the self-thinning phase in comparison to lower diversity stands (Pretzsch & Biber, 2016).

Second, particular life-history trait values (i.e. functional identity; FI) may also influence competitive intensity regardless of trait dissimilarity (Grossman et al., 2018; Kunstler et al., 2015) and thus the self-thinning process. For example, previous studies showed that mean stand-level wood density was negatively correlated with maximum stand density (Andrews et al., 2018; Ducey et al., 2017). The reasoning is that for a given diameter, stands dominated by hardwoods (higher wood density) can support larger crowns. Thus, fewer trees are required to close the canopy and begin the self-thinning process, compared to stands dominated by softwoods (but see Forrester et al., 2021). Few studies have tested the effects of particular traits on the self-thinning process. However, the extent to which communities' functional identity and diversity affect this process is poorly explored.

The objective of this study was to examine how the functional composition (i.e., identity and diversity) of tree communities affect the self-thinning process. We conducted this study in the IDENT-MTL tree diversity experiment, which was planted in spring 2009 (Tobner et al., 2014). This experiment is ideally suited to conduct such a study because its high-density design favors the development of competition and therefore self-thinning process. Self-thinning began as early as 2012 and increased steadily from then on based on our previous work (Urgoiti et al., 2022). Moreover, the IDENT-MTL site includes a wide range of even-aged tree communities throughout a functional diversity gradient with identical initial tree densities. Recently, Urgoiti et al. (2022) observed in this experiment that the emergence of positive diversity effects on productivity coincided with canopy closure and the beginning of the self-thinning process. This suggests that self-thinning differs among communities and that mixtures, overall, were more productive. We hypothesize that functional diversity and identity are key drivers of the self-thinning process. We expect that the rate of tree mortality, in relation to mean tree size, decreases as functional diversity increases (i.e., shallower slopes). We also expect that communities dominated by deciduous ‘fast-growing’ species start self-thinning at smaller mean tree size. The second objective of this study was to further explore how the functional diversity and identity of tree communities contributed independently to quadratic mean diameter and mortality over time to examine whether the diversity effects on self-thinning were influenced by differences in growth or in mortality.

MATERIALS AND METHODS

Experimental design

This study uses a high-density tree-diversity experiment established as part of the International Diversity Experiment Network with Trees (IDENT; Tobner et al. 2014). The experiment was established in Ste-Anne-de-Bellevue, McGill MacDonald Campus (near Montreal, Quebec, Canada, 45°25’30.1”N, Long 73°56’19.9”W, 39 m.a.s.l.) in the spring of 2009 on a flat, former agricultural field with sandy soil (approximately 70 cm deep, overtopping clay) that was intensively managed for decades. Mean annual temperature is 6.2°C and mean annual precipitation totals 963 mm (climate.weatheroffice.gc.ca).

Tree seedlings of 12 North American temperate-boreal forest species were planted 0.5 m apart in square plots of 4 x 4 m in size (16m^2; 64 trees per plot). Plots were spaced 1.25 m apart to allow movement and minimize inter plot interactions (Tobner et al. 2014). The experiment includes 37 different plots (i.e. unique tree communities): 12 monocultures, 14 two-species mixtures, 10 four-species mixtures and one twelve-species mixture (Tobner et al. 2014). Each community was replicated four times in a randomised block design for a total of 148 plots and 9,472 trees (note that the site includes more communities addressing other questions that were not used in this experiment; see Tobner et al. 2014 for the complete design). The proportion of species within mixtures was equal and their distribution randomised with restrictions to prevent monospecific patches (see Tobner et al. 2014 for details). The distribution of trees within the communities remained constant in all the blocks; however, the distribution of communities within blocks was randomised.

Two orthogonal gradients were established: 1) a species richness gradient, and 2) a functional diversity gradient. This design allows separating the two different diversity effects. The functional diversity gradient consists of communities with species combinations of equal species richness but increasing functional diversity (see Tobner et al. 2014 for details). The site was fenced to protect against large herbivores. All plots were regularly hand-weeded regularly during the first years to eliminate herbaceous competition until canopy closure, which occurred early due to the removal of competition and site fertility.

Tree measurements

For each year and plot (a given community in a block) we computed the tree density (N; trees ha-1) and quadratic mean diameter ($\overline{d}_q$). We only used the inner 6 x 6 trees of each plot to minimize edge effects from neighbouring plots. The basal diameter (at 15 cm aboveground; d) of every live tree was measured at the end of each growing season from 2009 to 2019, hereafter years 1 to 11, from which quadratic mean d ($\overline{d}_q$) were computed for each year and plot. We measured the status of every tree yearly (Alive, Dead) to estimate tree density related to the plot surface. This value was then transformed into number of live trees per hectare (N trees ha-1). We attributed tree mortality solely to competition for limited resources as any visible damage by biotic (pathogens or insect herbivores) or abiotic factors were negligible over the first 11 years of the experiment. Data from year 12 onwards were compromised by a spongy moth (*Lymantria dispar dispar*) outbreak and could not be used for this analysis.

Estimation of self-thinning trajectories

We estimated the self-thinning or maximum-density lines using quadratic mean diameter ($\overline{d}_q$) to represent tree mean size as Reineke's (1933) original formulation (Eq 1) because it can be measured accurately and is closely related to crown size (del Río & Bravo, 2001; Zeide, 1987). In order to fit and interpretate the linear $lnN \sim ln\overline{d}_q$ allometry relationship, we used the ordinary least square method (OLS). We chose OLS over other methods such as stochastic frontier analysis (SFA) or dynamic mortality models because it is less data demanding to work correctly (Trouvé et al., 2017). However, unlike the other methods, OLS requires stands that are strictly located along the self-thinning line and therefore relies on prior data selection. To eliminate any bias and subjectivity in data selection we followed Satopää et al. (2011) approach to detect the "knee" point of the $lnN \sim ln\overline{d}_q$ curve (i.e. maximum curvature) for each plot (Figure S2.1A). The "knee" of the $lnN \sim ln\overline{d}_q$ curve is the point where the trajectory bends from flat or almost flat to sharply decreasing. Therefore, the "knee" point represents the quadratic mean diameter at which a given community began to suffer tree mortality in direct relation to the growth of trees (i.e., self-thinning). We then selected the data from the "knee" point onwards for each plot (i.e., data under self-thinning process) and calculated the $lnN \sim ln\overline{d}_q$ allometry relationship using OLS (Figure S2.1B). From each plot we extracted 1) the quadratic mean diameter at which each plot began the self-thinning process (i.e., knee), and 2) the rate of tree mortality in relation to the size of trees from that point on (i.e., self-thinning slope).

Trait data collection and calculation of functional indices

We used seven functional traits that are linked to tree light-use strategies and competition capacities to compute functional diversity and identity at the initial stage of the experiment. They include specific leaf area (SLA), leaf nitrogen content by mass (LNmass), leaf nitrogen content by area (LNarea), net maximum photosynthesis by unit leaf mass (Amass), wood density (WD), specific root length (SRL), and seed mass (seedmass). All trait data used in the study were collected from the literature (Belluau, 2020).

Then, we performed a Principal Component Analysis (PCA) of the trait values at the species level to avoid collinearity among traits and identify species main axes of life-history strategies (see Chapter 1 for details; Figure 1.1). The first two principal components explained 80% of the variance in traits. The first principal component (PC1) was correlated to wood density (Pearson correlation; WD: $r = 0.94$), leaf nitrogen content by unit mass (LNmass: $r = 0.95$), specific leaf area (SLA: $r = 0.92$), and specific root length (SRL: $r = 0.81$), clearly separating evergreens from deciduous (Urgoiti et al. 2022). These functional traits are involved in the acquisition, processing, and conservation of resources. Therefore, they define species' life history strategy largely by influencing growth vs survival trade-offs (Reich, 2014) The second principal component (PC2) was related only to seed mass (Urgoiti et al. 2022). Seed mass is considered an indicator of the trade-off between colonization (early vs late successional species) and competitive capacity (Turnbull et al. 2004). For example, small-seeded species are typically better colonizers but less shade tolerant and thus, lesser competitors. Using the species scores over these two life-history axes (i.e. principal components), we calculated the tree communities' FD and FI using functional dispersion (Fdis, Laliberté and Legendre 2010) and community weighted means (CWMs, Lavorel et al. 2008) respectively (i.e. $Fdis_{PC1}$, $Fdis_{PC2}$, CWM_{PC1} and CWM_{PC2}). We used the R package FD to calculate CWM and Fdis (Laliberté & Legendre 2010).

Statistical Analysis

We performed linear mixed-effect models with REML estimation to test the effects of functional diversity (Fdis) and functional identity (CWM) on both the slope and "knee" point of the self-thinning process. We set block and plot (i.e., the 37 different tree communities replicated in each block) as random factors (noted *R*), yielding the following models:

$$Slope = Fdis_{PC1} + Fdis_{PC2} + CWM_{PC1} + CWM_{PC2} + \\ Plot\ (R) + Block\ (R) + \varepsilon$$

$$knee = Fdis_{PC1} + Fdis_{PC2} + CWM_{PC1} + CWM_{PC2} + \\ Plot\ (R) + Block\ (R) + \varepsilon$$

where 'Fdis' is functional dispersion, and 'CWM' community weighed means. The subscripts 'PC1' and 'PC2' refer to the principal components obtained from the PCA. To find the most parsimonious model, we used the function 'dredge' of R package 'MuMIn' (Bartoń, 2016) that generates a list of models with all possible combinations of the fixed effects ranked based on the lowest AICc (corrected Akaike information criterion). Top-ranked models with similar likelihood (ΔAICc < 2) were further evaluated to provide a final model with significant predictors only.

We subsequently explored the effects of Fdis and CWM on cumulative quadratic mean diameter and mortality over time (Year) independently. For these models, we only selected the diversity parameters that had a significant effect on the self-thinning slope (i.e., $Fdis_{PC1}$ and CWM_{PC1}). For the model for quadratic mean diameter, we used a linear mixed-effects model with REML estimation, and for the model on mortality, a generalized linear mixed-effects model with a negative binomial distribution. In the case of the mortality model, we only used data from year 4 onwards as mortality in the previous years was negligible (Tobner et al., 2016; Urgoiti et al., 2022). Block and plot were again set as random factors for both models. We followed the same approach as in the previous model to find the most parsimonious model.

$$\overline{d}_q = Year \times Fdis_{PC1} + Year \times CWM_{PC1} + \\ Plot\ (R) + Block\ (R) + \varepsilon$$

$$Mortality = Year \times Fdis_{PC1} + Year \times CWM_{PC1} + \\ Plot\ (R) + Block\ (R) + \varepsilon$$

RESULTS

Self-thinning trajectories were fit for every plot (a given tree community in a block) of the experiment over the first 11 years of development (Figure 2.1; Table S2.1). Our results show significant differences in the self-thinning trajectories among the different tree communities depending on their functional trait-based composition. First, functional identity had a substantial effect on the “knee” point, the quadratic mean tree diameter at which a community begins the self-thinning process (Table 2.1). Our results show that CWM of seed mass had a negative relationship with the “knee” point. In communities with lower values of seed mass, the self-thinning began at larger quadratic mean diameters compared to communities with larger mean seed mass (Figure 2.2).

Second, once self-thinning was initiated in a community, we observed that the rate of tree mortality in relation to the tree mean size (i.e., slope) decreased as the functional diversity of the first principal component increased (Fdis_PC1; Figure 2.3A; Table

2.2). Communities characterized by species with contrasting resource-use strategies (i.e., high values of Fdis_PC1) developed shallower self-thinning slopes compare to communities with similar resource-use strategies (i.e., low values Fdis_PC1). In addition, we also observed a positive relationship between the self-thinning slope and functional identity of the first principal component (CWM_PC1; Figure 2.3B; Table 2.2). Communities dominated by deciduous species with acquisitive economic traits (i.e., high values of CWM_PC1) had shallower self-thinning slopes than communities dominated by species in the “slow” end of the resource economic spectrum (i.e., low values of CWM_PC1; mostly evergreens).

Further analysis of the effects of tree communities’ functional composition on quadratic mean diameter and mortality over time shows that both vary substantially among communities during the first 11 years of the experiment. First, the functional diversity and identity of the first principal component (i.e., Fdis_PC1 and CWM_PC1) show negligible effects on quadratic mean diameter during the first 7 years of the experiment. These effects then became positive, strengthening over time (Figure 2.4; Table S2.2). Second, the effects of functional diversity and identity of the first principal component (i.e., Fdis_PC1) on mortality changed over time (Figure 2.5; Table S2.3). On the one hand, the effects of functional diversity were positive in the year 5, became flat from year 6 to 8, and then negative from year 9 onward. On the other hand, the effects of functional identity were positive from year 5 to 8, and then negative from year 9 onward.

DISCUSSION

Using a biodiversity experiment with trees in which all the communities were planted with identical initial conditions and grown for 11 years, we tested the effects of functional diversity and identity on the self-thinning process. This study provides evidence that a tree community’s functional diversity and identity are key drivers of self-thinning which, in turn, is a critical process of stand development influencing forest functioning. A recent study conducted on the same experiment found that the emergence of the diversity effects on productivity coincided with canopy closure and the beginning of the self-thinning process (Urgoiti et al. 2022). The present results complement that study and help explain how more diverse communities become more productive through the self-thinning phase.

The effects of functional diversity and identity on self-thinning trajectories

The study shows substantial variation in self-thinning trajectories among the 37 communities assessed over the first 11 years of the experiment. First, our results show that communities dominated by species with low seed mass began the self-thinning process at a higher mean tree size (i.e., knee point). Seed mass is considered an indicator of the trade-off between colonization (early vs late successional species) and competitive capacity (Turnbull et al., 2004). Early successional species (i.e., species with low seed mass) take advantage of recently disturbed areas (similar to the initial conditions in IDENT) where the high availability of light, water and nutrients enable rapid growth and faster occupation of dominant canopy positions. Fast growth during the initial stages of stand development (and consequently better access to resources) is directly linked to their reduced ability to tolerate competitive pressures, such as shading from other species (Kunstler et al. 2016). In this context, the intense agricultural activity on the site before experiment establishment, the complete removal of herbaceous competition during the first years, and the open canopy context resulted in resource-abundant conditions, favoring the rapid growth of early successional tree species (Tobner et al. 2016; Williams et al. 2017). These results suggest that communities dominated by early successional species benefited from the high availability of resources at the onset of the experiment, growing rapidly and quickly dominating the canopies. Greater access to resources, in turn, reduced competitive pressures, and ultimately, allowed these communities to reach greater diameter before the self-thinning process was initiated. Indeed, Tobner et al. (2016)

found that by year 4 of the experiment (one year before stands, in general, entered the self-thinning process; Urgoiti et al. 2022) communities dominated by early successional species were more productive.

Second, this study shows that once the communities were undergoing self-thinning, mixing slow-developing evergreen with fast-developing deciduous species decreased the rate of tree mortality in relation to mean tree size (i.e., shallower self-thinning slopes) compared to low-diversity communities. These trajectories, in turn, strongly determine the productivity of tree communities in the long term (Figure S2.2) which helps explain the emergence of positive diversity effects reported by a recent study on the same experiment. In diverse communities, the magnitude of density-related competition may be reduced, since the likelihood of two individuals competing for the same resource-based niche decreases (Clark 2010). Numerous studies have found that mixing species with contrasting life strategies promotes light partitioning through the more efficient occupation of the canopy space, either as canopy strata or fully differentiated canopies (Jucker et al. 2015; Sapijanskas et al. 2014). A typical example is the development of multi-layered canopies where shade-tolerant species grow under dominant, light-demanding species (Jucker et al., 2015; Niinemets, 2010). This decreases competition for light allows diverse communities to capture a greater amount of incoming light, thereby growing faster compared to monocultures (Jucker et al., 2019; Pretzsch, 2014b; Sapijanskas et al., 2014). Higher productivity in more diverse communities might be also due to reduced belowground competition. A previous study conducted in the same experiment showed a negative diversity effect on root biomass, thus possibly less competition belowground in more productive communities aboveground (Archambault et al. 2019). However, this reduction in the intensity of competition in more diverse communities can also promote higher stand densities (Pretzsch & Biber, 2016), suggesting a reduction in the intensity of competition-based mortality. Our analysis of functional composition effects on quadratic mean diameter and mortality shows that mixing fast-growing deciduous species with slow-growing evergreen species progressively increased mean tree size and reduced density-related mortality simultaneously over time. Therefore, the results suggest that the shallower self-thinning slopes we observed in more diverse communities are explained by both an increase in growth and a reduction in density-related mortality occurring simultaneously during self-thinning.

Similarly, we also found that the dominance of fast-developing deciduous species promoted shallower self-thinning slopes compared to communities dominated by slow-developing evergreens. Functional traits are directly related to the performance and the ecological strategies of trees species, ultimately determining their (competitive) fitness in a given environment (Adler et al., 2014; Reich, 2014). Competition under self-thinning is typically asymmetrical with the largest trees getting most of the incoming light (disproportionate to their sizes). Species exhibiting an acquisitive resource-use strategy (fast-growing) are associated with higher competitive ability and faster resource acquisition, which may give them an advantage in a competitive self-thinning environment over conservative slow-growing shade-tolerant species (Kunstler et al. 2016; Reich 2014). In this context, the effective light acquisition of tree communities dominated by deciduous “fast” developing species allows these to grow faster under self-thinning process (Hisano & Chen, 2020; Zheng et al., 2021), ultimately influencing its slope. However, the higher competitive tolerance of communities dominated by “slow” growing species should compensate for lower growth with lower competition-based mortality over time (i.e., higher shade tolerance), which in theory would balance the self-thinning slopes. Interestingly, we found that although during the first years of self-thinning tree communities dominated by “fast” developing species suffered higher levels of mortality, the trend changed over the last three years, with "slow" growing communities registering higher mortality. From a physiological point of view, the shade tolerance of a given species is defined as the minimum light under which it can survive (Valladares & Niinemets, 2007). Although “slow” shade-tolerant species are able to minimize respiratory losses and maximize long-term storage to survive in these environments (Craine & Reich, 2005), the extremely low light availability in the understory of the experiment over a long period could have reached a point where respiratory losses were greater than their photosynthetic production, resulting in their death. All the “slow” growing evergreen species of our study are considered to tolerate shade except red pine (*Pinus resinosa*), a light demanding species. Indeed, the monoculture of red pine is the community with the steepest self-thinning slope, probably caused by a relatively slow growth (Williams et al., 2017) and high mortality due to insufficient light during the self-thinning process. Moreover, regardless of light competition, during the first years of the experiment Archambault et al. (2019) observed that as the number of conifer species in a community increases, the proportion of belowground compared to aboveground biomass increases. This suggests that belowground competition might be proportionally higher in communities dominated by “slow” growing conifers, and consequently could also influence tree mortality during the self-thinning process. We conclude that the steeper self-thinning slopes of communities dominated by “slow” growing species are the result of slower growth and of higher mortality over time compared to "fast" growing communities.

CONCLUSION

Using eleven years of growth and mortality records from a tree diversity experiment, we find that tree communities’ functional composition plays a formative role driving development through the self-thinning phase. A previous study in the same experiment (IDENT) had shown how the emergence of diversity effects on productivity coincided with canopy closure and increased along the self-thinning process. The present study takes a further step and complements these results by explaining how tree communities’ functional diversity and identity affects these key phases of stand development that ultimately trigger positive diversity effects on productivity. We highlight that mixing species with contrasting resource-use strategies, and the dominance of deciduous, “fast” growing species, reduces tree mortality rate in relation to mean tree size during the self-thinning phase (i.e. lower self-thinning rates). We demonstrate that these communities achieve lower self-thinning rates by increasing trees’ growth and reducing tree mortality over time simultaneously, compared to less diverse communities dominated by “slow” growing conifer species. Moreover, the consequences of diversity on the self-thinning phase might also be conspicuous in the increasing tree communities’ variation in tree sizes and canopy complexity, which according to recent studies increase productivity in the later stages of forest development (e.g. Silva Pedro et al., 2017). Although the present study spanned only just over one decade of forest development, the results reinforce the growing evidence that management and conservation programs that favours increasing tree diversity have the potential to increase carbon sequestration in the long-term through better performance during the early stages of stand development when competition for resources is most intense.

ACKNOWLEDGEMENTS

This research would not have been possible without the dedication of the many grad students, postdocs and interns who worked on the IDENT-MTL experiment over the last 11 years. We also thank E. Searle for welcomed suggestions in data analysis. The research leading to these results was financially supported by grants from the National Research Council Canada (NSERC) and Fonds de Recherche du Québec – Nature et Technologies (FRQNT) to AP.

Table 2.1 Summary of the linear mixed-effects model testing the effects of functional identity of the second principal component (i.e., colonization strategy, CWM_PC2). on the “knee” point of the self-thinning (*N*=148). Summary includes degrees of freedom (df), denominator degrees of freedom (ddf), F-ratios (F) and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block and Plot as random effects).

Effects	**df**	**ddf**	**F**	**p-value**
CWM_PC2	1	35	15.512	< 0.001
R^2 conditional	0.45			
R^2 marginal	0.18			

Table 2.2 Summary of the linear mixed-effects model for the effects of functional diversity (Fdis_PC1) and identity (CWM_PC1) of the principal component (i.e., resource-use strategy, PC1) on self-thinning slopes (*N*=148). Summary includes degrees of freedom (df), denominator degrees of freedom (ddf), F-ratios (F) and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block and Plot as random effects).

Effects	**df**	**ddf**	**F**	**p-value**
Fdis_PC1	1	34	33.195	< 0.001
CWM_PC1	1	34	82.342	< 0.001
R^2 conditional	0.58			
R^2 marginal	0.51			

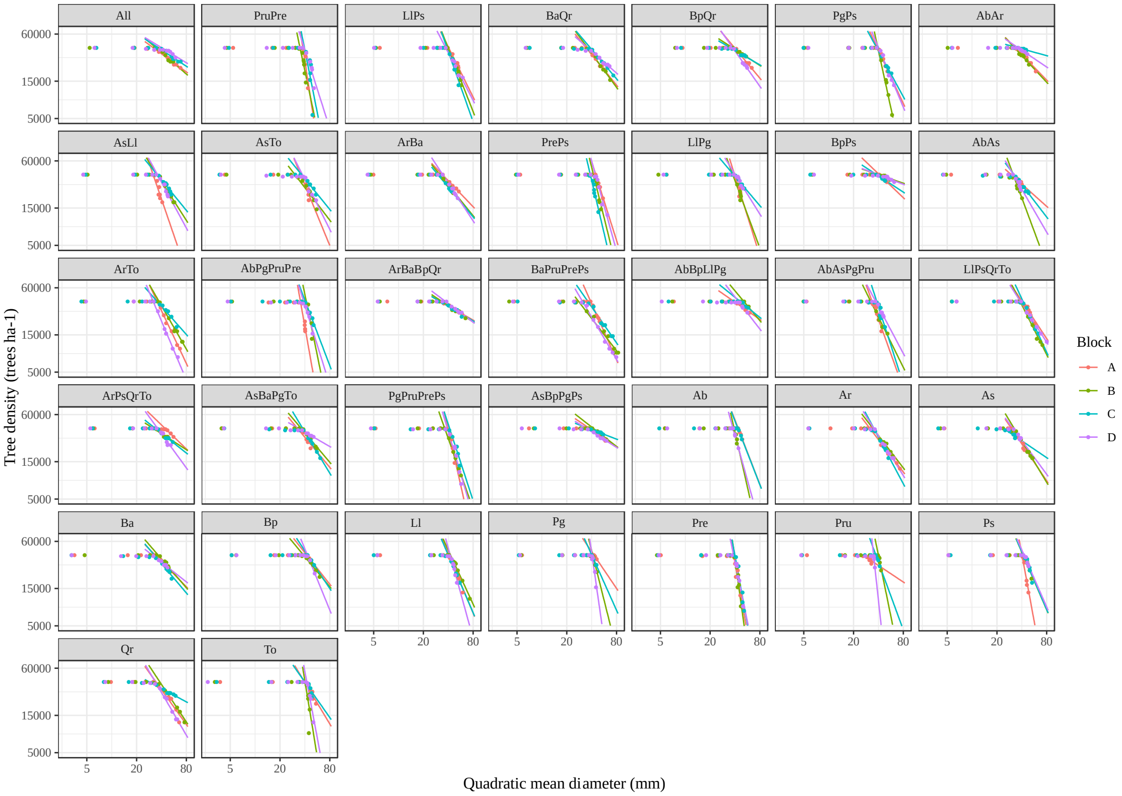


Figure 2.1 Estimated self-thinning trajectories for each tree community and block (i.e., plot). Coloured dots show the observed tree density in relation to quadratic mean diameter for each tree community (log-log relationship). Solid lines are tree community self-thinning trajectories (4 blocks) estimated from the “knee” point calculated following Satopaa’s et al. (2011) approach (Figure S2.1). Species codes are: Ab, *Abies balsamea*; Ar, *Acer rubrum*; As, *Acer saccharum*; Ba, *Betula alleghaniensis*; Bp, *Betula papyrifera*; Ll, *Larix laricina*; Pg, *Picea glauca*; Pru, *Picea rubens*; Pre, *Pinus resinosa*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; To, *Thuja occidentalis.*

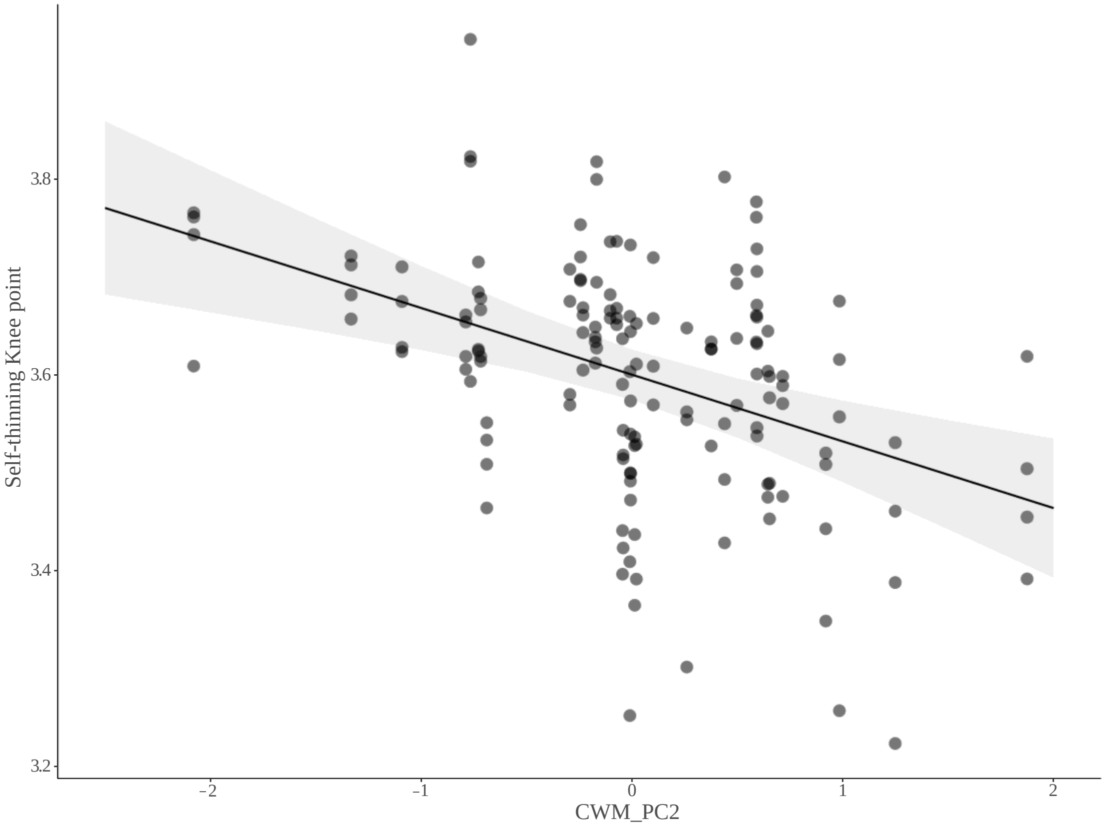


Figure 2.2 Predicted self-thinning knee point (black line ± confidence interval 95%, *N*=148) against functional identity of the second principal component (i.e., colonization strategy, CWM_PC2). Background points are estimated knee points for each plot of the experiment.

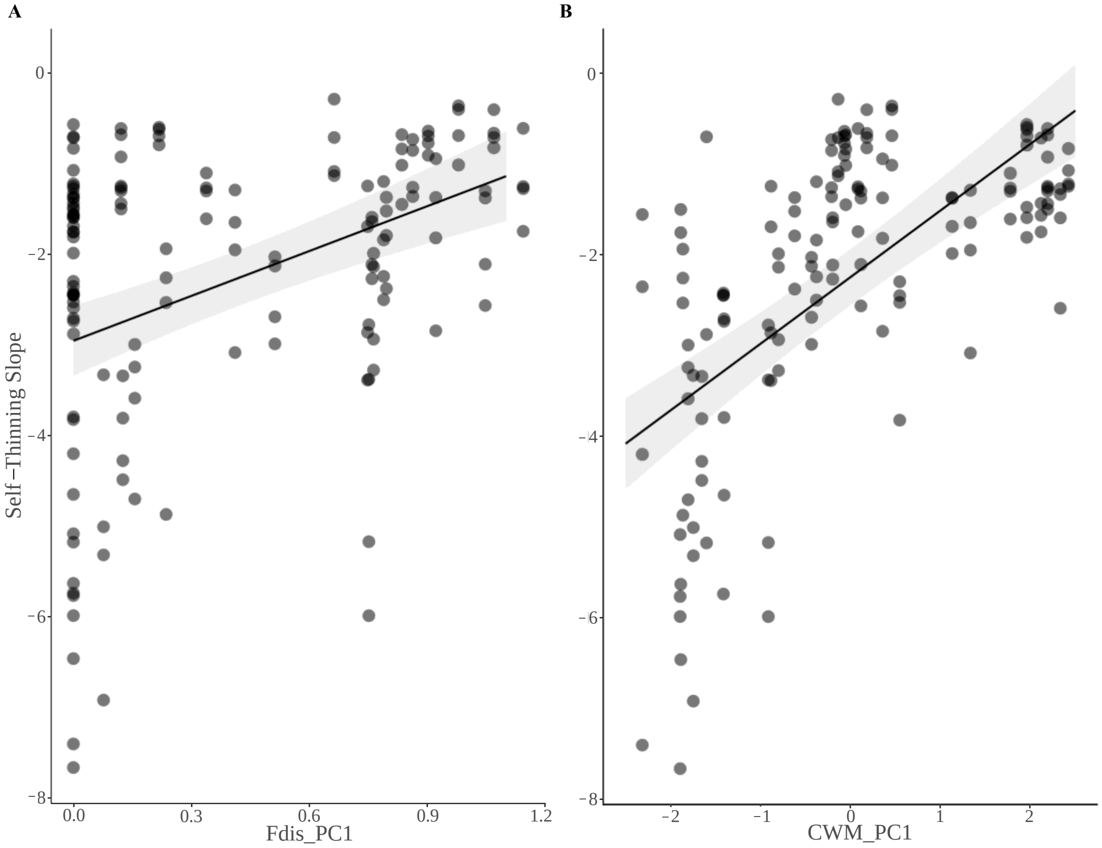


Figure 2.3 Predicted self-thinning slope (black line ± confidence interval 95%, *N*=148) against functional diversity (Fdis_PC1, A) and identity (CWM_PC1, B) of the principal component (i.e., resource-use strategy, PC1). Background points are estimated slopes for each plot of the experiment.

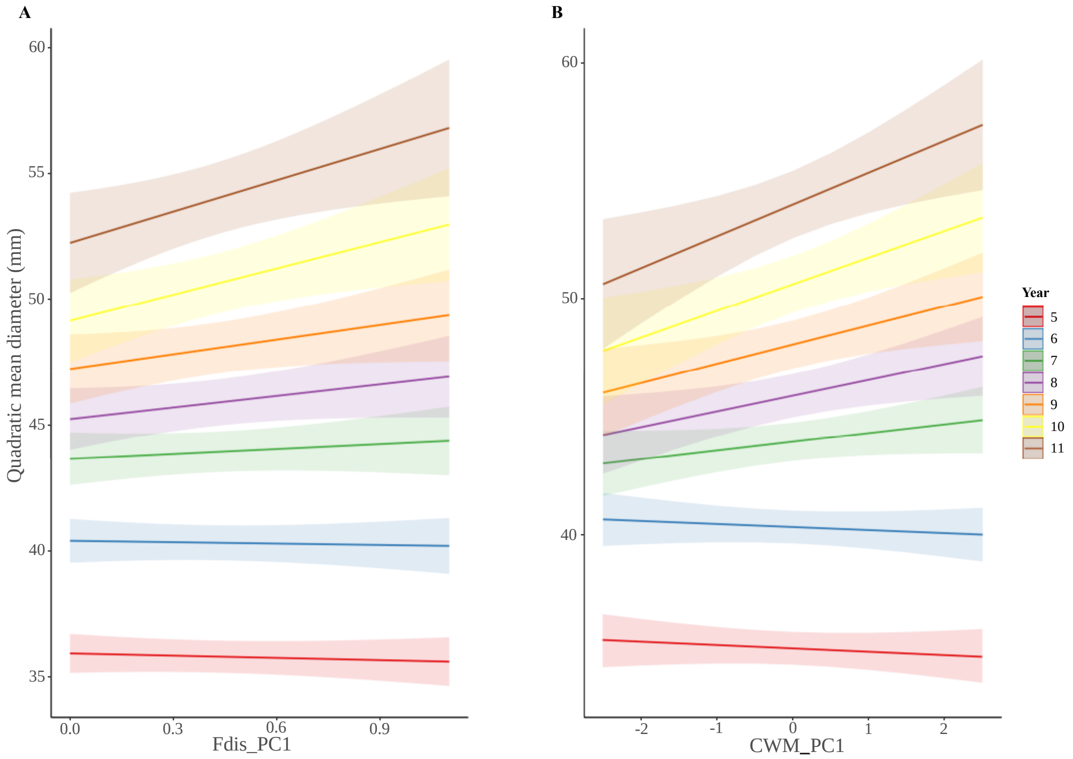


Figure 2.4 Predicted quadratic mean diameter against functional diversity (Fdis_PC1, A) and identity (CWM_PC1, B) of the principal component (i.e., resource-use strategy, PC1) over time (last 7 years only; coloured lines ± confidence interval 95%).

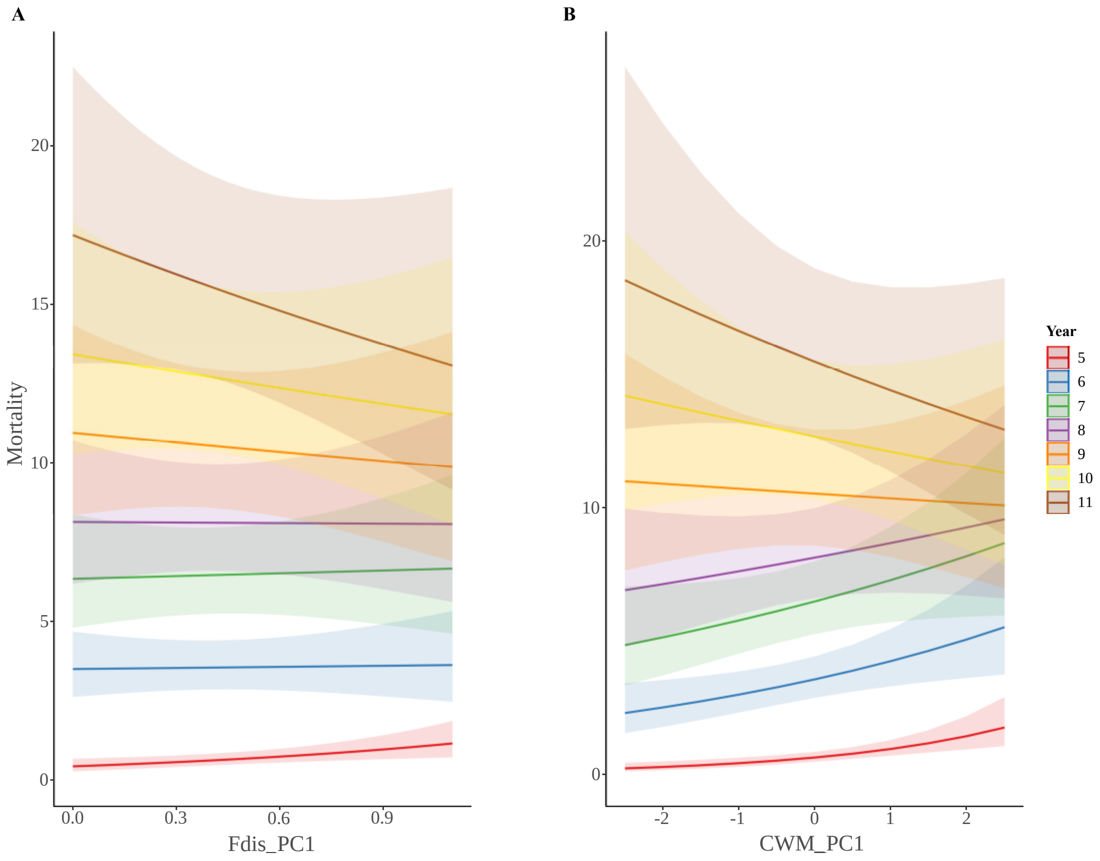


Figure 2.5 Predicted mortality against functional diversity (Fdis_PC1, A) and identity (CWM_PC1, B) of the principal component (i.e., resource-use strategy, PC1) over time (last 7 years only; coloured lines ± confidence interval 95%).

SUPPORTING INFORMARTION

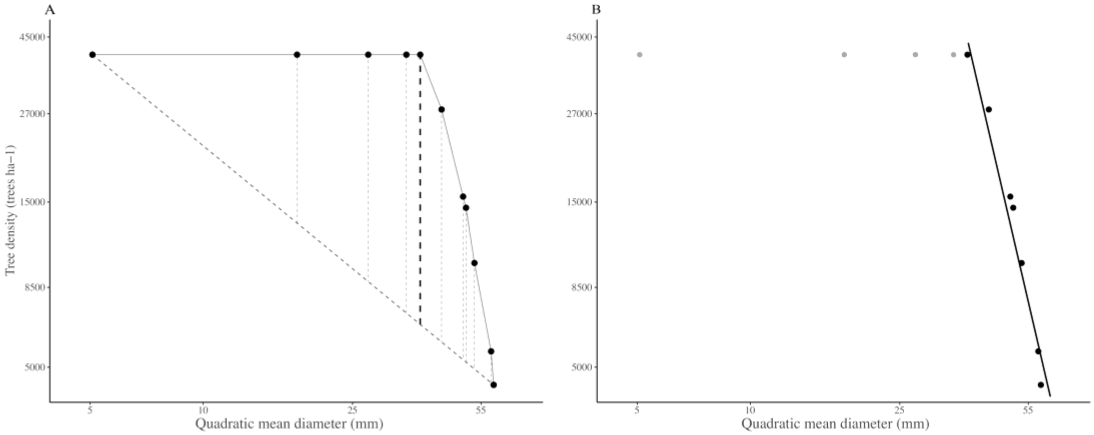


Figure S2.1 The approach we followed to estimate the knee point of the $lnN \sim ln\overline{d}_q$ curve (i.e., maximum curvature; A) for each plot. The knee point is the point at which the curve differs most from the straight-line segment connecting the first and last data point (bold dashed line). It is the point where the trajectory bends from flat or almost flat to sharply decreasing. Therefore, it represents the quadratic mean diameter at which a given community begins to suffer tree mortality in direct relation to the growth of trees (i.e., self-thinning). We then selected the data from the “knee” point onwards (i.e., data under self-thinning) and fitted linear regressions of the $lnN \sim ln\overline{d}_q$ relationship by ordinary least squares technique (i.e., self-thinning slope, B).

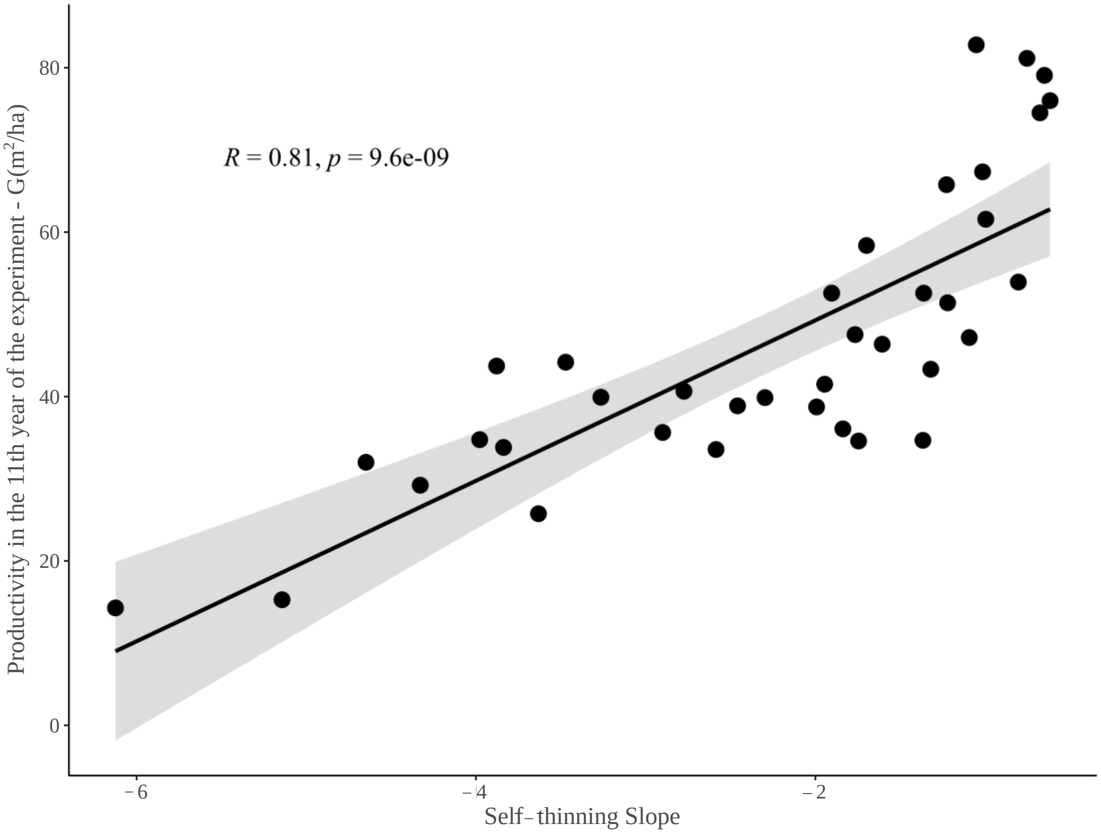


Figure S2.2 Correlation between tree community mean self-thinning slope and mean productivity in the last year of the study across blocks.

Table S2.1 Parameter estimates and fit statistics for self-thinning models based on Eq. (1) for each tree community across blocks; means (± standard deviation) of the knee and slope of the self-thinning trajectories, as well as the coefficient of determination (R^2) and square root of the mean square error (RMSE).

Tree community	**Knee**	**Slope**	**R^2**	**RMSE**
Ab	3.708 (± 0.071)	-3.471 (± 0.933)	0.960 (± 0.047)	0.036 (± 0.025)
Ac	3.559 (± 0.056)	-1.607 (± 0.293)	0.978 (± 0.009)	0.045 (± 0.006)
As	3.401 (± 0.132)	-1.367 (± 0.453)	0.894 (± 0.086)	0.046 (± 0.017)
Ba	3.515 (± 0.038)	-1.094 (± 0.191)	0.947 (± 0.029)	0.038 (± 0.019)
Bp	3.720 (± 0.074)	-1.700 (± 0.610)	0.977 (± 0.031)	0.031 (± 0.029)
Ll	3.693 (± 0.029)	-2.775 (± 0.705)	0.955 (± 0.033)	0.072 (± 0.026)
Pg	3.717 (± 0.027)	-3.878 (± 2.595)	0.964 (± 0.043)	0.047 (± 0.055)
Pre	3.645 (± 0.028)	-6.122 (± 1.094)	0.879 (± 0.038)	0.200 (± 0.026)
Pru	3.526 (± 0.186)	-4.647 (± 3.908)	0.847 (± 0.196)	0.042 (± 0.019)
Ps	3.685 (± 0.035)	-3.264 (± 1.648)	0.864 (± 0.069)	0.110 (± 0.053)
Qr	3.493 (± 0.096)	-1.363 (± 0.547)	0.953 (± 0.038)	0.077 (± 0.045)
To	3.663 (± 0.045)	-3.837 (± 2.572)	0.706 (± 0.241)	0.195 (± 0.162)
AbAr	3.529 (± 0.069)	-0.805 (± 0.392)	0.912 (± 0.108)	0.028 (± 0.018)
AbAs	3.455 (± 0.079)	-1.746 (± 0.814)	0.911 (± 0.042)	0.052 (± 0.015)
ArBa	3.467 (± 0.081)	-1.321 (± 0.210)	0.978 (± 0.008)	0.031 (± 0.007)
ArTo	3.547 (± 0.077)	-1.946 (± 0.568)	0.975 (± 0.034)	0.056 (± 0.014)
AsLl	3.500 (± 0.053)	-1.994 (± 0.775)	0.920 (± 0.042)	0.079 (± 0.029)
AsTo	3.517 (± 0.149)	-1.839 (± 0.606)	0.902 (± 0.056)	0.094 (± 0.034)
BaQr	3.615 (± 0.086)	-1.229 (± 0.217)	0.983 (± 0.009)	0.034 (± 0.015)
BpQr	3.655 (± 0.054)	-1.016 (± 0.437)	0.955 (± 0.032)	0.032 (± 0.018)
BpPs	3.659 (± 0.041)	-0.618 (± 0.302)	0.874 (± 0.106)	0.023 (± 0.009)
LlPg	3.635 (± 0.027)	-2.297 (± 0.995)	0.881 (± 0.047)	0.078 (± 0.032)
LlPs	3.644 (± 0.033)	-2.459 (± 0.457)	0.942 (± 0.022)	0.084 (± 0.019)
PgPs	3.633 (± 0.016)	-2.900 (± 1.335)	0.957 (± 0.021)	0.097 (± 0.050)
PrePs	3.735 (± 0.090)	-3.978 (± 0.511)	0.922 (± 0.064)	0.112 (± 0.058)
PruPre	3.604 (± 0.051)	-5.141 (± 1.470)	0.753 (± 0.127)	0.267 (± 0.142)
AbAsPgPru	3.553 (± 0.084)	-2.586 (± 0.620)	0.906 (± 0.086)	0.086 (± 0.049)
AbBpLlPg	3.794 (± 0.146)	-1.053 (± 0.306)	0.928 (± 0.031)	0.034 (± 0.010)
AbPgPruPre	3.652 (± 0.063)	-4.327 (± 1.501)	0.897 (± 0.091)	0.120 (± 0.074)
ArBaBpQr	3.516 (± 0.116)	-0.678 (± 0.087)	0.948 (± 0.039)	0.032 (± 0.015)
ArPsQrTo	3.569 (± 0.163)	-0.997 (± 0.332)	0.948 (± 0.029)	0.036 (± 0.020)
AsBaPgTo	3.546 (± 0.115)	-1.222 (± 0.466)	0.931 (± 0.085)	0.048 (± 0.039)
AsBpPgPs	3.633 (± 0.069)	-0.652 (± 0.178)	0.955 (± 0.025)	0.022 (± 0.011)
BaPruPrePs	3.481 (± 0.187)	-1.767 (± 0.443)	0.981 (± 0.011)	0.067 (± 0.035)
LlPsQrTo	3.678 (± 0.039)	-1.905 (± 0.338)	0.974 (± 0.033)	0.048 (± 0.017)
PgPruPrePs	3.639 (± 0.065)	-3.631 (± 0.752)	0.919 (± 0.050)	0.128 (± 0.064)
All	3.566 (± 0.113)	-0.755 (± 0.116)	0.930 (± 0.039)	0.039 (± 0.003)

Table S2.2 Summary of the linear mixed-effects model testing the effects of functional diversity (Fdis_PC1) and identity (CWM_PC1) of the principal component (i.e., resource-use strategy, PC1) on quadratic mean diameter over time (*N*=1628). Summary includes degrees of freedom (df), denominator degrees of freedom (ddf), F-ratios (F) and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block and Plot as random effects).

Effects	**df**	**ddf**	**F**	**p-value**
Year	10	1554	1081.883	< 0.001
Fdis_PC1	1	34	0.6284	0.433
CWM_PC1	1	34	0.8389	0.366
Fdis_PC1 : Year	10	1554	3.951	< 0.001
CWM_PC1 : Year	10	1554	7.790	< 0.001
R^2 conditional	0.93			
R^2 marginal	0.89			

Table S2.3 Summary of the generalized linear mixed-effects model with negative binomial distribution testing the effects of functional diversity (Fdis_PC1) and identity (CWM_PC1) of the principal component (i.e., resource-use strategy, PC1) on tree mortality over time (*N*=1036). Summary includes degrees of freedom (df), Chi-squared values (ChiSq) and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block and Plot as random effects).

Effects	**df**	**ChiSq**	**p-value**
Year	6	1519.138	< 0.001
FdisPC1	1	0.395	0.530
CWMPC1	1	0.011	0.918
Fdis_PC1 : Year	6	13.070	0.041
CWM_PC1 : Year	6	87.873	< 0.001
R^2 conditional	0.88		
R^2 marginal	0.69		

Chapter 3

Early tree community overyielding is explained by asymmetric species-specific responses to diversity

To be submitted for publication with the following coauthors: Messier C, Keeton WS, and Paquette A.

ABSTRACT

Recent long-term tree biodiversity experiments have shown that diversity effects on productivity tend to strengthen over time, as complementarity among constituent species increases over the course of forest development. However, these community-level metrics only account for the net outcome of multiple interactions among species and, thus, do not inform about the individual species' responses to diversity. In a tree diversity experiment spanning 11 years, we explored how species respond to diversity based on their functional traits and those of their heterospecific neighbors over time and analyzed their contribution to the community-level overyielding. We show species-specific responses to diversity, with fast-growing deciduous species rapidly performing better in mixtures relative to monocultures, than slow-growing evergreen species. Moreover, we find that species productivity in mixtures enhances over time as the proportion of slow-growing evergreen species in the heterospecific neighborhood increases. These patterns of response of species scale up and explain community overyielding, which occurs primarily in deciduous-evergreen mixtures and is explained by the overyielding of deciduous species over-compensating the poor performance of evergreen species. This study sheds light on the temporal dynamics of species responses to diversity, which together help improve our understanding of community-level overyielding over the course of stand development.

Key words: IDENT; biodiversity-ecosystem functioning; tree diversity experiment; functional traits; life-history strategy; competition; plant-plant interactions; overyielding

INTRODUCTION

There is robust evidence that tree diversity positively affects forest productivity (Liang et al., 2016; Paquette & Messier, 2011; Zhang et al., 2012), and that this relationship strengthens over time along forest development (Huang et al., 2018; Jucker et al., 2020; Taylor et al., 2020; Urgoiti et al., 2022). Recent results from long-term biodiversity experiments have shown that this temporal strengthening may result from an increase in the relative importance of complementarity over selection effects over time (*sensu* Loreau & Hector, 2001; Huang et al., 2018; Urgoiti et al., 2022). That is, overyielding (i.e., when mixtures' productivity is higher than their components' respective monocultures) is driven by an increasingly overall better performance of species in mixtures over monocultures. Yet, these community-level metrics only account for the net outcome of multiple interactions among species and, thus, do not reveal anything about individual species' responses to diversity. Unraveling the diversity effects on species-specific productivity is critical for a better understanding of the mechanisms leading to overyielding at the community level through time, with implications both theoretical and for the management of forests.

There is consensus that, aside from major abiotic disturbances (e.g. drought, wildfire), competition for light and/or growing space among neighbouring trees is the major driver of diversity effects on productivity during the early stages of forest development (Fichtner et al., 2018; Jucker et al., 2014; Morin et al., 2011). Recent studies have shown that the emergence of positive diversity effects on community productivity coincides with canopy closure and the subsequent self-thinning when trees begin to compete for light and growing space (Jucker et al. 2020; Urgoiti et al. 2022). This pattern has been attributed to the crown complementarity effect in diverse communities (Jucker et al., 2015; Jucker et al., 2020; Williams et al., 2017). This hypothesis predicts that by combining species with contrasting life history strategies and crown architectures, constituent individuals are able to utilize growing space more efficiently, packing their crowns more densely than in monocultures (i.e., crown complementarity; Williams et al. 2017). This reduces competition for light and may result in a more complete canopy filling, increased community leaf area and light interception, and, consequently, enhanced productivity (Kunz et al., 2019; Sapijanskas et al., 2014; Williams et al., 2020). However, given this spatial complementarity and the size-asymmetric nature of light competition – in which the largest trees intercept most of the incoming light – species are likely to respond differently to community diversity. Responses will depend on species' capacity to exploit the available resources and grow relative to others in competitive environments, leading to asymmetric species contributions to community overyielding (Jucker et al., 2014).

Throughout forest development, both the availability of resources and the competition for them undergo rapid changes over time as trees grow and occupy space (Chesson et al. 2001). This dynamism in the physical environment of trees provides challenges and opportunities for species within communities. Trees are able to adjust the shape and size of their crowns in response to changes in their local competitive environment directly influencing their productivity (Jucker et al., 2015; Pretzsch & Dieler, 2012; Vieilledent et al., 2010; Williams et al., 2017). A tree's competitive ability and fitness to a given environment are strongly related to its functional traits. They capture the inherent differences in species' resource-based niches, influencing their capacity to grow and survive in competitive environments (i.e., life-history strategies; Kunstler et al., 2015; Violle et al., 2007). For example, the so-called "acquisitive" species are characterized by fast rates of resource acquisition and processing, such as high specific leaf area (SLA)) but low tolerance to competitive pressures, such as shading from other species (Kunstler et al. 2016). Conversely, "conservative" species are associated with low rates of resource acquisition and processing (opposite trait expression) but high tolerance to competition.

The successional niche hypothesis suggests that species trade-off the ability to grow and exploit resources quickly when these are abundant early in the succession (i.e., stand establishment), with the ability to avoid mortality later in succession when resources are limiting (e.g. self-thinning) (Pacala & Rees, 1998; Reich, 2014). Under this hypothesis, when acquisitive and conservative species are mixed, the abundant availability of essential resources such as nutrients and light immediately following forest establishment, may favor acquisitive species. In such mixed stands, acquisitive species will have space to progressively expand their crown and occupy a dominant canopy position allowing them to have privileged access to the incoming light, and increase their productivity compared to when grown in pure stands. Because of their rapid growth and pre-emption of resources, acquisitive species dramatically reduce light availability, and temporarily suppress conservative species (Chesson et al., 2001). In this context, it is expected that acquisitive species will benefit from competitive reduction and an associated increase in light availability and contribute to a higher extent to community overyielding compared to conservative species (Jucker et al., 2014; Lasky et al., 2014).

In this study, we aim to analyze the temporal dynamics of species-specific performances in mixtures related to their functional traits and those of their heterospecific neighbors, and understand how they scale-up to community-level performance. We conducted this study within the IDENT biodiversity experiment near Montreal, Canada, which was established in spring 2009 (Tobner et al. 2014). This experiment has investigated the early stages of stand development including the stand establishment, canopy closure and the onset of self-thinning (47% of trees died over the first 11 years of the experiment; Urgoiti et al. *submitted*). We hypothesize that species respond differently to diversity, and thus contribute asymmetrically to community-level overyielding. If supported, we further hypothesize that both target species' and heterospecific neighbours' functional traits explain species-specific performances in mixtures over time. Given that this experiment covers the early stages of stand development, we expect acquisitive species to perform better than conservative species in mixtures relative to monocultures, leading to asymmetric contribution to community overyielding.

MATERIALS AND METHODS

Site description

We conducted this study in the IDENT-MTL biodiversity experiment which was established in Ste-Anne-de-Bellevue (near Montreal, Quebec, Canada, 45°25'30.1"N, Long 73°56'19.9"W, 39 m.a.s.l.) in the spring of 2009. Mean annual temperature is 6.2°C and mean total annual precipitation is 963 mm (climate.weatheroffice.gc.ca). The study area of 0.6 ha was planted with 1- or 2-years old tree seedling (depending on species) and established on a former high-input agricultural field. The soil is a 20-70 cm deep sandy layer overtopping clay (Tobner et al. 2016). The experiment includes 12 North American temperate forest species – five broad-leaf species and seven conifers, and is part of the "International Diversity Experiment Network with Trees" (IDENT) that includes several sites in North America, Europe and Africa, itself included in the larger TreeDivNet (Verheyen et al. 2015).

Experimental design

Trees were planted in square plots of 8 by 8 trees, 50 cm apart to stimulate early interactions among trees. We considered only the inner 6 by 6 trees of each plot in the analysis, to reduce the edge effect from neighbouring plots. Also, there is a 1.25 m spacing between plots to allow movement and minimise interplot interactions

(Tobner et al. 2014). The experiment includes 37 unique plot types (i.e., different tree communities): monocultures of all 12 species, 14 two-species mixtures, 10 four-species mixtures and one mixture including all 12 species (Tobner et al. 2014). Each tree community was replicated four times in a randomized block design for a total of 148 plots (note that the site includes more plots addressing other questions that were not used in this experiment) (Tobner et al. 2014). The proportion of species within plots was equal and their distribution randomized with restrictions to avoid monospecific patches (see Tobner et al. 2014 for details). The distribution of trees within the plots remained constant in all the blocks; however, the distribution of plots within blocks was randomised.

All plots were regularly weeded manually during the first years to eliminate herbaceous competition and a fence to protect against herbivory by large vertebrates was installed around the experiment. Around the outermost rows of the experiment, three rows of trees at 50 cm distance were planted to minimise edge effects.

Tree basal area as a proxy of cumulative productivity

We reported tree basal area (G; m^2/ha) as a proxy for cumulative aboveground productivity for each species within each mixture and monoculture from 2009 to 2019, hereafter year 1 to 11. We measured the basal diameter (at 15 cm aboveground) of every live tree at the end of each growing season from which species' basal area (m^2) was computed for each year and plot. We then related each species' basal area to the plot surface and transformed it into basal area per hectare (m^2/ha). Species basal area (m^2) was also used to calculate the mean basal area of the heterospecific neighbors as a proxy of competition intensity.

Diversity effects

There are several metrics to quantify the effects of diversity on productivity. In this study, we quantify them by calculating species' relative yield based on the comparison between a species' yield in mixture and its yield in monoculture (RY; de Wit, 1960). Relative yields calculated from experiments with a substitutive design like IDENT-MTL are considered robust indicators of overyielding. Relative yield of a species i (RYi) is the result of the ratio between the observed yield in mixture (Observed yield, Y_O) and the expected yield from monoculture (expected yield, Y_E):

$$RYi = \frac{Y_O}{Y_E} \tag{1}$$

To compare individual species performance across communities with different species richness (i.e., different proportions) we multiplied the observed relative yield (*RYi*) by plot species richness (SR). Thus, (*RYi* x *SR*) = 1 indicates that the species has the same performance in mixture and monoculture (i.e., the species performs as expected from monoculture). A (*RYi* x *SR*) > 1 indicates a better performance in mixture than in monoculture and (*RYi* x *SR*) < 1 a worse performance.

Relative yield can be also calculated for the whole community (Relative yield total, RYT; Vandermeer & Goldberg, 2004). We calculated the RYT for each mixture and year. The RYT is defined as the sum of relative yields of all constituent species of a mixture:

$$RYT = \sum_{i=1}^{n} RYi \tag{2}$$

where *n* is the total number of species. A RYT = 1 means that the mixture has, overall, the same yield as expected from its constituent monocultures. RYT > 1 indicates an overall better performance of the mixture than expected from its constituent monocultures, and a RYT < 1 a worse performance.

DATA ANALYSIS

Quantification of the functional identity of target species and their neighbors

To examine the role of the functional traits of target species as well as those of their heterospecific neighbors in tree species performance in mixtures, we selected seven traits (specific leaf area, SLA; leaf nitrogen content by mass, LNmass; leaf nitrogen content by area, LNarea; net maximum photosynthesis by unit leaf mass, Amass; wood density, WD; specific root length, SRL; and seed mass) which are linked to resource-use strategies and competition capacities. They define species life-history strategy largely by influencing growth vs survival trade-offs in competitive environments (Reich 2014). The functional trait values used in this study were collected from the literature (Belluau 2020).

We first conducted a principal component analysis (PCA) on standardised species traits values (see Chapter 1 for details; Figure 1.1). The first two axes explained 80% (PC1: 61%, P2: 19%) of the overall trait variation among species. The first principal component (PC1) was correlated to wood density (Pearson correlation; WD: r = 0.94), leaf nitrogen content by unit mass (LNmass: r = 0.95), specific leaf area (SLA: r =0.92), and specific root length (SRL: r = 0.81), which allowed us to rank tree species along a conservative (i.e., low PC1 values) to acquisitive (i.e., high PC1 values) resource-use gradient. This axis clearly separated evergreen (i.e., more conservative) from deciduous species (i.e., more acquisitive). This matches with previous studies on the same experiment that showed that evergreen species –

including the considered fast-growing pines (*P. resinosa* and *P. strobus*) – had systematically lower growth rates than deciduous species – including the considered slow-growing *A. saccharum* – at least initially (Archambault et al., 2019; Tobner et al., 2016; Williams et al., 2017). The second principal component (PC2) was related only to seed mass (r = 0.88) which proved to be uninformative. We, therefore, used only the species scores over the first principal component (i.e., conservative–acquisitive axis) to calculate the functional identity of the target species (simply its score on the axis), and of their heterospecific neighbors. The functional identity of the heterospecific neighbors is defined as the mean score of all species present in the mixture (except the target species) weighted by their relative abundances (i.e., Community Weighted Mean; CWM; Lavorel et al. 2008).

Statistical Analysis

We first used a linear mixed effect model with REML estimation to test for the effects of species identity, species richness ($\log_2 SR$; 1, 2, 4, and 12), and year, and their interaction on species accumulated basal area (*G*) over time. Block and plot (i.e., the different tree communities) were set as random factors (*R*). Basal area (*G*) was log-transformed to conform to the assumption of normality. Because the variance in these models was heterogeneous across years, we weighted the model variance by year (using VarIdent = Year, in nlme, Pinheiro et al., 2016).

$$\begin{gathered} log\_G = \log_2 SR \times Year \times SpeciesID + \\ Plot\ (R) + Block\ (R) + \varepsilon \end{gathered} \tag{3}$$

We performed a similar linear mixed model to test for the effects of species' functional identity ($PC1_{target}$), the functional identity of the heterospecific neighbours ($PC1_{neigh}$), year, and their interactions on the species' specific productivity in mixtures relative to monocultures (i.e., relative yield). We controlled for the effect of neighborhood competition intensity by including the mean basal area of the heterospecific neighbors for each year (log-transformed). Relative yield (*RY*) was log-transformed to meet model assumptions for normally. As in the previous model we weighted the model variance by year. For this model we set block, plot, and speciesID as random factors yielding the following equation:

$$\begin{gathered} log\_RY = Year \times PC1_{target} \times PC1_{neigh} + log\_NeighBA + \\ Block\ (R) + Plot\ (R) + SpeciesID\ (R) + \varepsilon \end{gathered} \tag{4}$$

where ‘PC1’ is the first principal component that represents species’ resource-use strategy spectrum (i.e., conservative-acquisitive gradient). The subscripts *‘target’* and *‘neigh’* refer to the scores of both target species and their heterospecific neighbors on the first principal component, respectively. To find the most parsimonious model we compared several models with different structures of the fixed effect terms using likelihood ratio tests and comparing AIC values between models. The best model was chosen based on the lowest AIC, with a minimum difference of two ΔAIC compared to other competing models. Models with similar likelihood ($\Delta AICc < 2$) were further evaluated to provide a final model with significant predictors only. We subsequently performed a cluster analysis for the heterospecific neighbors’ functional identity effect (i.e., $PC1_{neigh}$). This analysis classified the different heterospecific neighborhoods relative to a target species into similarity groups (i.e., clusters) according to a defined distance based on their CWM values. It grouped the different heterospecific neighborhoods into “deciduous” (i.e., dominated by fast-growing deciduous species), “mixed” (i.e., mixed of deciduous and evergreen species) and “evergreen” (i.e., dominated by slow-growing evergreen species).

We further analyzed whether tree communities' relative yield totals (i.e., RYT) changed over time with repeated measures ANOVA. We included year as treatment and relative yield totals as response variable. In case of significant effect of year, we performed multiple pairwise paired t-tests to test the differences in RYT between years. We also applied two-tailed t-tests to determine when tree communities' RYT and constituent species' RY values were different from 1 (same performance in mixture and in monoculture) for each year.

RESULTS

Our results show significant differences among species in productivity (Figure 3.1). These differences depended on species richness and year (Table 3.1). When analysed separately, the effects of species richness on productivity of 10 out of 12 species (10 out of 12) differed over time (Figure 3.1). These were increasingly negative for most of the evergreen species (except *P. glauca*) and negligible or increasingly positive for deciduous species. Only two species (*B. papyrifera* and *Q. rubra*) showed a consistent, increasingly positive effect of species richness over the first 11 years of the experiment.

Regarding species performance in mixtures relative to monocultures (RY) we found that heterospecific neighbors' size explained the greatest proportion of variance (Table 3.2) with lower relative yields as heterospecific neighbors increase in size (Figure S3.1). However, we also found strong differences among species in their relative yields depending on their functional identity (PCI_{target}; Figure 3.2). We observed that species with acquisitive resource economic traits (i.e., high values of $\mathrm{PC1}_{\mathrm{target}}$; deciduous species) performed, on average, better in mixtures relative to monocultures, than species with conservative traits (i.e., low values of $\mathrm{PC1}_{\mathrm{target}}$; evergreen species), and this difference increased over time (Figure S3.2). Whereas acquisitive deciduous species, in general, showed a rapid and progressive overyielding in mixtures over time, conservative evergreen species progressively decreased their productivity in mixtures compared to monocultures.

Importantly, the effect of the target species' functional identity depended on the functional identity of the heterospecific neighbors over time (Table 3.2). For instance, we observed that the performance of both slow-growing evergreen species and fast-growing deciduous species (i.e., low and high values of $PC1_{target}$ respectively) in mixtures decreased as the proportion of deciduous species in the heterospecific neighborhood (i.e., high values of $PC1_{neigh}$) increased (Figure 3.2). This pattern was noticeable between year 3 and 8 of the experiment while from year 9 onwards only deciduous fast-growing species benefited from growing with a heterospecific neighborhood dominated by evergreen, slow-growing species.

Mixtures relative yields

The RYT of the mixtures were greater or equal to one in all years of the experiment. The RYT of only six mixtures out of 25 changed significantly over time (Table 3.3; Figure 3.3). From these six mixtures only four showed a consistent increase of RYT over time, performing significantly better than their respective monocultures during the last few years (All, AbBpLlPg, ArBaBpQr, AsBaPgTo). The other two mixtures (AbAsPgPru, ArPsQrTo) showed significant increases and decreases from year to year, but no significant differences in their performance relative to monocultures. In addition, the RYT of two mixtures did not change significantly over time, but they did perform significantly better than the monocultures during the last few years (BpPs, AsBpPgPs). All the six mixtures that overyielded during the last years of the experiment were driven largely by the performance of one or more fast-growing deciduous species at the expense of slow-growing evergreen species (i.e., RY). Moreover, despite that the rest of the deciduous-evergreen mixtures showed similar yields to their monocultures, in most of them, these were explained by the increase in yield of one or more acquisitive species compensating for the co-occurring decreases in yield of conservative species (Figure S3.3). In particular, *B. papyrifera* showed a consistent increase in RY over time in all the mixtures, being the species that most benefited from growing in mixtures (Figure S3.4).

DISCUSSION

This study shows that both the functional identity of species and that of their heterospecific neighbors are key drivers of species-specific productivity in tree mixtures over time. These differences in the response to diversity among species are key to understanding the mechanisms leading to overyielding at the community level. A recent study in the same experiment found that mixtures were, overall, more productive than their respective monocultures, and that this relationship strengthened over time as stands developed (Urgoiti et al., 2022). The present study shifts the focus from communities to species, bringing new insight into effects that aggregate to community level processes; showing that these are primarily explained by the rapid increase in productivity of fast-growing deciduous species in mixtures compensating or even over-compensating for the co-occurring decreases of the yield of slow-growing evergreen species.

Effects of species' functional identity

As we hypothesized, species with acquisitive traits performed, on average, better in mixtures relative to monocultures, than species with conservative traits, and this difference increased over time. As evidenced in our PCA, this conservative-acquisitive resource-use spectrum clearly separates deciduous species, with acquisitive traits, from evergreen species, having conservative traits. Although this classification does not fit classic literature (e.g. shade tolerance rankings) for some species – e.g. fast-growing evergreen *P. resinosa* and *P. strobus* and slow-growing deciduous *A. saccharum* - previous studies on the same site observed that deciduous species had systematically faster growth rates than evergreen species during the early years (Tobner et al., 2016; Williams et al., 2017). This may be due to the fact that in the early years of the experiment, evergreen species allocated a larger proportion of their total biomass to roots than deciduous species, as documented by another early study on the same experiment (Archambault et al., 2019), making them less competitive at capturing what quickly became the restricting resource, light. Note that *P. strobus* and *A. saccharum* were also planted in three other IDENT experiments in North America (Auclair, Cloquet, and Sault-Ste-Marie) where they performed as expected – fast for the former, and slow for the latter (relative to other species on those sites) (Belluau et al., 2021a; Belluau et al., 2021b). Interestingly, those sites are on poor to very poor soils (of forest or low-input agriculture origin), especially in comparison with the high-input, very fertile conditions found at IDENT-MTL. The effects of functional identity on species-specific responses to diversity appeared quickly, and by the second year onwards, deciduous species were already performing, overall, significantly better in mixtures than evergreen species. Whereas deciduous species showed a rapid and progressive increase in their productivity in mixtures compared to monocultures over time, the evergreen species progressively decreased in productivity in mixtures over the same period.

The overall (in both mixtures and monocultures) better initial growth of deciduous species is consistent with the successional niche hypothesis, which posits that early in succession competitive ability is characterised by high productivity while later in the succession it is characterised by the ability to persist under low resource availability (Goldberg, 1990; Lasky et al., 2014; Pacala & Rees, 1998; Reich, 2014). In this context, the intense agricultural activity on the site prior to the establishment of the experiment, the complete removal of herbaceous competition during the first three years, and the open canopy context resulted in resource-abundant conditions, favoring fast-growing deciduous species. When mixed with slow-growing evergreens, this faster growth allowed them to quickly dominate the canopy space (Tobner et al., 2016; Williams et al., 2017). Greater access to light (compared to monocultures), in turn, reduced competitive pressures from neighbors, and allowed these fast-growing species to overyield during the early stages of stand development, as also observed by Jucker et al. (2014). In our study, all deciduous species showed similar or greater performance in mixtures than in monocultures (Figure S3.4). In particular, *B. papyrifera*, a light-demanding acquisitive species, showed robust overyielding in all mixtures. In contrast, the slow-growing evergreen species of our study (except *P. resinosa*) showed a consistent decrease in their performance over time in mixtures relative to monocultures. This overall negative performance in mixtures of slow-growing evergreen species suggests that interspecific competition for light reduced their growth, particularly in mixtures with fast-growing deciduous species, as also observed by Belluau et al. (2021b) (see next section). A previous study conducted in the same experiment showed that spatial complementarity of tree crowns in mixtures was strongly and positively related to mixtures' overyielding (Williams et al. 2017). Our results take a step further and show that at the species level this spatial complementarity-productivity relationship is explained primarily by the performance of fast-growing deciduous species at the expense of slow-growing evergreens during the early stages of stand development.

Effects of heterospecific neighbors’ functional identity

Our results also show that how target species responded to diversity depended on their own functional identity, as well as that of their heterospecific neighbors, during the first decade of stand development. Immediately after stand establishment (c. from year 3 to 8) both deciduous species and evergreen species performed better in mixtures when growing with slow-growing evergreen neighbors than with fast-growing deciduous neighbors. From year 9 on, however, only fast-growing deciduous species benefited from growing with a heterospecific neighborhood dominated by evergreen species.

This raises the question of why evergreen species did not benefit from growing with neighbors with a contrasting life-history strategy (i.e., deciduous acquisitive species). Tree diversity studies have shown that mixing species with contrasting life-history strategies and crown architectures lessens the overall competition for light, thereby enabling communities to improve light interception and growth (Jucker et al., 2015; Sapijanskas et al., 2014; Williams et al., 2017). However, those are average responses, measured at the community level. We argue that species response to neighbors' identity in our study is related to the directional nature of light that leads to size-asymmetric competition among trees (Craine & Dybzinski, 2013; DeMalach et al., 2016; Pretzsch & Biber, 2010). Tree growth and crown display play a central role for light-related tree interactions, which in turn affect carbon assimilation (Pretzsch, 2014a). Having a crown above those of competitors allows species to 1) maximize their growth and 2) slow the growth of competitors (Falster & Westoby, 2003; Jucker et al., 2014). In this context, the rapid growth and crown development allow fast-growing deciduous to quickly dominate canopy space when mixed with slower growing evergreen species, at least initially. These species then benefit from the reduced competition by increasing light interception and growth, while temporally suppressing the growth of evergreen species compared to monocultures (Chesson et al., 2001). Shading by neighbors, however, can affect tree growth either negatively by reducing light availability (i.e., competition; Freckleton & Watkinson, 2001) or positively by ameliorating microclimate conditions (i.e., facilitation; Mcintire & Fajardo, 2014; Montgomery et al., 2010), and these effects can be species-specific

(Valladares et al., 2008). However, given the high tree density and the extremely low light availability in the understory of our experiment, we can assume that growth inhibition due to lack of light was the most likely outcome. Indeed, our results point to a strong negative relationship between species relative yields and neighbors' mean tree size, suggesting that species' productivity in mixtures decreases as the size of heterospecific neighbors increases (i.e., shading).

How do species-specific responses to diversity scale to community-level

Collectively, results at the species level scale up and explain mixtures' productivity compared to their respective monocultures through time during the first decade of stand development. We observed that 1) mixture overyielding mainly occurs when deciduous species are mixed with evergreen species; and that 2) overyielding is explained by asymmetric species-specific performance relative to their monocultures (Caspersen et al., 2018; Jucker et al., 2015; Niinemets, 2010). Our results show that mixture overyielding is led by the rapid increase in the productivity of deciduous species, over-compensating the co-occurring decreases of evergreen species. These results suggest that the presence of evergreen species allowed mixtures' to overyield by reducing intra- and interspecific competition for deciduous species, allowing them to intercept more light and grow faster (Caspersen et al., 2018; Forrester & Bauhus, 2016; Jucker et al., 2014; Jucker et al., 2015). More specifically, we observe that all the mixtures that overyielded contained *B. papyrifera*. This light-demanding species benefited the most from reduced competition in mixtures, ultimately dominating and leading them to overyield. The emergence of mixtures overyielding was shown previously to result from increases in the relative importance of complementarity over selection effects during stand development (*sensu* Loreau & Hector 2001; Urgoiti et al. 2022). That is, overyielding was driven by an increasingly, overall, better performance of constituent species in mixtures than in monocultures. These seemingly contradictory results suggest that in young stands, fast-growing deciduous species took advantage of reduced competition in mixtures, thus leading to overyielding at the community-level despite the poor contribution of evergreen species (Grossman et al., 2018; Zheng et al., 2021).

While our results supported our hypotheses, a limitation is the relatively short time frame covering early stand establishment and development, including canopy closure and initiation of self-thinning (47% of trees died over the 11 years of the experiment; Urgoiti et al., *submitted*). As stands mature, the availability of nutrients and light decrease substantially likely shifting the asymmetric species-specific overyielding towards conservative species as they are better competitors in resource-limited environments (Pacala & Rees, 1998; Reich, 2014; Van Ruijven & Berendse, 2005). Indeed, our results show that the performance of deciduous species in mixtures compared to evergreens seems to have reached or is close to its maximum (Figure S3.2), suggesting a possible shift the asymmetric species-specific overyielding towards more conservative evergreen species in the coming years. Future research should focus, therefore, on tracking how the performance of acquisitive and conservative species in mixtures are likely to change in the later stages of stand development.

CONCLUSION

Using 11 years of growth records from a tree diversity experiment, we show species-specific responses to diversity over time. We highlight that species' responses to diversity are trait-dependent, with deciduous, fast-growing species rapidly performing better in mixtures relative to monocultures, when compared to evergreen, slow-growing species. Furthermore, these responses are strongly influenced by heterospecific neighbors' composition. We show that both deciduous and evergreen species increase their productivity in mixtures as the proportion of the latter in the heterospecific neighborhood increases. Ultimately, these patterns of species response scale up and help explain communities' overyielding over time. These primarily occur in deciduous-evergreen mixtures by the rapid increase in productivity of deciduous species over-compensating the poor contribution of evergreen species. Overall, this study sheds light on the temporal dynamics of species responses to diversity, which together help improve our understanding of community-level overyielding over the course of stand development.

This study is relevant for both conservation and forest management, as it shows through species performances in mixtures how and why more diverse tree communities end up overyielding and how these diversity effects change over time. Combined with previous studies from this and similar experiments, a more detailed, albeit still incomplete portrait of the mechanisms leading to biodiversity effects and overyielding in forests is starting to emerge. We argue that more research is needed looking into later stages of forest development, but also in still poorly documented areas such as belowground dynamics and trophic relationships involving insects and microorganisms, for example.

FIGURES

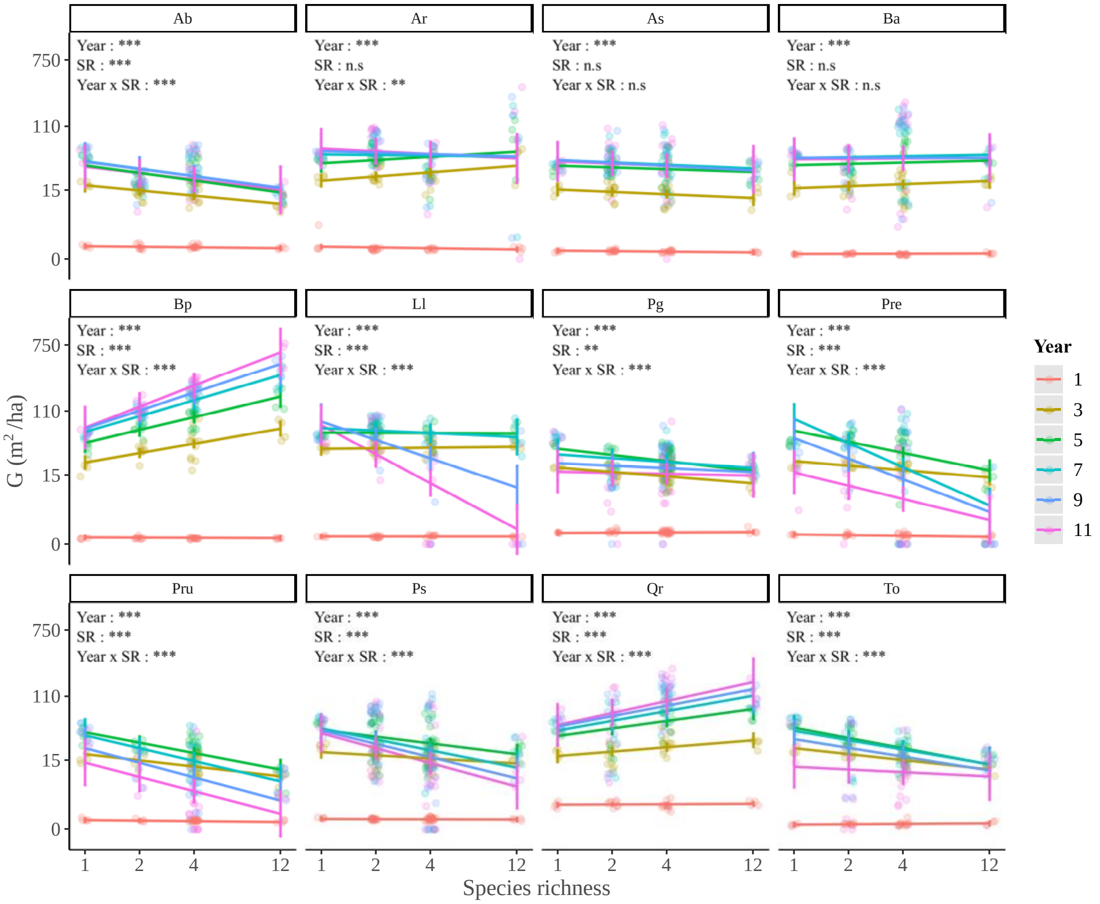


Figure 3.1 Species specific basal area (G ± 95% confidence interval; log scale) as a function of tree species richness from 2009 to 2019 (years 1 to 11; showing only odd years). Coloured dots represent raw data for each year. SR = species richness, year, *** p < 0.001, ** p < 0.01, * p < 0.05, n.s = not significant. Species codes are: Ab, *Abies balsamea*; Ar, *Acer rubrum*; As, *Acer saccharum*; Ba, *Betula alleghaniensis*; Bp, *Betula papyrifera*; Ll, *Larix laricina*; Pg, *Picea glauca*; Pru, *Picea rubens*; Pre, *Pinus resinosa*; Ps, *Pinus strobus*; Qr, *Quercus rubra*; To, *Thuja occidentalis.*

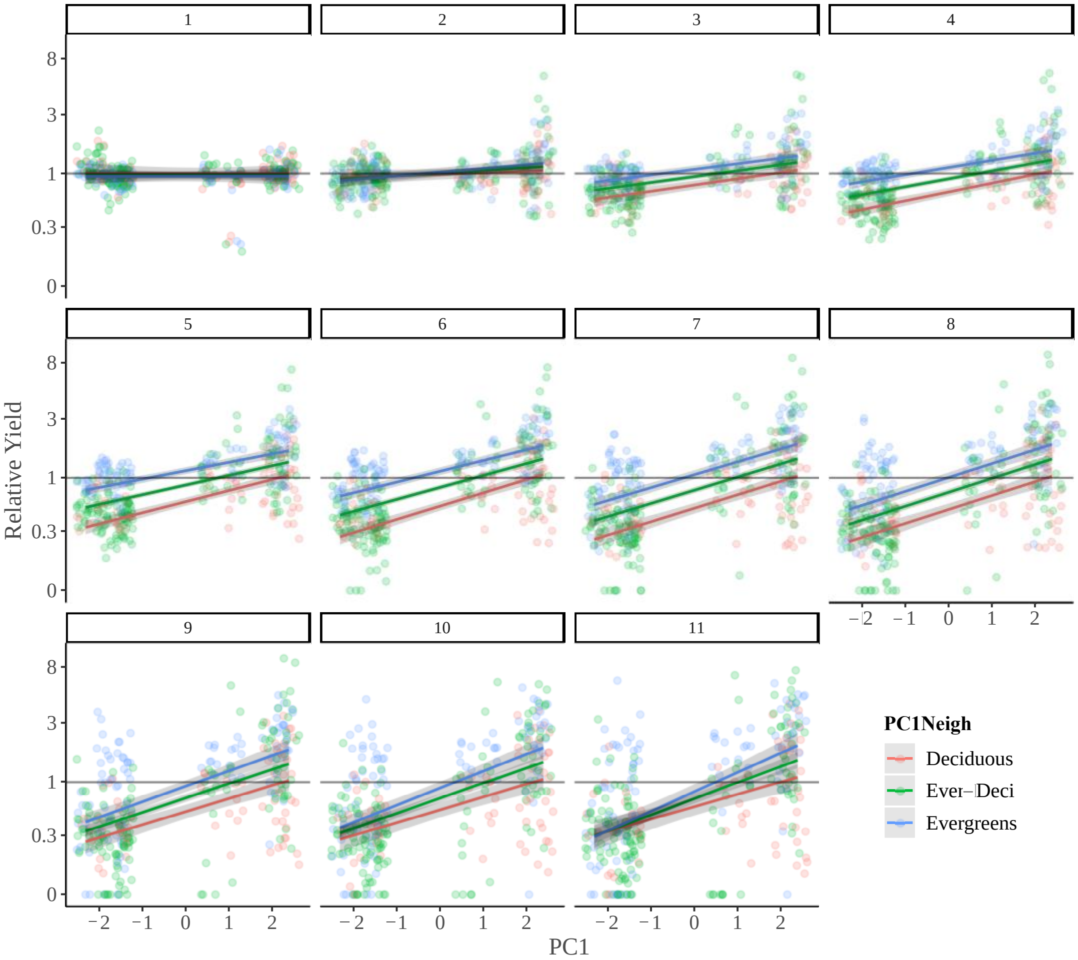
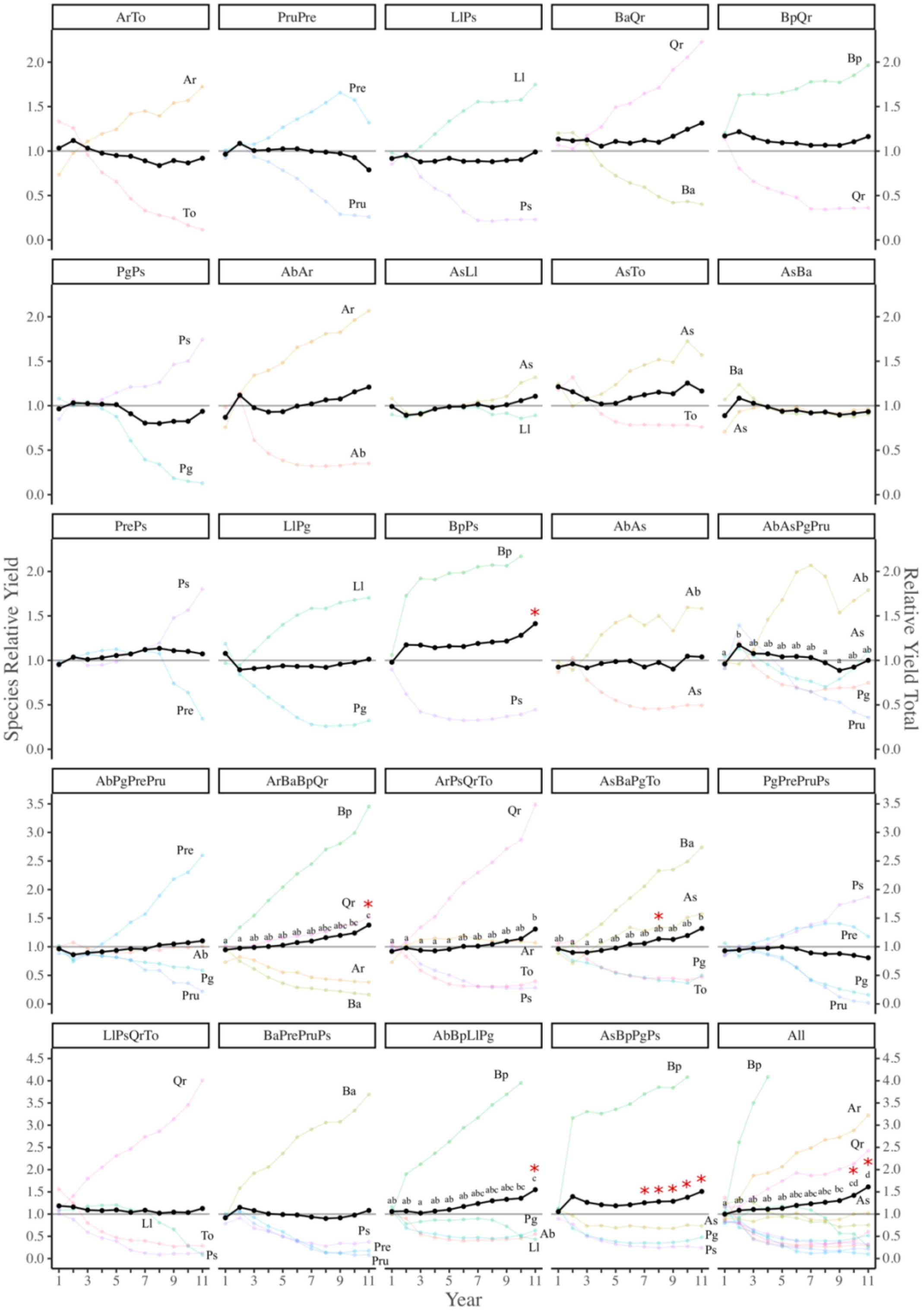


Figure 3.2 Fitted (eqn 4) species relative yields (RY) on *G* (m^2/ha) over time against the gradient of the first principal component (i.e., $PC1_{target}$) when growing with heterospecific neighborhood composed by "deciduous", a mix of "evergreens-deciduous" or "evergreens" (i.e., red, green, and blue lines respectively ± 95%, $PC1_{neigh}$). Coloured dots represent raw data for each group of the heterospecific neighbors.



ArTo
PruPre
LlPs
BaQr
BpQr
Ar
To
Pre
Pru
Ll
Ps
Qr
Ba
Bp
Qr
PgPs
AbAr
AsLl
AsTo
AsBa
Ps
Pg
Ar
Ab
As
Ll
As
To
Ba
As
PrePs
LlPg
BpPs
AbAs
AbAsPgPru
Ps
Pre
Ll
Pg
Bp
Ps
*
Ab
As
Ab
As
Pg
Pru
AbPgPrePru
ArBaBpQr
ArPsQrTo
AsBaPgTo
PgPrePruPs
Pre
Ab
Pg
Pru
Bp
Qr
*
Ar
Ba
Qr
Ar
To
Ps
Ba
As
*
Pg
To
Ps
Pre
Pg
Pru
LlPsQrTo
BaPrePruPs
AbBpLlPg
AsBpPgPs
All
Qr
Ll
To
Ps
Ba
Ps
Pre
Pru
Bp
*
Pg
Ab
Ll
Bp
* * * * *
As
Pg
Ps
Bp
Ar
Qr
* *
As
a
ab
b
abc
bc
c
cd
d
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
1
3
5
7
9
11
Year
Species Relative Yield
Relative Yield Total

Figure 3.3 Mixtures' relative yield totals (RYT; black line and dots) and constituent species relative yield (RY; coloured lines and dots) over time (note that the scales differ among rows to better show differences between treatments). Red asterisks indicate a significant difference in RYT from 1. Different letters indicate significant differences between years in RYT. RYT and RY >1 indicate positive mixture effects, RYT and RY< 1 indicate negative mixture effects. Note that species RY were scaled back to 1 for ease of comparison (some are cut for better resolution). Ab – *Abies balsamea*, Ar – *Acer rubrum*, As – *Acer saccharum*, Ba – *Betula alleghaniensis*, Bp – *Betula papyrifera*, Ll – *Larix laricina*, Pg – *Picea glauca*, Pru – *Picea rubens*, Pre – *Pinus resinosa*, Ps – *Pinus strobus*, Qr – *Quercus rubra* and To – *Thuja occidentalis*.

Table 3.1 Summary of the linear mixed model (REML estimation) testing the effects of species identity (i.e., species ID), year, and species richness ($\log_2$ transformed) on species-level productivity (*G*; *N* = 4048). Summary includes numerator degrees of freedom (df), denominator degrees of freedom (ddf), F ratios (F), and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block and Plot as random effects).

Effects	**df**	**ddf**	**F**	**p-value**
Species ID	11	3638	325.991	< 0.001
Year	10	3638	6047.588	< 0.001
$\log_2$(SR)	1	143	2.536	0.113
Species ID : Year	110	3638	21.912	< 0.001
Species ID : $\log_2$(SR)	11	3638	15.710	< 0.001
Year : $\log_2$(SR)	10	3638	8.140	< 0.001
Species ID : Year : $\log_2$(SR)	110	3638	4.891	< 0.001
R^2 conditional	0.94			
R^2 marginal	0.90			

Table 3.2 Summary of the linear mixed model (REML estimation) testing the effects of target species' functional identity (i.e., $PC1_{target}$), heterospecific neighbors' functional identity (i.e., $PC1_{neigh}$), year, and heterospecific neighbors' basal area (i.e., log_NeighBA) on species relative yields (RY; *N* = 3520). Summary includes numerator degrees of freedom (df), denominator degrees of freedom (ddf), F ratios (F), and p-values, as well as the conditional and marginal coefficient of determination (R^2) of the model (including Block, Plot, species ID as random effects).

Effects	**df**	**ddf**	**F**	**p-value**
$PC1_{target}$	1	217	249.642	< 0.001
$PC1_{neigh}$	1	217	109.968	< 0.001
Year	10	3159	38.612	< 0.001
log_NeighBA	1	3159	572.497	< 0.001
$PC1_{target}$: $PC1_{neigh}$	1	217	1.384	0.241
$PC1_{target}$: Year	10	3159	68.948	< 0.001
$PC1_{neigh}$: Year	10	3159	33.502	< 0.001
$PC1_{target}$: $PC1_{neigh}$: Year	10	3159	3.862	< 0.001
R^2 conditional	0.69			
R^2 marginal	0.46			

Table 3.3 Summary of the repeated measures ANOVA testing whether mixtures' RYT changed over time (Year). Summary includes F ratios (F) including the numerator degrees of freedom and denominator degrees of freedom, and p-values. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s = not significant.

Tree community	**Year**	**Tree community**	**Year**
ArTo	$F_{10,30} = 0.536^{n.s}$	AbAs	$F_{10,30} = 0.807^{n.s}$
PruPre	$F_{10,30} = 0.400^{n.s}$	AbAsPgPru	$F_{10,30} = 0.933^{n.s}$
LlPs	$F_{10,30} = 0.359^{n.s}$	AbPgPruPre	$F_{10,30} = 0.356^{n.s}$
BaQr	$F_{10,30} = 0.791^{n.s}$	ArBaBpQr	$F_{10,30} = 6.751^{***}$
BpQr	$F_{10,30} = 0.408^{n.s}$	ArPsQrTo	$F_{10,30} = 3.274^{**}$
PgPs	$F_{10,30} = 0.804^{n.s}$	AsBaPgTo	$F_{10,30} = 3.166^{**}$
AbAr	$F_{10,30} = 2.051^{n.s}$	PgPrePruPs	$F_{10,30} = 0.788^{n.s}$
AsLl	$F_{10,30} = 1.262^{n.s}$	LlPsQrTo	$F_{10,30} = 0.440^{n.s}$
AsTo	$F_{10,30} = 0.282^{n.s}$	BaPrePruPs	$F_{10,30} = 2.928^{**}$
ArBa	$F_{10,30} = 0.969^{n.s}$	AbBpLlPg	$F_{10,30} = 6.744^{***}$
PrePs	$F_{10,30} = 0.156^{n.s}$	AsBpPgPs	$F_{10,30} = 1.407^{n.s}$
LlPg	$F_{10,30} = 0.334^{n.s}$	All	$F_{10,30} = 9.741^{***}$
BpPs	$F_{10,30} = 0.942^{n.s}$		

SUPPORTING INFORMATION

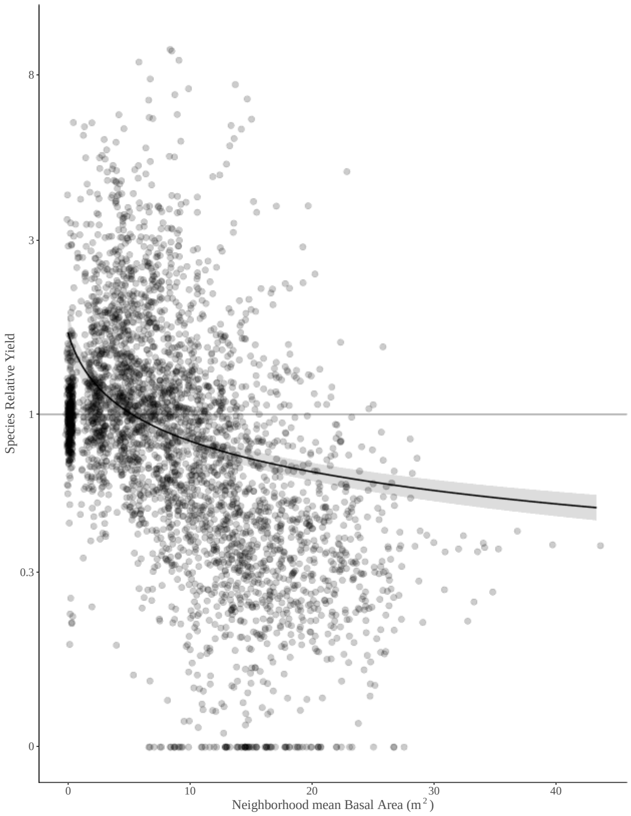


Figure S3.1 Fitted (eqn 4) species relative yields (RY; Black line ± confidence interval 95%; N=3520) on *G* (m^2/ha) against the heterospecific neighbors mean basal area (m^2).

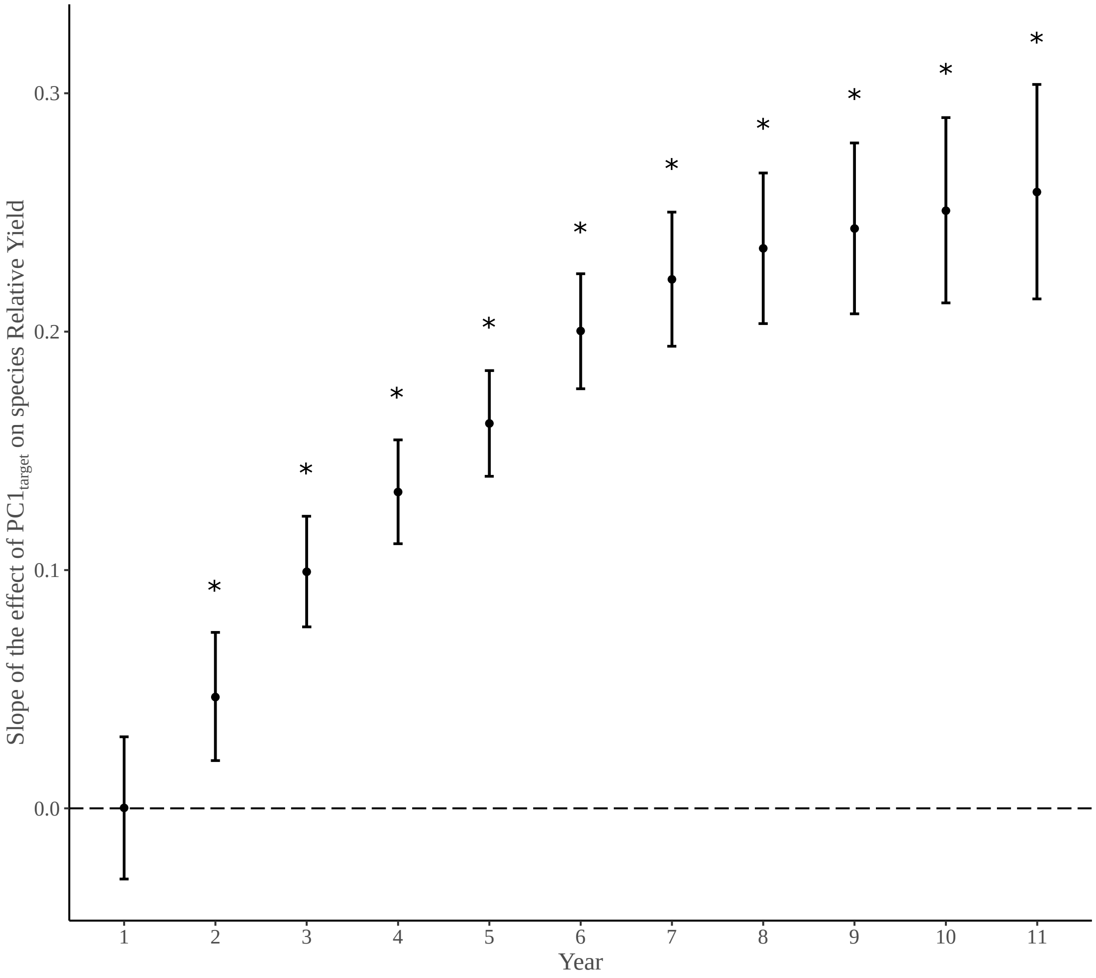


Figure S3.2 Estimates of the effect of functional identity of the target species ($PC1_{target}$) on species relative yield over the 11 years of the experiment. Significant differences among species in their performance in mixtures based on their functional identity ($PC1_{target}$) start at the 2nd year of the experiment and progressively strengthens over time. Estimates are calculated using the full model. Error bars represent the 95% confidence intervals of the effect. *$P < 0.05$.

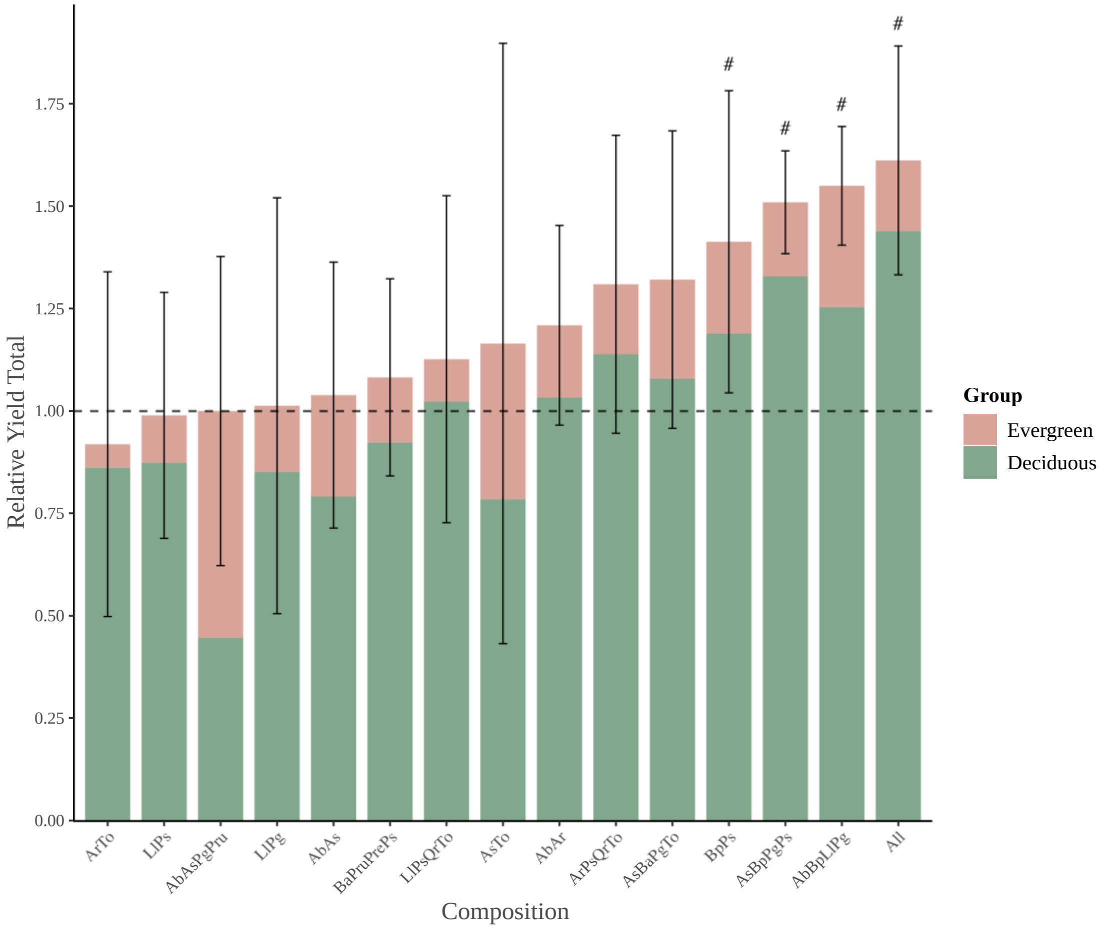


Figure S3.3 Relative yield total (± standard deviation across blocks) for each mixture of the experiment that contains deciduous and evergreen species for the final year of the experiment. The bars are showing the respective contributions of each group (i.e., the sum of relative yields of deciduous and evergreen species; green and brown respectively) to the relative yield total of the mixtures. RYT >1 indicate mixture overyielding. Mixtures with significant overyielding are annotated with # ($P < 0.05$).

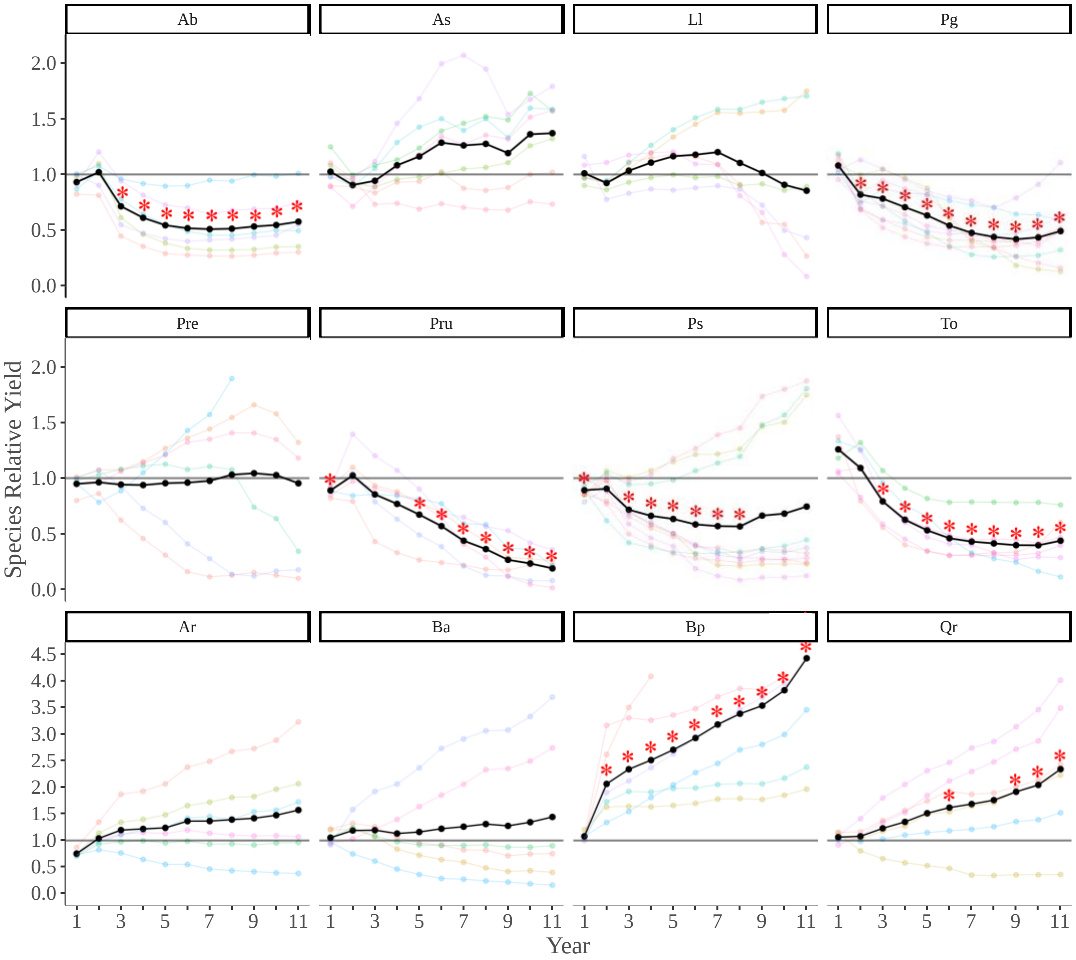


Figure S3.4 Species' mean relative yield across blocks and plots (RY; black line and dots) over the first 11 years of the experiment (note that the scales differ among rows to better show differences between species). Colored lines and dots represent species' relative yield in each mixture they grow (some are cut for better resolution). Red asterisks indicate a significant difference in RY from 1. RY >1 indicate positive mixture effects, RY< 1 indicate negative mixture effects.

CONCLUSION

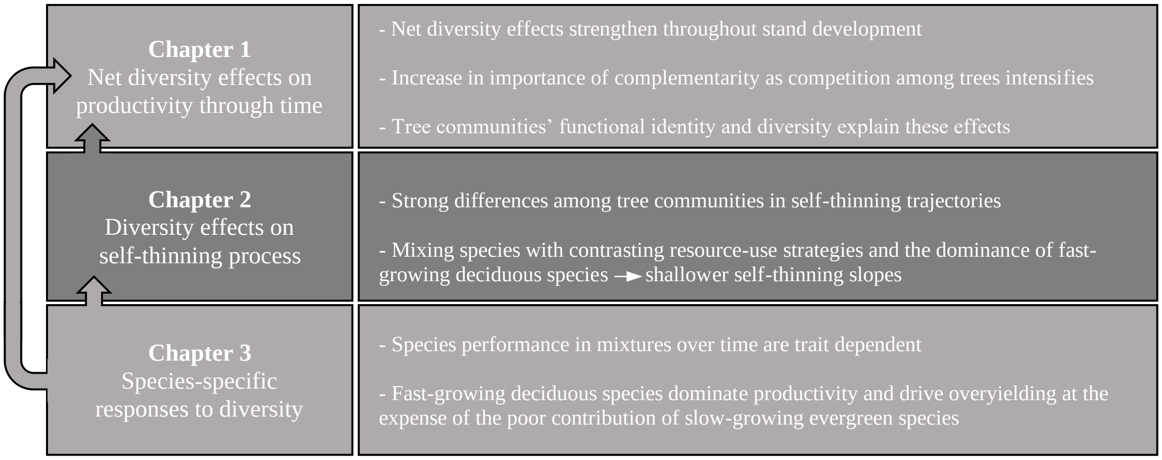
Exploring the relationship between tree diversity and ecosystem functioning has been a recent focus of forest ecology (Bauhus et al., 2010; Grossman et al., 2018). In particular, understanding the impacts of tree diversity on productivity has received special attention. After more than two decades of intensive research, there is now a general consensus that tree diversity positively affects forest productivity (Liang et al., 2016; Paquette & Messier, 2011; Zhang et al.,2012). This research has also revealed mechanisms and environmental factors that, together, can strongly influence such effects across space (Jactel et al., 2018; Jucker et al., 2016; Mori, 2018). However, how and why tree diversity effects on productivity vary over time along stand development remain elusive.

The aim of this thesis was to fill important knowledge gaps surrounding the role of stand development in the temporal dynamics of diversity effects on productivity. More specifically, I sought to better understand the mechanisms and processes that occur at both the species and community levels over the course of stand development. I have addressed this research throughout three chapters that put forward different aspects and mechanisms of how tree diversity may affect community productivity through time. Overall, this study provides a complete picture that helps explain the temporal shifts of this relationship along stand development. I briefly report the main findings of the individual chapters before bridging them together to provide an overall perspective (Figure 4.1).

Chapter 1 stands out to be the first study with trees to test how diversity effects on productivity change during the first decade of stand development and how the relative importance of complementarity over selection explains these effects over time. Here I demonstrated that diversity effects strengthen non-linearly over time, primarily driven by gradual increases in complementarity effects as stands develop. Moreover, I showed that mixing species with contrasting resource-acquisition strategies (i.e., functional diversity), and the dominance of deciduous, fast-growing species (i.e., functional identity), promote positive diversity effects on productivity through time.

In **Chapter 2** I tested how tree communities' functional identity and diversity influence the self-thinning process that ultimately may help explain mixtures' overyielding in the long term. I highlighted that mixing slow-growing evergreen species with fast-growing deciduous species and the dominance of the latter reduce the tree mortality rate in relation to mean tree size during the self-thinning phase (i.e., shallower self-thinning slopes). I also showed that the shallower slopes of these communities are due to simultaneous increases in trees' growth and reductions of tree mortality over time compared to less diverse communities dominated by slow-growing evergreen species.

In **chapter 3**, I sought to better understand the underlying species-level mechanisms leading to overyielding at the community level. More specifically, I explored the temporal dynamics of species-specific performances in mixtures related to their functional traits and those of their heterospecific neighbors, and how they scale-up and explain community-level overyielding as stands develop. Overall, this chapter highlighted that mixture overyielding primarily occurs in deciduous-evergreen mixtures by the rapid increase in productivity of fast-growing deciduous species over-compensating the poor contribution of slow-growing evergreen species.



Chapter 1
Net diversity effects on productivity through time

- Net diversity effects strengthen throughout stand development
- Increase in importance of complementarity as competition among trees intensifies
- Tree communities’ functional identity and diversity explain these effects

Chapter 2
Diversity effects on self-thinning process

- Strong differences among tree communities in self-thinning trajectories
- Mixing species with contrasting resource-use strategies and the dominance of fast-growing deciduous species → shallower self-thinning slopes

Chapter 3
Species-specific responses to diversity

- Species performance in mixtures over time are trait dependent
- Fast-growing deciduous species dominate productivity and drive overyielding at the expense of the poor contribution of slow-growing evergreen species

Figure 4.1. Overview of the main findings of each of the three chapters.

Diversity effects on productivity over the course of stand development: Causes and processes

There is consistent evidence that tree diversity generally positively affects productivity, especially in mature forests (Liang et al., 2016; Paquette & Messier, 2011; Zhang et el., 2012). However, in young stands, the necessary conditions may not exist for these effects to emerge. This is because the mechanisms causing mixtures overyielding rely on some degree of tree-tree interactions. For example, one of the most commonly proposed mechanisms to explain these positive effects of diversity is that spatial complementarity in tree crowns between species enhances the light interception of mixtures, thereby increasing their productivity (Jucker et al. 2015; Sapijanskas et al. 2014; Williams et al., 2017). Differences in the state of stand development might explain why studies carried out in the early years of tree diversity experiments found negligible or marginal positive diversity effects (Healy et al., 2008; Li et al., 2014; Tobner et al., 2016; Verheyen et al., 2015), whereas studies conducted in older experiments highlighted strong positive effects (Huang et al., 2018; Schnabel et al., 2019; Van de Peer et al., 2017). Everything seems to indicate, that canopy closure and the initiation of self-thinning is a critical moment when mixtures begin benefiting from light partitioning, and thereby increasing productivity relative to monocultures. Nonetheless, the emergence of these diversity effects is probably more complex. Indeed, these effects are the outcome of the sum of positive and negative performances of constituent species. These, in turn, depend on how these species exploit the limited resources relative to others and how they tolerate their limitations.

This thesis relies on the first 11 years of growth and mortality records from the IDENT-MTL experiment that covers the early stages of stand development; stand establishment, canopy closure, and self-thinning. Therefore, the conclusions of this research should be framed in these early stages and not extrapolated to more mature stages of stand development. Monitoring existing experiments like this one over longer temporal scales should allow us to track eventual shifts of diversity effects through more advanced stages of stand development. However, since all biodiversity experiments with trees are still relatively young, we must be patient and let them mature to conduct such research. Meanwhile, the available long-term observational data or even simulation studies could be complemented with the findings from these young experimental communities (e.g. Jucker et al., 2020; Morin et al., 2014).

The more competition, the more complementarity. The more complementarity, the more diversity effects on productivity

First, this research confirmed the evidence that trees first have to develop before tree-tree interactions are strong enough to trigger positive diversity effects. I showed how diversity effects on productivity increase non-linearly over time and how these emerge as stands underwent canopy closure and entered the self-thinning phase (*Chapter 1*). In addition, I separated these diversity effects into complementarity and selection effects over time, stressing the increasing importance of the former over time. I also showed that mixing species with contrasting resource-use strategies (“slow” evergreens and “fast” deciduous) and the dominance of fast-growing deciduous species promotes the emergence of complementarity, and ultimately the positive diversity effects on productivity over time. Overall, these results suggest that the increasing competition that follows from canopy closure and initiation of the self-thinning phase is a key factor in allowing conditions for mixtures to overyield through niche partitioning or facilitation (Jucker et al., 2020).

The emergence of complementarity through the self-thinning perspective

I demonstrated that the emergence of complementarity leading to positive diversity effects on productivity is explained by differences among tree communities in how they develop through the self-thinning phase of stand development (*Chapter 2*) (Figure 4.1). Specifically, I highlighted that once stands underwent self-thinning, mixing slow-growing evergreen species with fast-growing deciduous species and the dominance of the latter reduced the rate of tree mortality in relation to mean tree size (i.e., shallower self-thinning slopes). That is to say, for a given increment in tree mean size, these communities suffered fewer reductions in tree density (i.e., less mortality). Moreover, I showed that these shallower self-thinning slopes were achieved by increases in tree mean size and reductions in tree mortality over time simultaneously. In literature, it is hypothesized that mixing species with contrasting life history strategies and crown architectures may be important factors in determining self-thinning trajectories. This is because this type of mixture might influence crown packing into a specified volume, reduce competition for light, and thereby enhance light interception at the community level (Forrester et al., 2021; Lonsdale and Watkinson, 1983). I did not directly test how crowns and canopy structure affected the self-thinning process, but the results suggest that communities benefited from this spatial complementarity when slow-growing evergreen species grew under dominant, fast-growing deciduous species (Jucker et al., 2015; Niinemets, 2010), allowing them to increase their productivity in the long-term.

Spatial complementarity leading to asymmetric contributions to mixtures' overyielding

At the species level, spatial complementarity and the size-asymmetric nature of light competition – in which the largest trees intercept most of the incoming light – lead to species-specific responses to diversity, and therefore asymmetric contributions to mixtures' overyielding over time (*Chapter 3*) (Figure 4.1). I found that this intense asymmetric competition between species in mixtures led fast-growing deciduous species to rapidly dominate productivity and drive overyielding over-compensating the poor contribution of slow-growing evergreen species. In this study, the resource-abundant conditions and the open canopy context at the onset of the experiment clearly favored more acquisitive fast-growing deciduous species to dominate the canopy space. They then benefitted from the reduced competitive pressure by increasing light interception and growth, while temporally suppressing the growth of evergreen species. The emergence of mixtures overyielding was shown previously to result from increasing importance of complementarity during stand development. That is, overyielding was driven by an increasingly overall better performance of constituent species in mixtures than in monocultures. These seemingly contradictory results suggest that in young stands, fast-growing deciduous species took advantage of reduced competition in mixtures, thus leading to overyielding at the community-level despite the poor contribution of evergreen species

In short, this body of research contributes significantly to BEF science by disentangling the role of stand development on the temporal shifts of diversity effects on productivity. Taken together, it shows that mixtures can better cope with increasing competition as stands develop. The inherent differences among species in their life-history strategies promoted space partitioning over time where fast-growing deciduous species benefited the most from reduced competition, thus leading mixtures overyielding in the long term. This study has important implications for forest management and conservation, as it provides from an ecological perspective fundamental information to enhance productivity and carbon sequestration in the long term.

Limitations and future research perspectives

I finish this study by pointing out some limitations of it as well as some research perspectives in the context of BEF science to improve and expand further our knowledge about biodiversity impacts on the functioning of forest ecosystems.

Context-dependency of diversity effects on productivity

This study benefited from the long-term growth and mortality data of a very local biodiversity experiment with trees (IDENT-MTL). These kinds of experiments are immensely important for BEF research, as their design allows us to directly focus on the causal effects of biodiversity on ecosystem functioning while minimizing variation in other factors such as environmental conditions (Kambach et al., 2019). However, the literature has often reported that BEF relationships change significantly across space due to variations in abiotic factors and stand structure (Jactel et al., 2018; Jucker et al., 2016; Paquette & Messier, 2011; Ratcliffe et al., 2017). For example, Paquette & Messier (2011), showed that diversity effects on productivity become progressively stronger under harsher environmental conditions where beneficial complementarity effects among species become more relevant (but see Belluau et al. 2021). Given that BEF relationships result from interactions among constituent species and their environments, a clear follow-up question to this research, is: to what degree do environmental conditions and stand structure affect the temporal dynamics of diversity effects on productivity over the course of stand development?

In the present study, fast-growing deciduous species benefited the most from the initial resource-abundant conditions and open canopy context, rapidly dominating canopy space. This promoted niche partitioning (i.e., complementarity effects) through the development of multilayered canopies when they were mixed with slow-growing evergreen species (Jucker et al., 2015; Niinemets, 2010), ultimately leading to overyielding at the community level when competition for light was most intense (i.e. self-thinning) (Figure 4.1). However, in harsh environments, where nutrients and/or water are scarce, trees tend to allocate more biomass to roots to compete for acquiring these resources (Bai et al., 2010; Dai et al., 2009; Deng et al., 2006; Zhang et al., 2017). Contrary to competition for light, below-ground competition is size-symmetric where trees obtain nutrients and water proportionally to their root biomass (Lin et al. 2014, 2016). Numerous studies have shown that tree communities' development through the self-thinning phase changes across water and nutrient availability conditions (Bai et al., 2010; Dai et al., 2009; Zhang et al., 2017), which as we have seen in this research has a crucial impact on productivity in the long term.

Utilizing a network of tree experiments across a gradient of environmental conditions has the potential to generate essential insights into the context-dependency shaping BEF relationships (Paquette et al., 2018; Verheyen et al., 2015). For example, as more forest BEF experiments reach a similar state of development, we will be able to merge their data and capture the environmental and experimental contrasts between sites and test their impact. Some studies have performed site comparisons in the diversity-productivity relationships (e.g. Haase et al.,2015; Van dee Peer et al., 2017). But these studies often merge data from a few experimental sites over a short period of time. Also, a recent synthesis work evaluating all the studies performed across TreeDivNet experiments has shown prominent variation in the strength and direction of diversity effects on productivity (Grossman et al., 2018). However, we are still missing a meta-analysis including a large number of these experiments that quantitatively explores the effects of environmental conditions as well as the differences in experimental designs (i.e., tree density, plot size, etc.). This would be an important contribution to our understanding of the context-dependency of the dynamics of diversity-productivity.

LongER-term monitoring

The present research stands out to be the first study with trees to test how diversity effects on productivity change during the first decade of stand development, providing novel insights into these dynamics as well as the underlying mechanisms. Primarily, we have seen how diversity effects progressively strengthen over time driven by increases of complementarity effects as competition for light intensifies with fast-growing deciduous species dominating community productivity. However, logically, this study misses disentangling the role of stand development over more advanced stages. How long will positive net diversity effects due to complementarity last is unknown, but as stands further develop, they may become progressively dominated by slow-growing late-successional species with the gradual senescence of overstorey fast-growing deciduous species (Chen & Popadiouk, 2002; Taylor et al., 2020; White, 1979). This probably will allow selection effects to take over in determining the diversity effects on productivity in more advanced stages of stand development. Therefore, understanding how diversity effects on productivity are likely to change in these latter stages remains a priority.

Monitoring existing experiments over longer temporal scales should allow us to track the many trajectories that diversity effects could take through more advanced stages. However, all these experiments are still relatively young. Therefore, first, they must be allowed to mature to provide us with relevant information. Meanwhile, the available data from forest inventories and comparative forest plots could provide important some insights in this regard. For example, Taylor et al. (2020) using a space-for-time substitution design – where plots at different stages of stand development are compared – showed that in boreal forests mid-successional stages of high functional diversity exhibited the strongest diversity-productivity relationships. However, in this kind of studies is difficult to account for the differences in management practices and the conditions under which each plot has developed (Jucker et al., 2022). Simulation models could be useful to extend and complement the findings from both experiments and observational studies and explore the diversity effects on productivity over longer scales (e.g. Morin et al. 2011). The co-development of experiments with simulated models and observational data has the potential to provide a significant step towards disentangling the underlying mechanisms of tree diversity on productivity in more advanced stages of stand development.

Functional traits and the mechanistic approach

Another important objective of BEF research must be to elucidate further the biological processes that stimulate the emergence of overyielding in mixtures through time. In this thesis, I related the diversity effects and its partitioned components, i.e. complementarity and selection, with the functional composition at the community levels. I highlighted that mixing species with contrasting resource-use strategies (slow-growing evergreens and fast-growing deciduous) resulted in aboveground niche partitioning (i.e. complementarity effects) that led the community to make better use of incoming light (i.e. complementarity effects), and thereby to overyield.

Nonetheless, this study presents some limitations in explaining the processes leading to mixtures overyielding. First, as in other studies using a trait-based approach, complete trait data is often not available, which can influence the accuracy of functional diversity indices and the possible biological interpretation (Pakeman, 2014). For instance, in this thesis species' traits values are the average of multiple trait data sources (Belluau, 2020). However, evidence shows that species respond to variations in their environment by multiple adjustments in their morphological and physiological traits to alleviate resource stress and increase the uptake of limiting resources (Abakumova et al., 2016; Freschet et al., 2018; Williams et al., 2017). Moreover, species' functional traits are also known to vary during tree development (ontogeny) (Havrilla et al., 2021). Therefore, trait data ideally would need to be directly measured at the focal trees at different points in time to link these physiological variations to changes in ecosystem functioning.

Second, this study focused primarily on the competition for light as a determining factor in the functioning of communities. I provided strong evidence that light partitioning through species spatial complementarity is a crucial process leading to positive diversity effects on productivity. However, other biological processes may occur simultaneously through which diversity enhances productivity, such as reduced pest and pathogen loads, trophic interactions or improved nutrient and water uptake belowground (Ammer, 2019; Jactel & Brockerhoof, 2007), which this research did not cover (Figure 4.2). In particular, there is a special need to understand better the role of the belowground system in BEF relationships and its interrelationships with the aboveground system. Although both systems have traditionally been studied in isolation from one another (Wardle et al. 2004), they inherently rely on each other. Trees supply organic carbon resources to the belowground food web in the form of litter. In turn, decomposers affect trees' performance via their role in nutrient cycling. Also, similarly to aboveground light partitioning, differential use of available belowground resources (e.g. water and nutrients) contribute to complementary interactions between species leading to overyield at the community level (Bu et al., 2017; Sun et al., 2017). Moreover, above- and belowground systems can respond coordinately to variations in their environment through changes in biomass allocation (Bai et al., 2010; Zhang et al., 2017). For example, in resource-abundant sites, trees tend to allocate more biomass into aboveground growth and less into roots. In sites where nutrients and/or water are limited, trees allocate more biomass into roots. Therefore, investigating BEF relationships within a complete aboveground-belowground framework will likely yield deeper mechanistic insights into the drivers of such relationships.

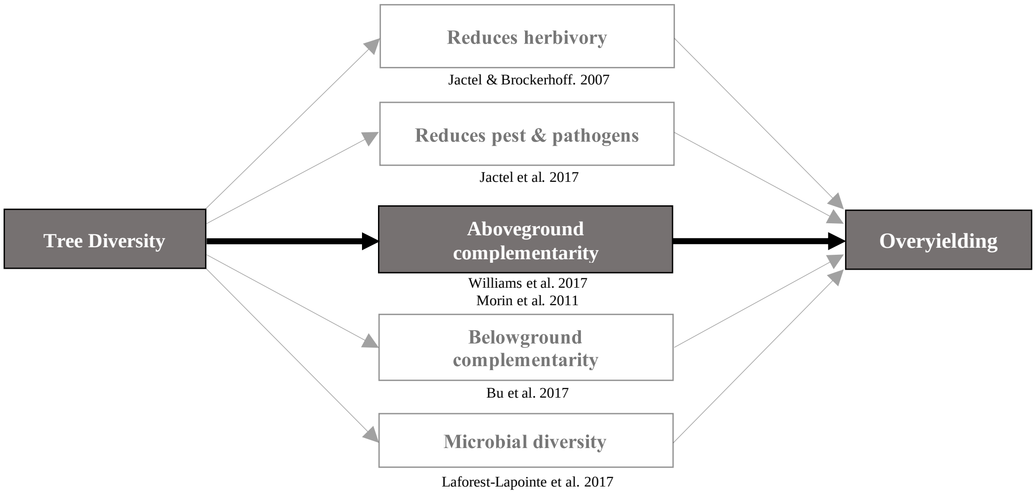


Figure 4.2 Outline of some mechanisms proposed in BEF literature to explain positive diversity effects on productivity. In this thesis, I have focused on light partitioning through spatial complementarity between species to explain mixtures overyielding over time.

BEF beyond ecosystems boundaries: From ecosystems to meta-ecosystems

An emerging issue in BEF research is understanding the extent to which diversity effects are relevant in an explicit spatial context. Biodiversity effects on ecosystem functioning have been studied almost exclusively ‘within’ a given ecosystem but not ‘across’ its boundaries (Scherer-Lorenzen et al., 2022). Nonetheless, ecosystems are connected by important flows of energy, matter, and organisms across their boundaries (i.e. meta-ecosystems) (Loreau et al. 2003), which, in turn, can impact their functioning.

Theory and empirical evidence suggest that variations in biodiversity in one ecosystem can strongly impact the functioning of other ecosystems through many co-occurring processes (i.e. cross-boundary diversity effects). Moreover, the impact can be either positive or negative, depending on the context. For instance, tree diversity often enhances forest productivity (Liang et al., 2016; Zhang et al., 2012). Greater forest productivity, in turn, promotes higher levels of litter production (von Arx et al., 2013). Litter inputs into freshwater systems provide a significant source of energy and nutrients that allows greater biomass production across different trophic levels (Stoler & Relyea, 2019). On the other hand, plant diversity can increase the retention of nutrients in soils, thus reducing their leaching to aquatic ecosystems (Scherer-Lorenzen et al., 2003), ultimately limiting the processes dependent on nutrient supplies (e.g. Mulholland et al., 2008). Therefore, since multiple processes can simultaneously contribute to cross-boundary diversity effects, the strength and direction of these effects will vary based on the relative contribution of each process pathway. A cross-boundary framework that aims to unravel the role of biodiversity in functionally interconnected ecosystems presents a promising frontier for BEF science with the potential to provide new dimensions and realism of the role of biodiversity.

In conclusion, the future of BEF research in forests is exciting and full of opportunities for new discoveries and innovations. By pursuing these research perspectives within and across its boundaries, we can better understand and manage forest ecosystems for the benefit of both biodiversity and human well-being.

REFERENCES

Abakumova, M., Zobel, K., Lepik, A., & Semchenko, M., (2016). Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist*, *211*(2), 455–463.

Aarssen, L. W. (1997). High Productivity in Grassland Ecosystems : Effected by Species Diversity or Productive Species? *Oikos*, *80*(1), 183–184.

Adler, P. B., Salguero-Gomez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, *111*(2), 740–745.

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*(10), 1294–1306.

Ammer, C. (2019). Diversity and forest productivity in a changing climate. *New Phytologist*, *221*(1), 50–66.

Andrews, C., Weiskittel, A., D'Amato, A. W., & Simons-Legaard, E. (2018). Variation in the maximum stand density index and its linkage to climate in mixed species forests of the North American Acadian Region. *Forest Ecology and Management*, *417*(2), 90–102.

von Arx, G., Pannatier, E. G., Thimonier, A., & Rebetez, M. (2013). Microclimate in forests with varying leaf area index and soil moisture: Potential implications for seedling establishment in a changing climate. *Journal of Ecology*. *101*(5), 1201–1213

Archambault, C., Paquette, A., Messier, C., Khlifa, R., Munson, A. D., & Handa, I. T. (2019). Evergreenness influences fine root growth more than tree diversity in a common garden experiment. *Oecologia*, 189(4), 1027–1039

Bai, Y., Zhang, W., Jia, X., Wang, N., Zhou, L., Xu, S., & Wang, G. (2010). Variation in root:shoot ratios induced the differences between above and belowground mass-density relationships along an aridity gradient. *Acta Oecologica*, *36*(4), 393–395

Bartoń, K. (2016). *Package" MuMIn": Multi-Model Inference – R package ver. 1.15.6. <https://CRAN.R-project.org/package=MuMIn>.*

Bauhus, J., Van der Meer, P., & Kanninen, M. (2010). *Ecosystem Goods and Services from Plantation Forests*. London: Earthscan.

Belluau, M. (2020) Data from: IDENT_TRAIT_DATABASE_2020- 10- 20.xlsx. Figshare Digital Repository. Available at: https://doi. org/10.6084/m9.figsh are.13118 132.v1

Belluau, M., Paquette, A., Gravel, D., Reich, P. B., Stefanski, A., Messier, C. (2021). Exotics are more complementary over time in tree biodiversity-ecosystem functioning experiments. *Functional Ecology* 00, 1-12. https://doi.org/10.1111/1365-2435.13900

Belluau, M., Vitali, V., Parker, W. C., Paquette, A., & Messier, C. (2021). Overyielding in young tree communities does not support the stress-gradient hypothesis and is favoured by functional diversity and higher water availability. *Journal of Ecology*, *109*(4), 1790–1803

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(1), 191–193

Bremer, L. L., & Farley, K. A. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation*, *19*(14), 3893–3915.

Bu, W., Schmid, B., Liu, X., Li, Y., Härtle, W., von Oheimb, G., … Ma, K. (2017). Interspecific and intraspecific variation in specific root length drives aboveground biodiversity effects in young experimental forest stands. *Journal of Plant Ecology*, *10*(1), 158–169.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., … Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, *417*(6), 844–848.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail. P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *489*(7415), 59–67.

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., … Gonzalez, A. (2011). The functional role of producer diversity in ecosystems. *American Journal of Botany*, *98*(3), 572–592.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M. & Jouseau, C. (2006). Effects of biodiversity on the functioning of tropic groups and ecosystems. *Nature*, *443*(7114), 989–992.

Caspersen, J. P., Thürig, E., Rigling, A., & Zimmermann, N. E. (2018). Complementarity of gymnosperms and angiosperms along an altitudinal temperature gradient. *Oikos*, *127*(12), 1787–1799.

Chen, H. Y. H., & Popadiouk, R. V. (2002). Dynamics of North American boreal mixedwoods. *Environmental Reviews*, *10*(3), 137–166.

Chesson, P., Pacala, S., & Neuhauser, C. (2001). Environmental Niches and Ecosystem Functioning. In A. P. Kinzig, S. W. Pacala, & D. Tilman (Eds.), *The Functional Consequences of Biodiversity - Empirical Progress and Theoretical Extensions* (pp. 213–245). Princeton, NJ: Princeton University Press.

Clark, J. S. (2010). Individuals and the variation needed for high species diversity in forest trees. *Science*, *327*(5969), 1129–1132.

Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, *27*(4), 833–840.

Craine, J. M., & Reich, P. B. (2005). Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytologist*, *166*(1), 710–713.

Dai, X., Jia, X., Zhang, W., Bai, Y., Zhang, J., Wang, Y., & Wang, G. (2009). Plant height-crown radius and canopy coverage-density relationships determine above-ground biomass-density relationship in stressful environments. *Biology Letters*, *5*(4), 571–573.

Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favored races in the struggle for life*. London: J. Murray.

Dawson, T. E. (1993). Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, *95*(4), 565–574.

De Wit, C. T. (1960). *On Competition*. Versl. Landbouwkd. Onderz.

del Río, M., Montero, G., & Bravo, F. (2001). Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands.

Forest Ecology, *142*(1), 79–87.

DeMalach, N., Zaady, E., Weiner, J. & Kadmon, R. (2016). Size asymmetry of resource competition and the structure of plant communities. *Journal of Ecology*, *104*(4), 899–910.

Deng, J. M., Wang, G. X., Morris, E. C., Wei, X. P., Li, D. X., Chen, B. M., … Wang, Y. (2006). Plant mass-density relationship along a moisture gradient in north-west China. *Journal of Ecology*, *94*(5), 953–958.

Ducey, M. J., & Knapp, R. A. (2010). A stand density index for complex mixed species forests in the northeastern United States. *Forest Ecology and Management*, *260*(9), 1613–1622.

Ducey, M. J., Woodall, C. W., & Bravo-Oviedo, A. (2017). Climate and species functional traits influence maximum live tree stocking in the Lake States, USA. *Forest Ecology and Management*, *386*(1), 51–61.

Falster, D. S., & Westoby, M. (2003). Leaf size and angle vary widely across species: What consequences for light interception? *New Phytologist*, *158*(3), 509–525.

FAO (2020). *Global Forest Resources Assessment 2020 - Key findings*. Rome.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y., & Von Oheimb, G. (2018). Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications, 9,* 1144.

Forrester, D. I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests : From pattern to process. *Forest Ecology and Management*, *312*(1), 282–292.

Forrester, D. I., Baker, T. G., Elms, S. R., Hobi, M. L., Ouyang, S., Wiedemann, J. C., … Pulkkinen, M. (2021). Self-thinning tree mortality models that account for vertical stand structure, species mixing and climate. *Forest Ecology and Management*, *487*(1), 118936.

Forrester, D. I., & Bauhus, J. (2016). A Review of Processes Behind Diversity—Productivity Relationships in Forests. *Current Forestry Reports*, *2*(1), 45–61.

Freckleton, R. P., & Watkinson, A. R. (2001). Predicting competition coefficients for plant mixtures: Reciprocity, transitivity and correlations with life-history traits.

Ecology Letters, *4*(4), 348–357.

Freschet, G. T., Violle, C., Bourget, M. Y., Scherer-Lorenzen, M., & Fort, F. (2018). Allocation, morphology, physiology, architecture: the multiple facets of plant above- and below-ground responses to resource stress. *New Phytologist*, *219*(4), 1338–1352.

Goldberg, D. E. (1990). Components of resource competition in plant communities. In J. B. Grace & D. Tilman (Eds.), *Perspectives on Plant Competition* (pp. 27–49). San Diego: Academic Press.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910.

Grossman, J. J., Cavender-Bares, J., Hobbie, S. E., Reich, P. B., & Montgomery, R. A. (2017). Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment. *Ecology*, *98*(10), 2601–2614.

Grossman, J. J., Vanhellemont, M., Barsoum, N., Bauhus, J., Bruelheide, H., Castagneyrol, B., … Verheyen, K. (2018). Synthesis and future research directions linking tree diversity to growth, survival, and damage in a global network of tree diversity experiments. *Environmental and Experimental Botany*, *152*(1), 68–89.

Guerrero-Ramírez, N. R., Craven, D., Reich, P. B., Ewel, J. J., Isbell, F., Koricheva, J., … Eisenhauer, N. (2017). Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nature Ecology and Evolution*, *1*(11), 1639–1642.

Haase, J., Castagneyrol, B., Cornelissen, J. H. C., Ghazoul, J., Kattge, J., Koricheva, J., … Jactel, H. (2015). Contrasting effects of tree diversity on young tree growth and resistance to insect herbivores across three biodiversity experiments. *Oikos*, *124*(12), 1674–1685.

Havrilla, C. A., Munson, S., Yackulic, E., & Butterfield, B. J. (2021). Ontogenetic trait shifts: Seedlings display high trait variability during early stages of development. *Functional Ecology*, *35*(11), 2409–2423.

Healy, C., Gotelli, N. J., & Potvin, C. (2008). Partitioning the effects of biodiversity and environmental heterogeneity for productivity and mortality in a tropical tree plantation. *Journal of Ecology*, *96*(5), 903–913.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., … Lawton, J. H. (1999). Plant Diversity and Productivity Experiments in European Grasslands. *Science*, *286*(5442), 1123–1127.

Hisano, M., & Chen, H. Y. H. (2020). Spatial variation in climate modifies effects of functional diversity on biomass dynamics in natural forests across Canada. *Global Ecology and Biogeography*, *29*(1), 682–695.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., … O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as major driver of ecosystem driver of ecosystem change. *Nature*, *486*(1), 105–108.

Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., … Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*(1), 3–35.

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., & Li, Y. (2018). Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, *363*(6423), 80–83.

Hulvey, K. B., Hobbs, R. J., Standish, R. J., Lindenmayer, D. B., Lach, L., & Perring, M. P. (2013). Benefits of tree mixes in carbon plantings. *Nature Climate Change*, *3*(10), 869–874.

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, *110*(4), 449–460.

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., … Brockerhoff, E. G. (2007). Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Current Forestry Reports*, *3*(1), 223–243.

Jactel, H., & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters*, *10*(9), 835–848.

Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., … Castagneyrol, B. (2018). Positive biodiversity–productivity relationships in forests: Climate matters. *Biology Letters*, *14*(4), 12–15.

Jucker, T., Avăcăritei, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., & Coomes, D. A. (2016). Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology, 104*(2), 388-398.

Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., & Coomes, D. A. (2014). Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *Journal of Ecology*, *102*(5), 1202–1213.

Jucker, T., Bouriaud, O., & Coomes, D. A. (2015). Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology*, *29*(1), 1078–1086.

Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G., & Coomes, D. A. (2020). Good things take time—Diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology*, *108*(6), 2198–2211.

Kinzig, A. P., Pacala, S. W., & Tilman, D. (2001). *The Functional Consequences of Biodiversity - Empirical Progress and Theoretical Extensions*. Princeton, NJ: Princeton University Press.

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., … Westoby, M. (2015). Plant functional traits have globally consistent effects on competition. *Nature*, *486*(1),1–15.

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., & von Oheimb, G. (2019). Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecology Letters*, *22*(12), 2130–2140.

Laforest-Lapointe, I., Paquette, A., Messier, C., & Kembel, S. (2017). Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. *Nature*,546(7656), 145–147.

Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305.

Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., John Kress, W., & Chazdon, R. L. (2014). The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters*, *17*(9), 1158–

1167.

Lavorel, S., & Garnier, E. (2002). Predicting Changes in Community Composition and Ecosystem Functioning from Plant Traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., … Bonis, A. (2008). Assessing functional diversity in the field - Methodology matters! *Functional Ecology*, *22*(1), 134–147.

Li, Y., Härdtle, W., Bruelheide, H., Nadrowski, K., Scholten, T., von Wehrden, H., & von Oheimb, G. (2014). Site and neighborhood effects on growth of tree saplings in subtropical plantations (China). *Forest Ecology and Management*, *327*(1), 118–127.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., … Ferreira, L. V. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*. aaf8957. https://doi.org/10.1126/ science.aaf8957

Lindenmayer, D. B., & Franklin, J. F. (2002). *Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach*. Island Press.

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*(1), 72–76.

Loreau, M., Mounquet, N., & Holt, R. (2003). Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, *6*(8), 673–679.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185.

Mcintire, E. J. B., & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, *201*(1), 403–416.

Montgomery, R. A., Reich, P. B., & Palik, B. J. (2010). Untangling positive and negative biotic interactions: views from above and below ground in a forest ecosystem. *Ecology*, *91*(12), 3641–3655.

Mori, A. S. (2018). Environmental controls on the causes and functional consequences of tree species diversity. *Journal of Ecology*, *106*(1), 113–125.

Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology*, *54*(1), 12–27.

Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, *14*(12), 1211–1219.

Morris, E. C. (2003). How does fertility of the substrate affect intraspecific competition? Evidence and synthesis from self-thinning. *Ecological Research*, *18*(3), 287–305.

Mulholland, P., Helton, A. M., Poole, G. C., Hall, R. O., Hamilton, S. K., Peterson. B. J., … Thomas, S. M. (2008). Stream denitrification across biomes and its response to anthropogenic nitrate loading. *Nature*, *452*(7184), 202–205.

Naeem, S. (2002). Disentangling the Impacts of Diversity on Ecosystem Functioning in Combinatorial Experiments. *Ecology, 83*(10), 2925-2935.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50.

Niinemets, Ü. (2010). A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecological Research*, *25*(4), 693–714.

Pacala, S. W., & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist*, *152*(5), 729–737.

Pakeman, R. (2014). Functional trait metrics are sensitive to the completeness of the species' trait data?. *Methods in Ecology and Evolution, 5*(1), 9–15.

Paquette, A., Hector, A., Castagneyrol, B., Vanhellemont, M., Koricheva, J., & Verheyen, K. (2018). A million and more trees for science. *Nature Ecology & Evolution*, *2*(1), 763–766.

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity : from temperate to boreal forests. *Global Ecology & Biogeography*, *20*(1), 170–

180.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Ranke, J. (2016). *nlme: Linear and non- linear mixed effects models. 2014. – R package ver. 3.1-120. <https://CRAN.R-project.org/package=nlme>.*

Plas, F. Van Der, Manning, P., Soliveres, S., Allan, E., Scherer-lorenzen, M., Wirth, C., … Verheyen, K. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, *113*(18), 3557–3562.

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., … Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, *134*(5), 927–947.

Pretzsch, H. (2005). Diversity and Productivity in Forests: Evidence from Long-Term Experimental Plots. In Scherer-Lorenzen, M., Körner, C., & Schulze, E. D. (Eds.), *Forest Diversity and Function* (pp. 41–64). Springer Berlin Heidelberg.

Pretzsch, H. (2006). Species-specific allometric scaling under self-thinning : evidence from long-term plots in forest stands. *Oecologia*, *146*(1), 572–583.

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, *327*(1), 251–264.

Pretzsch, H., & Biber, P. (2005). A re-evaluation of Reineke's rule and stand density index. *Forest Science*, *51*(4), 304–320.

Pretzsch, H., & Biber, P. (2010). Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. *Canadian Journal of Forest Research*, *40*(2), 370–384.

Pretzsch, H. & Biber, P. (2016). Tree species mixing can increase maximum stand density. *Canadian Journal of Forest Research*, *46*(1), 1179–1193.

Pretzsch, H. & Del Río, M. (2020). Density regulation of mixed and mono-specific forest stands as a continuum: A new concept based on species-specific coefficients for density equivalence and density modification. *Forestry*, *93*(1), 1–15.

Pretzsch, H. & Dieler, J. (2012). Evidence of variant intra- and interspecific scaling of tree crown structure and relevance for allometric theory. *Oecologia, 169*(3), 637–649.

Puettmann, K. J., Hann, D. W., & Hibbs, D. E. (1993). Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. *Forest Science, 39*(1), 7–27.

Reich, P. B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology, 102*(2), 275–301.

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B., & Eisenhauer, N. (2012). Impacts of biodiversity loss escalate through time as redundancy fades. *Science, 336*(6081), 589–592.

Reineke, L. H. (1933). Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research, 46*(7), 627–638.

Reyes-Hernandez, V., Comeau, P. G., & Bokalo, M. (2013). Static and dynamic maximum size-density relationships for mixed trembling aspen and white spruce stands in western Canada. *Forest Ecology and Management, 289*(1), 300–311.

Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., … Schulze, E. D. (2012). Using plant functional traits to explain diversity-productivity relationships. *PLoS ONE, 7*(5). https://doi.org/10.1371/journal.pone.0036760

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology, 95*(9), 2479–2492.

Satopää, V., Albrecht, J., Irwin, D., & Raghavan, B. (2011). Finding a “kneedle” in a haystack: Detecting knee points in system behavior. *Proceedings - International Conference on Distributed Computing Systems, 15*(1),166–171.

Scherer-Lorenzen, M., Palmborg, C., Prinz, A., & Schulze, E. D. (2003). The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology, 84*(6), 1539–1552.

Scherer-Lorenzen, M., Gessner, M. O., Beisner, B. E., Messier, C., Paquette, A., Petermann, J. S., … Nock, C. A. (2022). Pathways for cross-boundary effects of biodiversity on ecosystem functioning. *Trends in Ecology and Evolution*, *37*(5), 454–467.

Schnabel, F., Schwarz, J. A., Dănescu, A., Fichtner, A., Nock, C. A., Bauhus, J., & Potvin, C. (2019). Drivers of productivity and its temporal stability in a tropical tree diversity experiment. *Global Change Biology*, *25*(12), 4257–4272.

Schulze, E. D., & Mooney, H. A. (1994). *Biodiversity and ecosystem function*. Springer Berlin Heidelberg.

Searle, E. B., & Chen, H. Y. H. (2020). Complementarity effects are strengthened by competition intensity and global environmental change in the central boreal forests of Canada. *Ecology Letters*, *23*(1), 79–87.

Shipley, B., Vile, D., & Garnier, É. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, *314*(5800), 812–814.

Silva Pedro, M., Rammer, W., & Seidl, R. (2017). Disentangling the effects of compositional and structural diversity on forest productivity. *Journal of Vegetation Science*, *28*(3), 649–658.

Spiecker, H. (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe-temperate zone. *Journal of Environmental Management*, *67*(1), 55–65.

Stoler, A., & Relyea. R. (2020). Reviewing the role of plant litter inputs to forested wetland ecosystems: leafing through the literature. *Ecological Monographs*, *90*(2), e01400, https://doi.org/10.1002/ecm.1400.

Sun, Z., Liu, X., Schmid, B., Bruelheide, H., Bu, W., & Ma, K. (20). Positive effects of tree species richness on fine-root production in a subtropical forest in SE-China. *Journal of Plant Ecology*, *10*(1), 146-157.

Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*(3), 451–459.

Taylor, A. R., Gao, B., & Chen, H. Y. H. (2020). The effect of species diversity on tree growth varies during forest succession in the boreal forest of central Canada.

Forest Ecology and Management, *455*(9), 117641.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, *75*(1), 2-16.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(9), 471–493.

Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, *379*(6567), 718–720.

Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J., & Messier, C. (2016). Functional identity is the main driver of diversity effects in young tree communities. *Ecology Letters*, *19*(6), 638–647.

Tobner, C. M., Paquette, A., Reich, P. B., Gravel, D., & Messier, C. (2014). Advancing biodiversity-ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, *174*(3), 609–621.

Trouvé, R., Nitschke, C. R., Robinson, A. P., & Baker, P. J. (2017). Estimating the self-thinning line from mortality data. *Forest Ecology and Management*, *402*(2), 122–134.

Turnbull, L. A., Coomes, D., Hector, A., & Rees, M. (2004). Seed mass and the competition/colonization trade-off: Competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*, *92(4)*, 97–109.

Urgoiti, J., Messier, C., Keeton, W. S., Paquette, A., & Belluau, M. (2023). Functional diversity and identity influence the self-thinning process in young forest communities (submitted for publication). *Journal of Ecology*.

Urgoiti, J., Messier, C., Keeton, W. S., Reich, P. B., Gravel, D., & Paquette, A. (2022). No complementarity no gain—Net diversity effects on tree productivity occur once complementarity emerges during early stand development. *Ecology Letters*, *25*(4), 851–862.

Valladares, F., & Niinemets, U. (2007). The Architecture of Plant Crowns: From Design Rules to Light Capture and Performance. In Pugnaire, F., & Valladares, F. C. (Eds.), *Functional plant ecology* (pp. 101–150). Taylor and Francis, New

York.

Valladares, F., Zaragoza-Castells, J., Sánchez-Gómez, D., Matesanz, S., Alonso, B., Portsmuth, A., … Atkin, O. K. (2008). Is shade beneficial for Mediterranean shrubs experiencing periods of extreme drought and late-winter frosts? *Annals of Botany*, *102*(6), 923–933.

Van de Peer, T., Verheyen, K., Ponette, Q., Setiawan, N. N., & Muys, B. (2017). Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. *Journal of Ecology*, *106*(3), 1096–1105.

Van Ruijven, J., & Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(3), 695–700.

Vandermeer, J. H., & Goldberg, D. E. (2004). *Population Ecology: First Principles*. Princeton, NJ: Princeton University Press.

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., … Scherer-lorenzen, M. (2015). Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Royal Swedish Academy of Sciences*.

Vieilledent, G., Courbaud, B., Kunstler, G., Dhôte, J. F., & Clark, J. S. (2010). Individual variability in tree allometry determines light resource allocation in forest ecosystems: A hierarchical Bayesian approach. *Oecologia*, *163*(3), 759–773.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*(5677), 1629–1633.

Wardle, D. A. (1999). Is " sampling effect " a problem for experiments investigating function. *Oikos*, *87*(2), 403–407.

White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *The Botanical Review*, *45*(3), 229–299.

Williams, L. J., Cavender-Bares, J., Paquette, A., Messier, C., & Reich, P. B. (2020). Light mediates the relationship between community diversity and trait plasticity in functionally and phylogenetically diverse tree mixtures. *Journal of Ecology*, *108*(4), 1617–1634.

Williams, L. J., Paquette, A., Cavender-Bares, J., Messier, C., & Reich, P. B. (2017). Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology & Evolution*, *1*, 0063.

Yoda, K., Kira, T., Ogawa, H., & Hozumi, K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology Osaka City University*, *14*, 107–129.

Zeide, B. (1987). Analysis of the 3/2 power law of self-thinning. *Forest Science*, *33*(1), 517–537.

Zhang, M., Ji, C., Zhu, J., Wang, X., Wang, D., & Han, W. (2017). Comparison of wood physical and mechanical traits between major gymnosperm and angiosperm tree species in China. *Wood Science and Technology*, *51*(6), 1405–1419.

Zhang, W. P., Jia, X., & Wang, G. X. (2017). Facilitation among plants can accelerate density-dependent mortality and steepen self-thinning lines in stressful environments. *Oikos*, *126*(8), 1197–1207.

Zhang, Y., Chen, H. Y. H., & Reich, P. B. (2012). Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. *Journal of Ecology*, *100*(3), 742–749.

Zheng, L. T., Chen, H. Y. H., Biswas, S. R., Bao, D. F., Fang, X. C., Abdullah, M., & Yan, E. R. (2021). Diversity and identity of economics traits determine the extent of tree mixture effects on ecosystem productivity. *Journal of Ecology*, 109(1), 1898-1908.