TREE FUNCTIONAL TRAITS.

UNDERSTANDING THEIR VARIATION -

FROM INTRASPECIFIC PLASTICITY TO THE EFFECTS OF TRAIT DIVERSITY ON ECOYSTEM FUNCTIONING

THÈSE

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AVANT –PROPOS

Ce projet de recherche doctorale a été divisé en trois chapitres, conçus sous le format d’articles de revue scientifique. Par choix personnelle, j’ai publié dès le départ avec le nom de famille de ma mère : Tobner. Le premier article a été publié dans la revue Frontiers in Plant Sciences (Tobner, Cornelia Marie, Alain Paquette, Christian Messier. 2013. Front. Plant Sci. 4 (424), 1-11). Le second regroupe les mêmes auteurs que le premier et a été accepté dans la revue Oecologia (Tobner, Cornelia Marie, Alain Paquette, Christian Messier. 2013. Oecologia, in press). Le troisième chapitre sera soumis sous peu avec Tobner, Cornelia Marie, Alain Paquette et Christian Messier comme auteurs. Ces trois chapitres sont présentés ici intégralement, dans leur version en langue anglaise. Ils sont accompagnés d’une introduction et d’une conclusion générales rédigées en anglais, visant relier les chapitres entre eux afin de former un tout cohérent.

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ABSTRACT

Rising awareness about the unprecedented rate of species extinctions created growing concern about the impacts of biodiversity loss on ecosystem functioning at the end of the 20h century. In consequence, a systematic and concerted search to understand the relation between biodiversity and ecosystem functioning (BEF) began. After more than 20 years of BEF research, general consensus leans toward increasing productivity, resource capture and decomposition with diversity. The two main mechanisms proposed to underlie this positive relationship are niche complementarity and selection effects. Both mechanisms emphasize the fundamental role of functional traits in explaining BEF relations. Especially complementarity (i.e. the greater exploitation of resources through increased trait diversity) has been shown to underlie positive BEF relations and to increase over time. Although most often used in BEF to measure diversity, species richness has been shown to not be the best predictor of EF as it assumes all species of being functionally equal. Functional diversity has shown great potential in explaining BEF relations. However, most BEF research was conducted in herbaceous systems and most knowledge about functional traits is derived from aboveground plant parts.

The main objectives of this thesis were to address some of the open research questions surrounding BEF in tree systems, particularly regarding niche complementarity and plant functional traits. In particular, the objectives were to improve our understanding of fine root trait variation within and across tree species, develop an experimental design testing specifically for the effects of functional diversity and the existence of complementarity in tree communities, and to implement the developed design to test for the effect of functional diversity on productivity in tree communities. For this purpose, the thesis is comprised of three chapters, each treating one of the objectives.

The first chapter analyses two datasets including three fine root traits. The first dataset compared interspecific correlations of these traits for 12 North American tree species grown in controlled, experimental conditions. The second dataset examined intraspecific variation along a gradient of soil conditions and tree age, among four tree species co-occurring in natural forests. Across species, root traits were strongly correlated and confirmed the emerging evidence for a root trait spectrum. Within species, variation to soils and age were trait specific. Out of the three fine root traits, diameter showed greatest phenotypic plasticity and was significantly higher in humid organic soils compared to xeric and mesic soils.

The second chapter reviews and synthesizes current knowledge surrounding the paradigm of biodiversity and ecosystem functioning (BEF) in tree systems and beyond. After identification of open research questions within the BEF paradigm, the second chapter proposes an experimental design addressing those gaps. The core of this experimental design is the variation of tree communities along a gradient of continuous functional diversity (FD) to specifically test for the effect of FD on EF and for underlying mechanisms such as complementarity. In addition, the design is characterized by a great flexibility allowing each site to simultaneously address other open research questions.

The third chapter describes the result of an experimental site following the approach developed in the second chapter. High-density tree communities that vary in functional diversity, independent of species richness were used to specifically test for the effect of those two metrics of diversity on productivity while separating their respective contributions. This chapter also specifically tested for the existence of complementarity in young tree communities. After four years of growth, positive diversity effects were documented for the majority of mixtures. However, those were largely due to selection effects. Some fast-growing, deciduous trees clearly overyielded in mixture while most evergreen species were competitively excluded. Functional traits involved in explaining this effect of functional identity included leaf longevity, seed mass and nitrogen. These traits reflect the life history strategy of the overyielding species. In addition, rooting depth and branching intensity significantly affected biomass and diversity effects, possibly reflecting the location of limiting resources belowground.

In conclusion, similar to aboveground traits, fine root traits may be bound by specific physiological trade-offs, forming specific spectra. Although often neglected, fine root diameter may be a better estimator of environmental change than the often-used specific root length. In respect to BEF, we reason that although great advances in the understanding of the effects of biodiversity on ecosystem functioning have been achieved, many crucial links and aspects have yet to be examined, especially for tree-dominated ecosystems. This is especially true for diversity metrics other than species richness. Despite the growing acknowledgement and understanding of the importance of FD in explaining BEF relations, only few experiments actually do manipulate FD in tree communities. In addition, trees are model systems to examine BEF relations offering multiple advantages compared to other systems. Through their size and the facility to assess their development on an individual basis over time, tree systems allow testing of new sets of questions thus bringing science closer to a more detailed understanding of how individuals regulate the way in which species interact to form both positive and negative outcomes. After presenting one of the first experiments testing for the effect of functional diversity on tree productivity, we reach the conclusion that in general, diversity positively affects productivity in young tree communities. However, this effect is largely due to selection effects.

Keywords : biodiversity, ecosystem functioning, tree, functional diversity, complementarity, experimental design, fine root plasticity

RESUME

Depuis la fin du 20ème siècle, la prise de conscience de l'effritement sans précédent du nombre d'espèces a mené les scientifiques à se questionner sur les impacts de la perte de la biodiversité sur le fonctionnement des écosystèmes (FE). Conséquemment, une recherche concertée et systématique a été entreprise afin de comprendre la relation entre la biodiversité et le fonctionnement des écosystèmes (RBFE). Plus que vingt ans de recherche ont dégagé un consensus associant l'accroissement de la productivité, de la capture des ressources et de la décomposition avec une augmentation de la biodiversité. Les deux mécanismes principaux expliquant cette relation positive sont la complémentarité des niches et l'effet de sélection. Ces deux mécanismes mettent en valeur le rôle fondamental des traits fonctionnels pour expliquer les corrélations sous-jacentes à la RBFE. En particulier, la complémentarité des niches (la plus grande exploitation des ressources due à une plus grande diversité des traits) a été montré à la base des RBFE positifs et d'augmenter au fil du temps. Souvent utilisée dans l'étude de la RBFE pour mesurer la diversité, la richesse spécifique n'est pas le meilleur prédicteur du FE puisqu'elle suppose que toutes les espèces sont fonctionnellement égales (c.-à-d., l'effet de n'importe quelle espèce est interchangeable avec l'effet de n'importe quelle autre). La diversité fonctionnelle a, quant à elle, montré un meilleur potentiel pour expliquer les RBEF. Par contre, la majorité des recherches sur la RBEF a été faite sur des systèmes herbacés. De plus, les connaissances sur les traits fonctionnels proviennent presque exclusivement des parties aériennes des plantes.

Les objectifs principaux de cette thèse étaient de développer la connaissance des RBEF au niveau des communautés d'arbres afin de mieux comprendre les effets de la complémentarité de niche et de la diversité fonctionnelle sur le fonctionnement de ces systèmes. Plus précisément, les objectifs étaient d'améliorer la connaissance des variations racinaires intraspécifiques et interspécifiques, de développer un design expérimental pour tester les effets de la diversité fonctionnelle et déterminer s'il y a présence de complémentarité dans les communautés d'arbres. Le dernier objectif était de mettre en œuvre le design développé pour tester l'effet de la diversité fonctionnelle sur la productivité dans les communautés d'arbres. La thèse est divisée en trois chapitres, traitant chacun un des objectifs.

Le premier chapitre analyse deux ensembles de données de traits de racines fines (le diamètre, l'intensité du branchement et la longueur spécifique des racines). Le premier jeu de données compare la corrélation interspécifique de ces traits pour 12 espèces nord-américaines d'arbres cultivées dans des conditions expérimentales contrôlées. Le deuxième jeu de données examine les variations intra-spécifiques pour quatre espèces co-occurrentes selon un gradient de conditions du sol et d'âge des arbres. Entre les espèces, les traits des racines étaient fortement corrélés ce qui supporte les preuves récentes de l'existence d'un spectre des traits racinaires. Pour une même espèce, les variations des traits racinaires dues au sol et à l'âge de la plante sont spécifiques à chaque trait. Des trois traits racinaires, le diamètre est celui qui montre la plus grande plasticité phénotypique et était significativement plus grand dans les sols riches et humides que dans les sols xériques et mésiques.

Le deuxième chapitre récapitule et résume les connaissances actuelles sur la RBEF dans les communautés d'arbres et au-delà. Suite à l'identification des avenues de recherche principales au sein des RBEF, le deuxième chapitre propose un système expérimental dont l'objectif est de répondre à ces questions. Le cœur de ce design expérimental est la variation des communautés d'arbres suivant un gradient de diversité fonctionnelle (DF) continu pour tester spécifiquement l'effet de la DF sur le FE et décrire les mécanismes sous-jacents tels que la complémentarité. De plus, le design est très flexible, ce qui permet à chaque site d'explorer simultanément d'autres questions pertinentes.

Le troisième chapitre expose les résultats obtenus sur un site expérimental suivant l'approche décrite dans le deuxième chapitre. Des communautés d'arbres très denses variant en termes de DF et de richesse spécifique de façon indépendante ont servi à tester les effets respectifs de ces deux caractéristiques sur la productivité. L'existence de la complémentarité au sein de communautés d'arbres jeunes a aussi été testée dans ce chapitre. Après quatre années de croissance, des effets positifs de la diversité ont été trouvés pour la majorité des communautés testées. Par contre, ces effets sont largement attribuables aux effets de sélection. Quelques espèces décidues à croissance rapide ont clairement surproduit au sein des peuplements mixtes pendant que la plupart des conifères étaient exclus du à la compétition. Les traits fonctionnels expliquant cet effet incluent la longévité des feuilles, la masse des graines et le contenu en azote. Ces traits reflètent les stratégies fondamentales des espèces ayant surproduit. De plus la profondeur des racines et la quantité de ramifications racinaires affectaient significativement la biomasse des arbres et l'effet de la diversité sur la productivité, ce qui pourrait indiquer des ressources limitantes dans le sol.

En conclusion, de même que pour les traits des parties aériennes des arbres, la variabilité des traits des racines fines semble être contrainte par des compromis physiologiques. De plus, même s'il est souvent négligé, le diamètre des racines fines pourrait être un meilleur estimateur de changements environnementaux que la

longueur spécifique des racines qui est fréquemment utilisée. En ce qui concerne les RBFE, on conclut que même si de grands progrès dans la compréhension des effets de la biodiversité sur le FE ont été atteints, de nombreux liens cruciaux doivent encore être examinés, en particulier pour les écosystèmes dominées par des arbres. Cela est particulièrement vrai pour des paramètres de diversité autres que la richesse en espèces. Malgré la reconnaissance croissante et la compréhension de l'importance de la DF par rapport aux RBFE, seules quelques expériences manipulent DF dans des communautés d’arbres. En outre, les arbres sont des systèmes modèles pour étudier les RBFE offrant de multiples avantages par rapport à d'autres systèmes. Grâce à leur taille et la facilité d'évaluer leur développement sur une base individuelle au fil du temps, les systèmes d'arbres permettent de tester de nouvelles séries de questions. En conséquence, ils rapprocher la science à une compréhension plus détaillée de la façon dont les individus règlementent la coexistence positivement ou négativement. Après avoir présenté l'une des premières expériences testant l'effet de la DF sur la productivité, nous arrivons à la conclusion qu’en général, la diversité influe positivement sur la productivité dans les jeunes communautés d'arbres. Cependant, cet effet est en grande partie due à des effets de sélection.

Mots-clés : biodiversité et fonctionnement des écosystèmes, arbre, diversité fonctionnelle, complémentarité, dispositif expérimental, plasticité racinaire

INTRODUCTION

One of the oldest quests in ecology is the search to understand the stable coexistence of species. To date, this quest has basically remained unresolved, especially in regard to plants. In grasslands for example, how is it possible that so many plant species can coexist while having fundamentally the same resource requirements (Silvertown, 2004)? A common null model assumes that species associations arise solely from species-specific responses to environmental variables (Holt, 2001). However, patterns of species associations emphasize the implication of species interactions. And indeed, species interact with one another either directly (e.g., via interference competition, predation, parasitism, mutualism) or indirectly (e.g., via altering abiotic conditions, resource competition, apparent competition) affecting their coexistence (Siepielski et McPeek, 2010). Among the many models proposed (Zobel, 1992), niche complementarity certainly got the most empirical support and has been considered one of the main candidate mechanisms to explain species coexistence even though it is likely that it is not the sole mechanism at work (Silvertown, 2004). According to the Volterra-Gause principle, the niche complementarity assumes that two or more species cannot coexist unless their requirements towards the limiting resource(s) (i.e. niche) differ at least partially (Holt, 2001).

Following this principle, species that differ in their functional traits (traits that strongly influence organismal performance, McGill *et al.*, 2006) should differ in their resource requirements (i.e. niche) and thus experience reduced competition. In other words, increased diversity of species' traits (i.e. functional diversity) should lead to increased ecosystem functioning. Indeed, the idea of increasing plant diversity leading to increased producer productivity is known at least since the 19th century. European forester von Cotta proposed in 1828 that "Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands…" (in Pretzsch, 2005) and three decades later, Darwin enunciated in his seminal work that a "divergence of character" would reduce interspecific competition and likely yield greater productivity (Darwin, 1859). However, it is not until the late 20th century with the considerable and accelerating change in the earth's biota that a systematic and concerted search for the effects of biodiversity on ecosystem functioning (BEF) began. A generally positive relation between plant diversity and plant community productivity was confirmed across a variety of biomes and taxa (Cardinale *et al.*, 2011). Niche complementarity has been evoked as the main candidate mechanism creating these positive mixture effects (Cardinale *et al.*, 2011 ; Hooper *et al.*, 2005). Most BEF research has been conducted on terrestrial plant systems with a strong bias towards artificial and natural grasslands (Caliman *et al.*, 2010). BEF research using trees or in forests is more recent and scarce (Nadrowski, Wirth et Scherer-Lorenzen, 2010). However, forests support ~80% of the world's terrestrial biodiversity and provide key services to humanity including climate regulation, not to mention the livelihoods of ~1.6 billion people and well over 300 billion $ generated from annual trade of forest products (FAO, 2010). This lack of BEF research on tree systems is mostly due to practical constraints (Scherer-Lorenzen *et al.*, 2007).

Although early BEF focused on manipulations of species richness (SR) to assess diversity, strong effects of species composition and especially the presence or absence of specific functional traits put doubts on SR as the best predictor of EF (Chapin III *et al.*, 1997 ; Díaz et Cabido, 2001). To better understand the effect of components of diversity (i.e. functional diversity and identity) on EF and specifically test for underlying mechanisms such as complementarity (i.e. different niche occupation through functional diversity), a more systematic study of plant traits began.

Through concerted effort, trait syndromes (i.e. strong correlation in suites of traits) in leaves (Wright *et al.*, 2004) and stems (Chave *et al.*, 2009) have been described and ameliorated our understanding of interspecific trait variation. Due mostly to the inaccessibility of the rhizosphere, our knowledge and understanding of root trait variation lacks behind those of aboveground traits. In addition, intraspecific variation in roots proved more variable than for aboveground traits (Ryser, 2006) and more research is needed to test root plasticity along gradients of environmental gradients and age, especially in trees.

The general objectives of this doctoral thesis were to address some of the open research questions surrounding BEF in tree systems, particularly regarding niche complementarity and plant functional traits. Specifically, the objectives were:

1) to improve our understanding on fine root trait variation within and across tree species,
2) to develop an experimental design testing specifically for the effects of functional diversity and the existence of complementarity in tree communities, and
3) to evaluate how tree diversity affects aboveground productivity.

In the following, I will expand on the fundamental ecological paradigms underlying this doctoral thesis (i.e. biodiversity and ecosystem functioning research, niche complementarity and plant functional traits) before introducing the structure of the thesis and the three chapters.

Biodiversity Ecosystem Functioning – BEF

Global change with its many biotic (e.g. exotic species, changes in phenology, extinction) and abiotic facets (e.g. land fragmentation and habitat loss, changing biogeochemical cycles) increasingly manifests itself on the planet’s face (Vitousek *et al.*, 1997). At the end of the 20th century, the great concern about the unprecedented rate of species loss resulted in a concerted and systematic search for the effects of biodiversity on ecosystem functioning (Balvanera *et al.*, 2006). Publications on BEF increased exponentially between 1990 and 2007 and their proportion of the overall ecological literature has exceeded the average publication effort since 2003 (Caliman *et al.*, 2010). Early BEF research focused on annual plants species grown in microcosm (Naeem *et al.*, 1996) or in controlled field experiments (Tilman, Wedin et Knops, 1996) and examined above all the relationship between species richness and productivity (Hector *et al.*, 1999 ; Tilman, Wedin et Knops, 1996) and stability (Lavorel, 1999 ; Tilman et Downing, 1994). After almost two decades of species richness manipulative research, general consensus leaned toward increased productivity and stability with diversity (Hooper et al. 2005, Kinzig 2001). These findings as well as critique on those early BEF experiments (Naeem, 2002a) triggered more comprehensive approaches. Strong effects of species composition in addition to species richness for example led to studies including different metrics of biodiversity such as functional or phylogenetic diversity (Cadotte *et al.*, 2009). More recent studies also broadened the array of EF under examination such as decomposition (Hättenschwiler, Tiunov et Scheu, 2005) or N-cycling (Niklaus, Wardle et Tate, 2006). This was accompanied by an expansion towards other systems (aquatic, animal, microbial) and the consideration of multiple trophic levels (Bastian, Pearson et Boyero, 2008).

In a recent meta-analysis summarizing more than 500 independent manipulations of species richness spanning 30 biomes, diversity increased producer biomass in 86% of all cases (Cardinale *et al.*, 2011). However, most of these studies still originated from grasslands.

Although forests are usually mixtures of species and mixed forest plantations are not a new concept in forestry, some naturally occurring constraints aggravate a straight-on approach to BEF in tree systems:

i) In comparison to herbaceous systems, a direct manipulation at the producer level, i.e. trees, is obviously a more difficult and long-lasting task. Therefore, we still have to rely mostly on observational (including large-scale plantations), comparative studies rather than on experimental, manipulative experiments (Scherer-Lorenzen, Körner et Schulze, 2005 ; Zhang, Chen et Reich, 2012). However, the verification of a mixture effect is more difficult in observational studies due above all to the variety of confounding factors and the lack of appropriate control (e.g. monoculture yields or replication) (Burkhart et Tham, 1992).

ii) Forest landscapes, especially in temperate regions, have been subjected to heavy anthropogenic influence. Natural forests have nearly always been converted to structurally and compositionally more simplistic forests (Puettmann, Coates et Messier, 2008).

First evidence suggests that tree diversity positively affects nutrient cycling (Rothe et Binkley, 2001), decomposition (Hättenschwiler, Tiunov et Scheu, 2005), damage by insect pests (Jactel, Brockerhoff et Duelli, 2005), fungal pathogens (Pautasso, Holdenrieder et Stenlid, 2005) and animal (bird) diversity (Kissling, Field et Böhning-Gaese, 2008). In addition, reviews and meta-analysis regrouping around 100 studies in tree systems confirm a general trend of increased productivity with tree diversity (Nadrowski, Wirth et Scherer-Lorenzen, 2010 ; Zhang, Chen et Reich, 2012).

To explain these positive mixture effects in tree systems and beyond, two main mechanisms have been proposed: complementarity and selection effects.

Complementarity effects occur, when increased EF is due to increased resource exploitation through niche differentiation or facilitation. Selection effects ascribe greater EF to the dominance of species with particular traits (i.e. a very productive species in monoculture will have increased yield in mixture) (Loreau et Hector, 2001). Both mechanisms are fundamentally based on the concept of functional traits that link species to the role they play in the ecosystem. Functional traits are by definition “morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance” (Cardinale *et al.*, 2011) and it is now widely accepted, that trait changes at the organismal level influence processes at higher organizational levels and indeed, functional traits have been shown to be the key mechanism to drive ecosystem processes and services through direct biotic control or indirect abiotic controls such as the availability of limiting resources (Violle *et al.*, 2007). In addition, functional components of diversity have been shown to exhibit strong explanatory power in a variety of systems (Díaz et Cabido, 2001) and in tree systems in particular (Nadrowski, Wirth et Scherer-Lorenzen, 2010). However, only few studies and ongoing projects actually manipulate continuous measures of functional diversity (instead of functional groups) and specifically test for niche complementarity, especially in trees.

Niche Complementarity

Niche complementarity or complementary resource use hinges on the idea of niche partitioning and leads back to the fundamental conceptions of competition and species coexistence. Following the competitive exclusion principle (an idea held by some naturalists in the late 19th century but first comprehensively described by Gause, 1934b), two very similar species will hardly ever co-exist due to competition for a certain and limited amount of energy (resource). Grinnell concluded in the following that two co-existing species must thus not occupy the same niche (Grinnell, 1914) – a view that got widely accepted.

To quantitatively detect a positive mixture effect, the rate of the ecosystem function under examination (most commonly yield) in mixture has traditionally been compared to its values in monoculture of the same species as found in the mixture; i.e. for a positive mixture effect, the EF rate per area in mixture divided by the EF rate per area in monoculture must exceed one (“overyielding”). In agriculture, this method is known as the ‘land equivalent ratio’ (LER) (Vandermeer 1989), the identical measure derived from replacement studies is known as the ‘relative yield total’ (RYT) (de Wit 1960). As Loreau (1998) pointed out however, positive values for LER or RYT can have different underlying processes and it does not allow deducing complementarity. Loreau and Hector (2001) proposed an explicit approach to separate the two major proposed effects: selection and complementarity by using additive partitioning of the observed and expected yields. Both components are based on the relative yield approach mentioned above. In this way, complementarity effects are the product of the monoculture yields and the relative yields and include the hardly distinguishable niche differentiation and facilitative interactions. Selection effects are calculated as the covariance between monoculture yields and the relative yield. Although not formally acknowledged, the selection effects corresponds to the mass ratio hypothesis that holds that ecosystem functioning is greatly due to the traits of the dominating species (Grime, 1998). In this sense, selection effects and the mass ration hypothesis are based on functional identity whereas complementarity effects are based on functional diversity.

Both components have been shown to be at work in creating positive mixture effects (Cardinale *et al.*, 2011). There is however evidence for greater importance of complementarity in a variety of systems such as grasslands (Fargione *et al.*, 2007 ; Marquard *et al.*, 2009 ; Spehn *et al.*, 2005 ; Van Ruijven et Berendse, 2005), pot experiments (Jiang, Zhang et Wang, 2007 ; Lanta et Leps, 2006), agricultural systems (Trenbath, 1974) and shrublands (Montès *et al.*, 2008). In addition, it has been shown that the importance and dominance of complementarity increased with time (Allan *et al.*, 2011 ; Cardinale *et al.*, 2007 ; Fargione *et al.*, 2007 ; Reich *et al.*, 2012). Evidence from tree systems however is scarce. There is ample evidence for positive mixture effects, mostly calculated in terms of relative yield (i.e. “overyielding”), experimental examination of underlying mechanisms such as complementarity and selection effects has been attempted in only a few cases (Sapijanskas, Potvin et Loreau, 2013 ; Zeugin *et al.*, 2010). Theoretical evidence of strong complementarity in tree systems comes from modeling approaches (Morin *et al.*, 2011 ; Perot et Picard, 2012). Besides documented cases of facilitation in tree mixtures with nitrogen fixers acacias (Forrester, Bauhus et Cowie, 2005 ; Piotto, 2008), architectural complementarity in canopies has long and often been proposed as mechanism for positive mixture effects (Assmann, 1961 ; Erskine, Lamb et Bristow, 2006 ; Pretzsch et Schütze, 2009). There is need to experimentally test for complementarity and selection effects to better understand underlying mechanisms of positive mixture effects.

Plant Functional Traits

The utilization and classification of plants according to their traits has long been known to plant ecology, at least since Raunkiaer’s plant life-form classifications

(Raunkiaer, 1937). In the face of global change, much hope was put on attempts to generalize complex community dynamics and predict changes in ecosystem processes by assessing plant functional traits (PFT) instead of species identities (Lavorel *et al.*, 2007). A first approach was to reduce complexity by classifying species into functional effect groups (i.e. species with a similar effect on one or several ecosystem functions) and functional response groups (i.e. groups of species with a similar response to a particular environmental factor) (Lavorel *et al.*, 1997). However, hopes to find an easily accessible and functionally comprehensive classification scheme have been attenuated and the quest has largely remained an “elusive Holy Grail” (Lavorel *et al.*, 2007). The high intraspecific trait variation has proved scaling-up from individuals to vegetation assembly and ecosystem processes more challenging than expected (Lavorel *et al.*, 2007). Trait values and their correlations change for example along gradients of climate, disturbance (Díaz *et al.*, 1999), nutrient availability (Schellberg et Pontes, 2012), plant age (Niinemets, 2010) and neighborhood diversity (Burns et Strauss, 2012). In addition, effect and response traits cannot strictly be separated due to strong overlap (i.e. a trait can exert an effect on the community which in turn may change the trait itself as it responds to the changed environment) (Schellberg et Pontes, 2012).

However, information about PFT has increased (Lavorel *et al.*, 2007) and improved our understanding of their link to key processes such as plant economics at a global scale (Wright *et al.*, 2004). Due to trade-offs between traits based on whole plant integration, suites of co-varying traits have been grouped along axes of plant specialization and are surprisingly consistent over biomes and taxa (Díaz *et al.*, 2004 ; Reich *et al.*, 2003). Probably the best understood axis is based on trade-offs between leaf longevity and specific leaf area (SLA) including repercussions on nutrient resident time, plant growth rate and herbivory (Díaz *et al.*, 2004 ; Wright *et al.*, 2004). Along this axis, plants with low structural costs (high SLA) exhibit high photosynthetic rates, fast turnover and increased herbivory.

The Hidden Half

As leaves are the factories that produce energy for a trees' growth, roots are the railways that spread out into the rhizosphere (often more than 20 m) to deliver water and the essential nutrients (not to mention the myriad of mycorrhizal contractors and numerous volatile couriers). Though their physiological and ecological importance is well established, the understanding of their functional linkages lacks behind the knowledge on aboveground traits. The overwhelming complexity and the inaccessibility have hampered exhaustive root research resulting in knowledge gaps about belowground traits, their linkages to other below- and aboveground traits as well the functional role they play in ecosystem processes. Whereas coarse roots are responsible for anchorage, transport and storage, fine roots actively absorb nutrients and water and thus contribute largely to a trees' competitive ability and finally overall performance. Consequently, understanding their functional role is essential to assess a trees' competitive ability the effects of their diversity on overall ecosystem processes.

First evidence suggests the possible existence of co-varying traits along economic axes similar to aboveground traits. Plant fine roots of higher diameter are usually associated with roots of low specific root length, low nitrogen and high lignin content (Comas et Eissenstat, 2004 ; Comas et Eissenstat, 2009 ; Craine *et al.*, 2001 ; Craine et Lee, 2003). This syndrome has been associated with slow growing species and growth-limiting conditions (Comas, Bouma et Eissenstat, 2002 ; Comas et Eissenstat, 2004 ; Reich *et al.*, 1998). However, studies and thus study conditions are limited and root responses to environmental conditions such as nutrient supply are highly variable (Ryser, 2006). A part of the reason of these inconsistencies may be explained by the greater belowground compared to aboveground heterogeneity and the multiple stresses plant roots experience that may shift trade-offs within root traits. On the other hand, responses of specific root length (SRL), probably the most studied fine root trait, have been shown to significantly change with type of fertilization, sampling method and size of the root sample (Ostonen *et al.*, 2007). In addition, most of root studies are conducted on non-woody plants, in pot experiments and on seedlings (Zobel, Kinraide et Baligar, 2007). More studies examining interspecific root variation as well as intraspecific root plasticity along natural environmental gradients (i.e. reflecting the multiple stresses in natural habitat) are needed to better understand

In addition, increased focus on phenotypic plasticity (PI, proportion of total variation due to changes in the environment) for above and belowground PFT may help choose traits better suited to predict responses (i.e. high PI) or effects (i.e. low PI).

Thesis plan

The thesis is divided into three chapters, each treating specific aspects of the above-mentioned objectives.

The first chapter uses two datasets of tree fine root traits – one from a common garden experiment and one from natural forests. The first dataset included 12 North American temperate tree species and was used to describe the interspecific correlations between three fine root traits: diameter, specific root length and branching intensity. This part of the study specifically tested for the existence of belowground trait syndromes and their link to aboveground life-strategies such as relative growth rate. The second dataset examined the same three fine root traits in four North American temperate tree species co-occurring on different soil conditions in natural temperate deciduous forests near Montreal, Canada. Here, intraspecific trait variation in relation to changes in ontogeny (i.e. juveniles and mature trees) and soil conditions (i.e. plasticity) was examined.

The second chapter reviews and synthesizes current knowledge surrounding the paradigm of biodiversity and ecosystem functioning (BEF) in tree systems and beyond. After identification of open research questions within the BEF paradigm, the second chapter proposes an experimental design addressing those gaps. This experimental design is the foundation of the International Diversity Experiment Network with Trees (IDENT) regrouping experimental sites in Europe and North America that all share the quest of examining the effect of functional diversity on ecosystem functioning.

The third chapter describes the results of the IDENT Montreal. The experimental design followed the approach developed in chapter two and was the first site within IDENT to being established in 2009. High-density tree communities that vary in functional diversity, independent of species richness were used to specifically test for the effect of those two metrics of diversity on productivity while separating their respective contributions. This chapter also specifically tested for the existence of complementarity in young tree communities.

CHAPTER I

INTERSPECIFIC COORDINATION AND INTRASPECIFIC PLASTICITY OF FINE ROOT TRAITS IN NORTH AMERICAN TEMPERATE TREE SPECIES

Abstract

Fine roots play an important role in nutrient and water absorption and hence overall tree performance. However, current understanding of the ecological role of belowground traits lags considerably behind those of aboveground traits. In this study, we used data on specific root length (SRL), fine root diameter (D) and branching intensity (BI) of two datasets to examine interspecific trait coordination as well as intraspecific trait variation across ontogenetic stage and soil conditions (i.e. plasticity). The first dataset included saplings of twelve North American temperate tree species grown in monocultures in a common garden experiment to examine interspecific trait coordination. The second dataset included adult and juvenile individuals of four species (present in both datasets) co-occurring in natural forests on contrasting soils (i.e. humid organic, mesic and xeric podzolic). The three fine root traits investigated were strongly coordinated, with high SRL being related to low D and high BI. Fine root traits and aboveground life-strategies (i.e. relative growth rate) were weakly coordinated and never significant. Intraspecific responses to changes in ontogenetic stage or soil conditions were trait dependent. SRL was significantly higher in juveniles compared to adults for *A. balsamea* and *A. rubrum*, but did not vary with soil condition. BI did not vary significantly with either ontogeny or soil conditions, while D was generally significantly lower in juveniles and higher in humid organic soils. D also had the least total variability most of which was due to changes in the environment (plasticity). This study brings support for the emerging evidence for interspecific root trait coordination in trees. It also indicates that intraspecific responses to both ontogeny and soil conditions are trait dependent and less concerted. D appears to be a better indicator of environmental change than SRL and BI.

Keywords : Specific root length, fine root diameter, branching intensity, tree fine roots, phenotypic plasticity, functional traits

Introduction

The search to understand the effects of species on ecosystem functioning has brought forward the functional role of various traits. Functional traits have been shown to link species to the roles they play in the ecosystem. Through changes at the organismal level they not only influence individual performance but also higher organizational levels and hence drive ecosystem processes and services (Díaz *et al.*, 2004 ; Garnier *et al.*, 2004). However, we know much more about aboveground traits, their coordination, phenotypic plasticity and linkages to ecosystem functioning than we know about belowground traits.

Although the physiological and ecological importance of roots is well established, the great variability of root systems, the small and varied size of fine roots and the relative inaccessibility of the belowground realm have all hampered exhaustive root research. In addition, the lack of consensus about how to classify and measure fine roots has constrained the development of a unified framework towards a root economics spectrum as was achieved for both leaves (Wright *et al.*, 2004) and wood (Chave *et al.*, 2009) traits. Fine roots have traditionally been distinguished from coarser roots using various diameter classes of arbitrary width, with 2mm being the most common threshold (Guo *et al.*, 2008 ; Hishi, 2007 ; Pregitzer *et al.*, 2002). Consequently, fine root samples of different or even the same species may include varying numbers of root orders. Fine root traits such as specific root length, diameter, root length density as well as nitrogen, lignin, non-structural carbohydrate and cellulose concentrations have been found to systematically change with root order (Guo, Mitchell et Hendricks, 2004 ; Pregitzer *et al.*, 2002 ; Wang *et al.*, 2006). Such morphological and physical changes with root order translate into potentially large differences in functional properties such as water uptake (Rewald, Ephrath et Rachmilevitch, 2011) , respiration (Jia *et al.*, 2011) or fine root mortality (Wells, Glenn et Eissenstat, 2002). More recently, a functional classification approach based on root orders has been applied (Guo *et al.*, 2008 ; Rewald, Ephrath et Rachmilevitch, 2011). In tree roots, a first order root would usually be the smallest (i.e. shortest) segment, which would be attached to a second order branch and so forth (Fitter, 2002). Although this approach attempts to control for confounding factors, comparisons across studies are restricted due to varying numbers of root orders included (see for example Alvarez-Uria et Körner, 2011 ; Chen *et al.*, 2013 ; Comas et Eissenstat, 2009 ; Yu *et al.*, 2007).

Above- and belowground organs share many functions, such as nutrient acquisition and transfer. Some functional coordination between above and belowground traits is therefore expected (Westoby et Wright, 2006). Despite examples of strong coordination in some traits and ecosystems (Craine *et al.*, 2001 ; Reich *et al.*, 1998 ; Tjoelker *et al.*, 2005), results remain inconsistent (Chen *et al.*, 2013 ; Freschet *et al.*, 2010 ; Westoby et Wright, 2006).

Apart from mean trait values used to coordinate and characterize species, trait plasticity has gained momentum as a driver of individual fitness and consequently, community dynamics. Evidence is accumulating that through changes in realized niches, trait plasticity can be linked to a species' competitive ability and hence overall fitness (Berg and Ellers, 2010). Due to higher spatial and temporal variability of resources belowground, phenotypic plasticity (i.e. plasticity due to environmental changes) is expected to be greater for below- than aboveground traits. There is also evidence of drastic ontogenetic changes in trait values (Cornelissen et al., 2003) that should be more pronounced in long living organisms such as trees. However, only little information about root acclimations to changes in the environment or in ontogeny is available, especially for trees. In addition, much of our knowledge about plant root function is based on seedling responses (Zobel et al., 2007) and on experiments conducted in pots or containers.

Probably the most studied fine root trait is specific root length (SRL), the ratio between root length and weight (Zobel, Kinraide et Baligar, 2007). Much like the well-known specific leaf area (SLA) for leaves, SRL is thought to describe the economical aspect of a root by weighing the costs (weight) per potential return (length) (Ryser, 2006). Under the assumption that investment in carbon per unit length should be minimized to exploit a larger volume of soil, SRL is expected to be highly plastic and increase under nutrient limitation. Despite examples confirming the assumption (see Ostonen *et al.*, 2007 for a meta-analysis), increases in SRL with increasing nutrient supply as well as no response to changes in nutrient supply have been reported (see Ryser, 2006 for a summary), with equally variable responses to changes in soil water (Bakker *et al.*, 2009 ; Cortina *et al.*, 2008 ; Ostonen *et al.*, 2007).

Through its link to surface area and volume, fine root diameter (D) is an important trait directly linked to nutrient and water absorption. Although D has been shown to be plastic and strongly dependent on nutrient supply (Eissenstat *et al.*, 2000), it is rarely a focus of fine root research except as average diameter (Zobel, Kinraide et Baligar, 2007). Research on the response of D to nutrient concentrations showed species specific responses with increases and decreases possibly depending on nutrient, species and their interaction (Zobel, Kinraide et Baligar, 2007).

Lastly, branching intensity (BI, also called root tip density) is a fine root trait describing the topology of fine roots by counting the number of tips per unit root length. Changes in BI to environmental factors have been assessed in only a handful of studies, with contrasting results (Ahlström, Persson et Börjesson, 1988 ; George *et al.*, 1997 ; Kakei et Clifford, 2002).

In the present study, we examined interspecific (coordination) and intraspecific variation across contrasting soil conditions (i.e. plasticity) as well as with ontogenetic stages (i.e. adults versus juveniles) for SRL, D and BI. A first dataset ("common garden", CG), including twelve North American temperate tree species grown in a common garden experiment was used to examine trait variation across species. We tested the hypotheses that under uniform controlled conditions:

1) SRL, BI and D are strongly coordinated across species of wide variation in root morphology; and

2) Belowground fine root traits are correlated to whole-plant life-strategies, such as relative growth rate.

A second dataset ("natural forest", NF) of four tree species (also present in the CG dataset) that included adults and juveniles co-occurring on contrasting soil conditions in natural forests was employed to examine trait variation in relation to species, ontogeny and soil conditions. More specifically, we tested the hypotheses that:

1) SRL and BI are greater and D smaller in juvenile compared to adult trees;

2) SRL and BI generally increase while D decreases with decreasing soil moisture and nutrient content;

3) Phenotypic plasticity is greater in fine root traits that are more strongly associated with resource uptake (i.e. SRL and D).

Materials and Methods

Common garden dataset – CG

Study site

The study site for the first dataset was located at Ste-Anne-de-Bellevue, near Montreal, Québec, Canada (45˚26’N, Long 73˚56’W, 39 m.s.l). Mean annual temperature is 6.2 ºC with a mean annual precipitation of 963 mm (climate.weatheroffice.gc.ca). On this former agricultural field that has been managed for several decades (Marc Samoisette, personal communication, October 2011), monocultures of twelve North American temperate forest species were established in spring 2009 with seedlings of one (broadleaf) or two (conifer) years of age. These monocultures are part of an ongoing experiment on biodiversity and ecosystem functioning with trees (Tobner *et al.*, 2013). Within the objectives of this biodiversity experiment, the twelve species were selected to cover a wide range of functional traits, including angio- and gymnosperms, and early and late successional species: *Acer saccharum* Marsh., *Acer rubrum* L., *Betula alleghaniensis* Britton, *Betula papyrifera* Marsh. and *Quercus rubra* L. as well as seven conifers: *Abies balsamea* (L.) Mill., *Larix laricina* (Du Roi) K. Koch, *Pinus strobus* L., *Pinus resinosa* Aiton, *Picea glauca* (Moench) Voss, *Picea rubens* Sarg. and *Thuja occidentalis* L. Each species was planted in a square plot of eight by eight individuals (50 x 50cm). Plots were replicated four times within an area of ~ 0.6 ha. Plots were weeded manually and a fence was installed to protect against ungulate herbivory.

Common garden trait measurements

Traits were measured in September 2011. From each plot, two individuals were selected that were growing in the outer rows (to minimize impacts on the ongoing experiment). This was repeated for each of the four replicate blocks blocs resulting in eight individuals sampled per species. Following the main axis (i.e. stem), a root that grew towards the inside of the plot was detected and followed until it branched off into roots < 2mm. Roots were then excavated and placed in a cooler for transport. Roots were then stored at 4ºC until processing that occurred no later than two weeks after sampling.

Roots were carefully washed and separated into segments of the first three orders. This classification approach (i.e. 1st to 3rd order roots) was chosen following Guo et al. (2008). Root samples were then scanned for subsequent image analysis (Winrhizo, Regent software, Québec). Total root length, average diameter and number of root tips were measured for each sample. Finally, root samples were oven-dried at 65 °C and weighed to calculate SRL (m g^{-1}). Relative growth rate (RGR) was calculated based on volume ([trunk diameter at 5 cm]^2 x total tree height): RGR = (log vol fall 2011- log vol spring 2009) / 3 growth periods (i.e. vegetation periods 2009 through 2011).

Natural Forest dataset – NF

Study site

The study site for the second dataset was situated at the Station de biologie des Laurentides of Université de Montréal in St-Hippolyte, Québec, Canada (Lat 45˚59'N, Long 73˚59'W, 366 m.s.l.). The research station consists of an area of about 16 km^2 of forest and lakes dedicated to research and has been protected from other human activities since 1963. Birch (*Betula papyrifera* and *Betula alleghaniensis*) and maple (*Acer saccharum* and *Acer rubrum*) communities are the dominating forest types covering more than 60% of the land surface in terms of canopy cover (Savage, 2001). Mean annual temperature is 3.9 ºC with a mean annual precipitation of 1164 mm (climate.weatheroffice.gc.ca).

Four forest species, also present in the CG dataset, co-occur in the forests of the research station on contrasting soil conditions: *Acer rubrum*, *Betula papyrifera*, *Abies balsamea* and *Thuja occidentalis*. Species were selected to include a broad spectrum of phylogeny and different life strategies (growth rate, life span, type of mycorrhization, etc.). We identified three different soil conditions where the studied species occur:

- Humisols with standing water level between 10 to 20 cm belowground and *T. occidentalis* as the dominant species, hereafter referred to as "humid organic",
- Orthic humoferric podzols (Courchesne et Hendershot, 1989)(Courchesne and Hendershot, 1989, personal communication Courchesne, March 2011) on slopes of 28 to 46 degrees and strong water runoff with *T. occidentalis* as the dominant species, hereafter referred to as "xeric podzol" and
- Orthic humoferric podzols with good drainage, nil to very gentle slope and *B. papyrifera* as the dominant species, hereafter referred to as "mesic podzol".

For each soil type, three plots covering at least 200 m^2 were established. Plots were located under closed canopy, with no recent sign of perturbation and at least four adult and four juvenile individuals of the target species. Exceptions were *T. occidentalis* that never occurred on mesic podzols and *B. papyrifera*, for which no juvenile individuals were found, as this species does not regenerate under closed canopies. Juveniles were defined as tree saplings between 25 and 100 cm in height and adult trees were defined as trees with a diameter at 1.3 m (DBH) > 10 cm.

Table 1. Soil and stand characteristics of the three soil conditions for the Natural Forest Dataset. Given are means ± sd of three sites per soil condition (HO - humid organic, MP - mesic podzol and XP - xeric podzol). CEC-cation exchange capacity, BS-base saturation.

	Soil moisture (%)	ppH	CEC (cmol kg^{-1})	BS%	Basal area (m^2 ha^{-1})				
					Abies balsamea	*Thuja occidentalis*	*Acer rubrum*	*Betula papyrifera*	others
HO	85.2 ±1.8	4.88 ±1.1	1.9 ±1.1	5.9 ±3.4	5.9 ± 2	14.85 ± 2.6	7.1 ± 0.4	6.3 ± 3.5	8.0 ± 4.2
MP	30.7 ±3.0	5.05 ±0.0	0.6 ±0.2	9.9 ±16.2	7.2 ± 3.0		4.7 ± 0.4	23 ± 14.1	9.95 ± 5.6
XP	19.2 ±7.2	4.70 ±0.3	0.5 ±0.1	9.1 ±4.7	6.0 ± 3.4	10.1 ± 5.6	4.0 ± 2.9	6.7 ± 3.0	11.6 ± 4.0

Soil characterization

At the center of each plot, one soil sample was taken at 20 cm depth on August 22, 2011. The average daily temperature in the two weeks preceding soil sampling was 17.5 °C. Precipitation for the same period amounted to 46 mm distributed over 6 days with 15 mm being the strongest precipitation event for one day.

Soil samples were placed in resealable plastic bags and immediately stored at -18 °C before further processing that occurred no later than one week after collection. Samples were then oven-dried at 65 °C until they reached constant weight and sieved through a 2 mm mesh prior to soil analyses. Soil moisture was the difference in sample weight before and after drying. Soil pH was measured in water in a ratio of one part soil (10 mg) to two parts water for mineral soil and one part soil (4 mg) to five parts water for organic soils (Canadian Society of Soil Sciences, 2007). Cation exchange capacity (CEC) and base saturation (BS%) were assessed through dissolving soil samples in barium chloride solution and atomic spectroscopy (Canadian Society of Soil Sciences, 2007) (Table 1.1).

Natural Forest Trait Measurements

On each plot, species and DBH of all adult trees (i.e. DBH > 10 cm) were recorded to calculate basal area (Table 1.1). Adult trees of the site are usually not older than 90 years as the last high-intensity fire passed through the research area around 1923 (Savage, 2001).

For the four target species, at least four adult and four juvenile individuals were sampled (i.e. total of 12 adults and 12 juveniles per soil condition). For each adult tree, two root samples were collected in opposite directions from each other. From the stem, roots were excavated and followed until they branched off into fine roots (< 2 mm diameter). Roots of adult individuals were excavated from the mineral or organic soil horizons, never from the humus or litter layers. Furthermore, for each adult individual, at least three of the highest branches were harvested with the help of a professional tree climber to obtain sun leaves. For juveniles, the entire plant was excavated for root samples and at least three leaves or 20 needles were collected.

Leaf and root samples were immediately put into sealed plastic bags, labeled and stored at about 4ºC until further processing, occurring no later than six weeks after sampling. For each individual, three to five leaves were punched with a hollow metal pin, yielding leaf samples of a standard surface area. A minimum of 20 needles of the previous year of growth were plucked off the branch and scanned. Samples were then oven-dried to constant weight to calculate SLA (foliage area/foliage weight, mm mg^{-1}).

Root samples (<2 mm) of each individual were carefully washed and scanned and analyzed in an identical fashion to the CG dataset. Once the complete sample was scanned, parts of the image containing first to third order roots were selected and re-analyzed. For these subsamples, average diameter, total length and number of tips were calculated. In addition, root diameter was assessed following the handbook of trait measurements (Cornelissen *et al.*, 2003), on first order roots, after the root hair zone (i.e. after tapering).

Hereafter for both datasets, traits measured on complete root samples (roots < 2mm) are noted using the subscript “c” (e.g. D_c), while results for fine roots defined as first to third order roots are noted with subscript “3” (e.g. D_3). Diameter measured on first order roots is noted as “D_1”.

Phenotypic plasticity

The total phenotypic variability of a population is the result of genetic and environmental sources and their interaction (Hartl et Clark, 1997 ; Whitman et Agrawal, 2009). To quantify the total variability of a trait we employed the coefficient of variance (CV), i.e. the standard deviation divided by the mean.

In a second step, for each trait and species we calculated an index of the variability, which is due solely to variation in the environment, the phenotypic plasticity index (PI). Determining the contribution of the environmental source of variability is essential in assessing a population's potential to adapt to heterogeneous or changing environments (Byers, 2008). The ability of a genotype to express different phenotypic values for a given trait under different environmental conditions, the phenotypic plasticity (Valladares, Sanchez-Gomez et Zavala, 2006), is strongly linked to individual fitness (Bell et Galloway, 2007 ; Nicotra et Davidson, 2010) and hence population demographics as it can generate novelty and facilitate evolution (Draghi et Whitlock, 2012). Phenotypic plasticity has gained increasing interest with the necessity to predict species responses to global change (Matesanz, Gianoli et Valladares, 2010 ; Richter *et al.*, 2012) . Several metrics have been proposed to assess this environmental source of variability (Valladares, Sanchez-Gomez et Zavala, 2006). In the present study, we employed the phenotypic plasticity index (PI), a metric recommended to explore functionally related traits. PI is based on maximum and minimum trait means across environmental conditions and was calculated for every trait and species as:

[max(trait mean among soil conditions) – min(trait mean among soil conditions)] / max[trait mean among soil conditions] (Valladares, Sanchez-Gomez et Zavala, 2006).

Finally, to compare the phenotypic plasticity with the overall phenotypic variability, we computed a ratio of PI to CV (PI:CV) as an expression of how much of the overall phenotypic variability is due to plastic responses to the environment. Both CV and PI vary between zero and one. Hence, a PI:CV of zero would indicate no environmental source of variability, whereas a PI:CV of one would indicate that the overall phenotypic variability is completely due to acclimations to the environment. Although the literature on trait variation and plasticity is rich, we are not aware of other studies using PI:CV to explore differences in relative plasticity between species and traits.

Data analysis

For both datasets, traits were tested for normality with the Shapiro test and transformations were applied where needed to correct for deviations. To test for species differences within the CG dataset, a one-way ANOVA with subsequent Tukey HSD test was performed. Trait correlations were assessed using the Pearson correlation coefficient. To test for effects of soil condition and ontogenetic stage on fine root traits in the NF dataset, linear mixed effect models (REML) with site (random effect) as well as the interaction of plot and ontogenetic stage nested within soil condition were applied for each species. The asymptotic inference test for coefficients of variation as described in Miller and Feltz (1997) was used to test for differences in CV as well as PI:CV between traits and species. Subsequent Dunn-Sidak correction (Šidák, 1967) were applied to correct alpha levels for multiple comparisons. To test for differences in PI, resampling methods were applied to create populations per species, ontogenetic stage and trait (N = 999). Data were then analyzed using ANOVA models to test for effects of trait and species.

Results

Interspecific trait coordination (CG)

In the common garden, fine root traits were highly coordinated across species, especially SRL_3 and D_3 (Table 1.2). SRL_3 increased with BI_3 and decreased with D_3. Consequently, BI_3 was negatively correlated with D_3. Correlations between fine root traits and whole plant strategies such as RGR were much weaker and never significant (Table 1.2). In general, conifers showed greater D_3, lower SRL_3, and BI_3 (Table 1.3).

Table 2. Correlation matrix for functional traits of 12 North American temperate forest species grown in a common garden. Traits include belowground specific root length (SRL), diameter (D) and branching intensity (BI) as well as whole-plant life-strategy measures (i.e., relative growth rate – RGR). Fine root traits were measured on first three root orders (subscript “3”). Significant correlations appear in bold type ($P<0.001$ in all cases).

	D_3	SRL_3	BI_3
SRL_3	**0.83**		
BI_3	**0.64**	**0.66**	
RGR	0.05	0.07	0.07

Table 3. Mean trait values for 12 North-American temperate forest species grown in a common garden. Traits include belowground specific root length (SRL), diameter (D) and branching intensity (BI) as well as whole-plant life-strategy measures (i.e., relative growth rate—RGR). Fine root traits were measured on first three root orders (subscript “3”). Different letters indicate significant differences between species. Angiosperms are underlined in gray.

Species	D_3	SRL_3	BI_3	RGR
Thuja occidentalis	0.57^{A}	13.9^{F}	1.2^{F}	0.79^{BC}
Pinus strobus	0.56^{AB}	16.1^{F}	3.2^{BCD}	0.70^{CD}
Abies balsamea	0.45^{BC}	23.9^{EF}	1.9^{EF}	0.59^{DE}
Larix laricina	0.38^{CD}	41.3^{DE}	2.8^{DE}	0.88^{AB}
Pinus resinosa	0.37^{CD}	39.5^{DE}	3.9^{D}	0.69^{CD}
Acer rubrum	0.35^{DE}	64.5^{ABC}	3.1^{CD}	0.75^{BC}
Acer saccharum	0.33^{DEF}	57.8^{BCD}	2.7^{DE}	0.67^{CD}
Picea glauca	0.33	48.3^{CD}	3.1^{CD}	0.59^{DE}
Betula alleghaniensis	0.28^{EFG}	90.3^{A}	4.0^{AB}	0.74^{C}
Quercus rubra	0.27^{FG}	71.9^{ABC}	4.6^{A}	0.68^{CD}
Picea rubens	0.27^{FG}	68.3^{ABC}	2.9^{ABC}	0.49^{E}
Betula papyrifera	0.26^{G}	74.0^{AB}	4.5^{A}	0.94^{A}

Intraspecific trait variation across ontogenetic stages and contrasting soil conditions (NF)

In the natural forest, fine root diameter in woody (i.e. D_c and D_3) as well as non-woody roots (i.e. D_1) was generally greater in humid organic than in mesic and xeric podzol conditions. However, differences were only significant for *A. balsamea* and *T. occidentalis* (Tables 1.4 and 1.5). D was also significantly lower for juveniles compared to adults in all three species (Tables 1.4, 1.5 and Fig. 1.1). While differences for *A. rubrum* were consistent across fine root classification (i.e. size versus functional) for *T. occidentalis* differences were only significant for the two functional classifications of fine roots (i.e. D_3 and D_1), and for *A. balsamea* there only were significant differences in non-woody roots (i.e. D_1, Tables 1.4 and 1.5).

Table 4. P-values for fixed effects (soil condition and ontogenetic stage - OS) of linear mixed models (REML) and their interactions on functional traits of four North-American temperate forest species (NF dataset). Traits include belowground specific root length (SRL), diameter (D) and branching intensity (BI) as well as aboveground specific leaf area (SLA). Fine root traits were measured on roots < 2mm (subscript ‘c’), first three root orders (subscript ‘3’) or first order roots only (subscript ‘1’).

		Diameter			SRL_c	Branching intensity		SLA
		D_c	D_3	D_1		BI_c	BI_3	
Abies balsamea	Soil	**0.03***	0.07•	**<0.01****	0.95	0.67	0.17	0.47
	OS	0.12	0.30	**0.03***	**0.01***	0.58	0.44	**<0.01****
	Soil+OS	0.72	0.43	0.20	0.71	0.98	0.96	0.34
Thuja occidentalis	Soil	0.09•	**0.02***	**0.03***	0.22	0.77	0.60	0.66
	OS	0.09•	**0.02***	**<0.01****	0.72	0.21	0.71	**<0.01****
	Soil+OS	0.71	0.95	0.67	0.51	0.66	0.59	0.42
Acer rubrum	Soil	0.13	0.76	0.14	0.55	0.11	0.10	0.09•
	OS	**0.04***	**0.04***	**<0.01****	**0.02***	0.63	0.13	**<0.01****
	Soil+OS	0.99	0.33	0.53	0.75	0.33	0.47	**0.04***
Betula papyrifera[1]	Soil	0.15	0.54	0.10	0.15	0.50	0.65	0.77

Significant effects are annotated as ‘**’ for $P < 0.01$, ‘*’ for $P < 0.05$ and ‘•’ for $P < 0.1$

[1] No *B. papyrifera* juveniles were found in the NF plots

SRL_c never varied significantly across soil conditions but was significantly greater for juveniles compared to adults in *A. balsamea* and *A. rubrum*. For juveniles of *T. occidentalis,* SRL_c was smaller as well, but it did not vary significantly (Tables 1.4, 1.5 and Fig. 1.1). Conversely, BI_c never varied significantly across soil conditions or ontogenetic stage (Tables 1.4 and 1.5).

PI was greatest in D_c except for *B. papyrifera* adults and *A. rubrum* juveniles. PI for SRL_c and BI_c was more variable and depended on species (Fig 1.2). The amount of total trait variability (CV), tended to be significantly higher in SRL_c and BI_c, compared to D_c (Fig 1.2). Consequently, D_c was also the trait with the highest PI:CV.

As expected, SLA was significantly higher in shade-grown leaves of juveniles compared to sun leaves of adults (Table 1.4). SLA did not vary significantly with soil conditions. The significant interaction term of soil condition and ontogenetic stage for *A. rubrum* is due to a slightly higher SLA for juveniles in mesic conditions (Table 1.4). When analyzed by species and ontogenetic stage, no significant correlation was found between SLA and SRL (data not shown).

Although fine root classification based on root orders did not uniformly reduce variation (i.e. CV) compared to fine root classification based on size (Table 1.5), in some cases, it helped detect treatment differences (e.g. D_c to D_3 for *T. occidentalis,* Tables 1.4 and 1.5).

Discussion

Interspecific trait coordination

The observed belowground trait correlations across various taxa indicate strong coordination among fine root morphological traits supporting the idea of a generalized tree root syndrome (Holdaway *et al.*, 2011).

As root diameter and root mass density constitute the two components of SRL, the strong negative correlation between SRL and D was expected (Chen *et al.*, 2013 ; Comas et Eissenstat, 2009 ; Fahey et Hughes, 1994). Branching patterns were found to negatively correlate with D when measured as BI (i.e. number of root tips divided by root length, Comas et Eissenstat, 2009) or as branching ratio (number of root tips divided by number of second order roots, Chen *et al.*, 2013) and positively with SRL (Comas et Eissenstat, 2009). As shown by Comas and Eissenstat (2009), there is a possible link between BI and mycorrhization that may in turn determine internal cell structure (e.g. layers of root cortex) and hence D and SRL.

Although evidence is still sketchy, root syndromes are based on a trade-off between life-history strategies (e.g. RGR) and tissue longevity. Thus, roots with high SRL, thin D and low tissue density are generally associated with greater root proliferation, greater RGR and shorter overall longevity (Eissenstat, 1992 ; Wright et Westoby, 1999). In previous studies, growth rates of juvenile and adult trees have been linked to root traits with fast-growing species showing higher SRL (Comas, Bouma et Eissenstat, 2002 ; Comas et Eissenstat, 2004 ; Reich *et al.*, 1998), smaller root diameter and greater degree of branching (Comas, Bouma et Eissenstat, 2002 note that for these papers, results are for phylogenetically constrained contrasts ; Comas et Eissenstat, 2004)). Other studies documented no or even negative relationships between SRL and SLA or RGR in grasslands (Kembel et Cahill, 2011 ; Laughlin *et al.*, 2010 ; Poorter et Remkes, 1990) and trees (with phylogenetic independent contrasts, Chen et al. 2013).

In the present study, no significant relationships were found between fine root traits and RGR based on volume, height or diameter (only volume is reported). Here, the two species with highest SRL were also the species with the highest and lowest RGR (*B. papyrifera* and *P. rubens*, respectively). The study site for the common garden experiment has been intensively cultivated for decades. Nutrient availability can be assumed to be abundant. Interestingly, the four species occurring in both datasets have markedly higher SRL (less so for *T. occidentalis*) in the common garden site, compared to the nutrient poorer natural forest, confuting the often-assumed increase in SRL with nutrient limitation. This indicates that in nutrient abundant habitat, SRL may not be a trait of primary importance for plant growth.

Trait variation between ontogenetic stages

Trait responses to ontogenetic stage were trait dependent. Similar trends of decreasing SRL with age as shown in our study have been reported in the literature for Japanese cedar (*C. japonica*) (Fujimaki, Tateno et Tokuchi, 2007), silver birch (*B. pendula*) (Rosenvald *et al.*, 2013), European spruce (*P. abies*) and Turkey oak (*Q. cerris*) (Claus et George, 2005) or in a comparison of laboratory-grown seedlings to field-grown adult trees of six temperate North American tree species (Comas and Eissenstat, 2004). D was also found to increase with tree age (Jagodziński et Kałucka, 2010 ; Rosenvald *et al.*, 2013).

Two possible mechanisms may explain differences in root morphology with age. On the one hand, higher SRL and lower D in juveniles could be an artifact of differences in root orders measured as it is likely that juvenile root samples < 2mm contain fewer root orders than their conspecific adults. For a multitude of species, SRL and D have been shown to significantly change with root order (Pregitzer *et al.*, 2002 ; Wang *et al.*, 2006). However, when controlling for root orders in both adults and juveniles, SRL was still higher in juveniles compared to adult trees (Comas et Eissenstat, 2004 ; Rosenvald *et al.*, 2013).

It appears thus more likely, that the observed changes in root morphology with ontogenetic stage may be an adaptation to rooting depth. In most of the above-mentioned studies examining the effect of tree age on root morphology, including the present study, soil depth was not accounted for. However, changes in SRL and diameter with soil depth have been reported in other studies (Makita *et al.*, 2011 ; Wang *et al.*, 2006). In the present study, root samples for adult trees were collected in the mineral horizons (often below 10 cm soil depth) while the entire root system of juveniles often did not exceed 10 cm soil depth. Furthermore, juveniles were frequently found on or near rotting logs. Increased SRL and lower D of juveniles could thus be an acclimation to shallow soil depth and possible higher nutrient availability. This is congruent with the assumption that species experiencing large shifts in height and therefore environmental conditions while maturing should experience corresponding shifts in traits (Grime, 2001 ; Smilauerova et Smilauer, 2007).

It was surprising that BI never changed significantly with ontogenetic stage. In fact, BI also never changed significantly with soil condition, pointing towards a rather conservative trait and fine root topology.

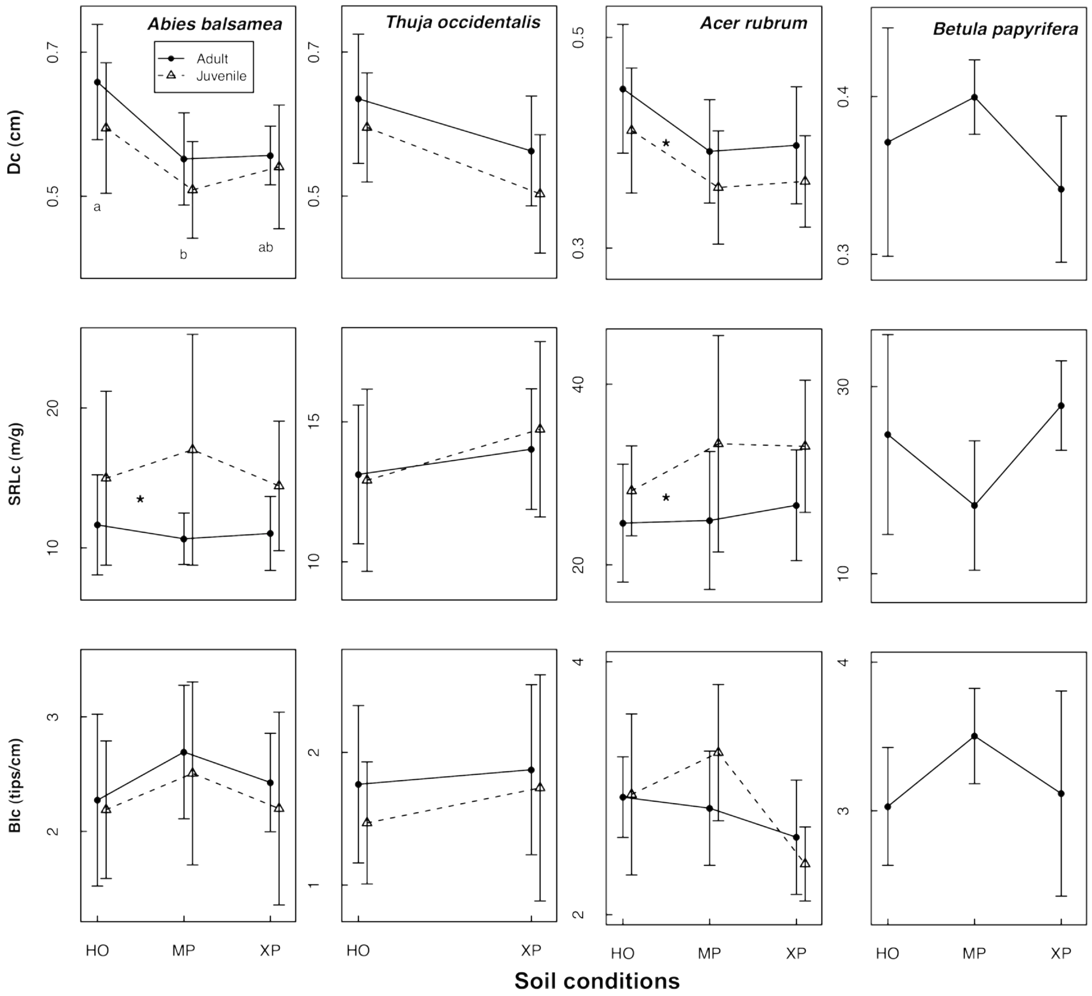

Figure 1. Mean ± standard deviation for three fine root traits along a gradient of soil conditions (NF dataset). Traits are measured on roots < 2mm: specific root length (SRLc), branching intensity (BIc) and fine root diameter (Dc). Soil conditions were identified as HO – humid organic, MP – mesic podzol and XP – xeric podzol. Different letters indicate significant differences between soil conditions; asterisks indicate significant differences between adults (solid line) and juveniles (dashed line) (for $P < 0.05$).

Trait plasticity across soil conditions

As shown above with ontogenetic stages, fine root responses to soil conditions were also trait specific. Despite the large gradient in soil nutrients and water (Table 1.1), SRL and BI never varied significantly across soil conditions for the four target tree species; only D tended to be greater in humid organic soils.

SRL has been studied extensively and it was often associated with root proliferation in response to nutrient heterogeneity (Hodge, 2004). For trees, SRL has even been described as a successful indicator of nutrient availability (Ostonen *et al.*, 2007). Empirical responses of SRL to increases in nutrients have been mixed however (Ryser, 2006). Initially, it was proposed that under growth limiting conditions, SRL should be greater (and D smaller) in order to decrease construction costs and invest in greater soil exploitation (Ryser, 2006). And indeed, decreases in SRL with nutrients have been documented (Ostonen *et al.*, 2007 ; Trubat, Cortina et Vilagrosa, 2006). However, positive (Majdi et Viebke, 2004 ; Yu *et al.*, 2007) or non-significant (George *et al.*, 1997 ; Mei *et al.*, 2010) responses of SRL to nutrients have been documented as well. Despite advances in root research, responses of SRL to nutrient availability still appear somewhat “mysterious” (Ryser, 2006) and SRL has been shown to vary significantly with type of fertilizer, sampling method (i.e. pot, soil coring or ingrowth core) and root diameter class sampled (i.e. 0-1 mm, < 2 mm, etc.) (Ostonen *et al.*, 2007).

As mentioned earlier, SRL has two components: diameter and root mass density. While SRL did not change significantly with soil conditions, D was higher in humid organic conditions compared to mesic and xeric podzolic conditions implying a possible inverse response of root mass density that could explain the lost signal in SRL. In grasses, decreases in nitrogen and phosphorus have been shown to decrease root diameter and increase tissue mass densiy (Ryser et Lambers, 1995). If the same applied to temperate tree species, then humid organic conditions with their greater water and nutrient content (Table 1.1) would constitute an improvement in plant nutrition. Tissue density in roots has been related to the proportion of stele and of cell wall in the stele, and to characteristics of the tracheary system (Wahl et Ryser, 2000). A reduced percentage of stele in fine roots with decreasing tissue mass density could indicate a reduced importance of conductive tissue in an environment of good plant nutrition as in humid organic soil conditions. Although some studies have reported increases in D with nutrients (Holdaway *et al.*, 2011) and water (Cortina *et al.*, 2008 ; Peek *et al.*, 2005), its potential as environmental indicator may have been underestimated so far.

A limited number of studies have examined responses of BI to soil nutrition, reporting mostly non-significant changes (Bakker, Garbaye et Nys, 2000 ; George *et al.*, 1997). Interestingly, among these few studies on BI, contrasting results were reported within species (i.e. *Pinus sylvestris*) (Ahlström, Persson et Börjesson, 1988 ; George *et al.*, 1997). In the present study, BI proved to be the least variable and least plastic fine root trait responding to neither ontogenetic stage nor soil conditions.

Trait plasticity

From the three fine root traits assessed in the present study, D clearly showed the greatest plasticity (PI) and was also the trait where phenotypic plasticity contributed the most to total phenotypic variability (highest PI:CV). This coincides with it being the most responsive trait to soil conditions (Tables 1.4 and 1.5). Although more often used to assess acclimations to changes in the environment, SRL_c had significantly greater CV and a lower PI:CV than D_c in most cases. Interestingly, the species with the greatest CV within SRL_c are the two ectomycorrhizal species, *A. balsamea* (juvenile) and *B. papyrifera* (Table 1.5 and Fig 1.2), indicating that this greater variability may be due in part to methodological challenges of hyphenated root samples.

Variability of BI was highly species specific. In adults and juveniles, CV for BI_c was similar to those of D_c for the two angiosperm species and significantly higher for the two gymnosperm species. In addition, CV was generally higher in juveniles compared to adults. This trend is reversed in many cases when measured on D_3, D_1 or BI_3 (Table 1.5), indicating a possible effect of greater variation in root orders comprised in samples < 2 mm for juveniles.

Table 5. Mean / coefficient of variance (CV) for three fine root traits measured on the same root samples but following different fine root classification approaches. Subscript ‘c’ indicates a trait measured on roots < 2mm, subscript ‘3’ indicates a trait measured on first to third order roots and subscript ‘1’ indicates a trait measured on first order roots (diameter only). Data shown separately according to ontogenetic stage (OS): A – Adults, J – Juveniles and soil conditions: HO – Humid organic, MP – Mesic podzol and XP – Xeric podzol soil conditions. Different letters to the left of a column indicate significant differences in mean; different letters to the right of a column indicate significant differences in CV between soil conditions. Letters for all sites indicate significant differences between species (upper case for adults, lower case for juveniles).

Species	OS	Soil Condition	Diameter			Specific root length	Branching intensity	
			D_c	D_3	D_1	SRL_c	BI_c	BI_3
Abies balsamea	A	HO	**a** 0.66 / 0.12	0.62 / 0.11	**a** 0.53 / 0.18	11.7 / 0.31	2.3 / 0.33	2.1 / 0.39
		MP	**b** 0.55 / 0.12	0.46 / 0.23	**b** 0.39 / 0.14	10.7 / 0.17	2.7 / 0.22	2.7 / 0.23
		XP	**b** 0.56 / 0.07	0.55 / 0.15	**a** 0.48 / 0.16	11.0 / 0.24	2.4 / 0.18	2.0 / 0.30
		All sites	0.59 / 0.14	0.55 / 0.20	0.47 / 0.20	11.1 / 0.25 **AB**	2.5 / 0.25 **AB**	2.3 / 0.32
	J	HO	**a** 0.60 / 0.15	0.55 / 0.19	**a** 0.45 / 0.12	15.0 / 0.41	2.2 / 0.27	2.2 / 0.34
		MP	**b** 0.51 / 0.13	0.47 / 0.15	**ab** 0.40 / 0.2	17.0 / 0.49	2.5 / 0.32	2.8 / 0.22
		XP	**ab** 0.54 / 0.2	0.50 / 0.13	**b** 0.39 / 0.12	14.4 / 0.32	2.2 / 0.38	2.2 / 0.28
		All sites	0.55 / 0.16	0.51 / 0.17	0.42 / 0.14	15.5 / 0.42 **a**	2.3 / 0.32 **ab**	2.4 / 0.29
Thuja occidentalis	A	HO	0.64 / 0.14	**a** 0.65 / 0.1	**a** 0.60 / 0.05	13.1 / 0.19	1.8 / 0.34	1.4 / 0.24
		XP	0.56 / 0.14	**b** 0.55 / 0.1	**b** 0.51 / 0.13	14.0 / 0.15	1.9 / 0.34	1.3 / 0.24
		All sites	0.60 / 0.15	0.60 / 0.18	0.55 / 0.14	13.6 / 0.17 **B**	1.8 / 0.33 **A**	1.3 / 0.24
	J	HO	0.59 / 0.13	**a** 0.57 / 0.1	**a** 0.51 / 0.09	12.9 / 0.25	1.5 / 0.31	1.6 / 0.37
		XP	0.50 / 0.16	**b** 0.46 / 0.1	**b** 0.40 / 0.18	14.7 / 0.21	1.7 / 0.49	1.4 / 0.42
		All sites	0.55 / 0.17	0.52 / 0.16	0.46 / 0.18	13.8 / 0.24 **b**	1.6 / 0.43 **a**	1.5 / 0.39
Acer rubrum	A	HO	0.45 / 0.14	0.40 / 0.14	0.42 / 0.13	24.6 / 0.27	2.9 / 0.11	3.6 / 0.21
		MP	0.39 / 0.13	0.36 / 0.17	0.36 / 0.19	24.9 / 0.31	2.8 / 0.16	3.6 / 0.24
		XP	0.40 / 0.14	0.39 / 0.17	0.36 / 0.14	26.6 / 0.23	2.6 / 0.17	3.1 / 0.28
		All sites	0.41 / 0.15	0.39 / 0.16	0.38 / 0.17	25.4 / 0.26 **AB**	2.8 / 0.15 **b**	3.4 / 0.25
	J	HO	0.41 / 0.14	0.32 / 0.18	0.36 / 0.11	28.2 / 0.18	3.0 / 0.22	3.0 / 0.23
		MP	0.36 / 0.15	0.33 / 0.14	0.31 / 0.15	33.4 / 0.36	3.3 / 0.16	3.5 / 0.21
		XP	0.36 / 0.12	0.35 / 0.13	0.34 / 0.14	33.1 / 0.22	2.4 / 0.12	2.7 / 0.25
		All sites	0.38 / 0.15	0.33 / 0.15	0.34 / 0.14	31.3 / 0.28 **b**	3.0 / 0.21 **BC**	3.1 / 0.24
Betula papyrifera	A	HO	0.37 / 0.20	0.29 / 0.32	0.30 / 0.16 **b**	24.9 / 0.43	3.1 / 0.13	3.7 / 0.29
		MP	0.40 / 0.06	0.26 / 0.35	0.22 / 0.26 **a**	17.3 / 0.40	3.5 / 0.09	3.8 / 0.20
		XP	0.34 / 0.14	0.26 / 0.21	0.23 / 0.17 **b**	28.0 / 0.17	3.1 / 0.22	4.1 / 0.23
		All sites	0.36 / 0.16	0.27 / 0.29	0.25 / 0.24	23.2 / 0.38 **A**	3.2 / 0.17 **B**	3.9 / 0.24

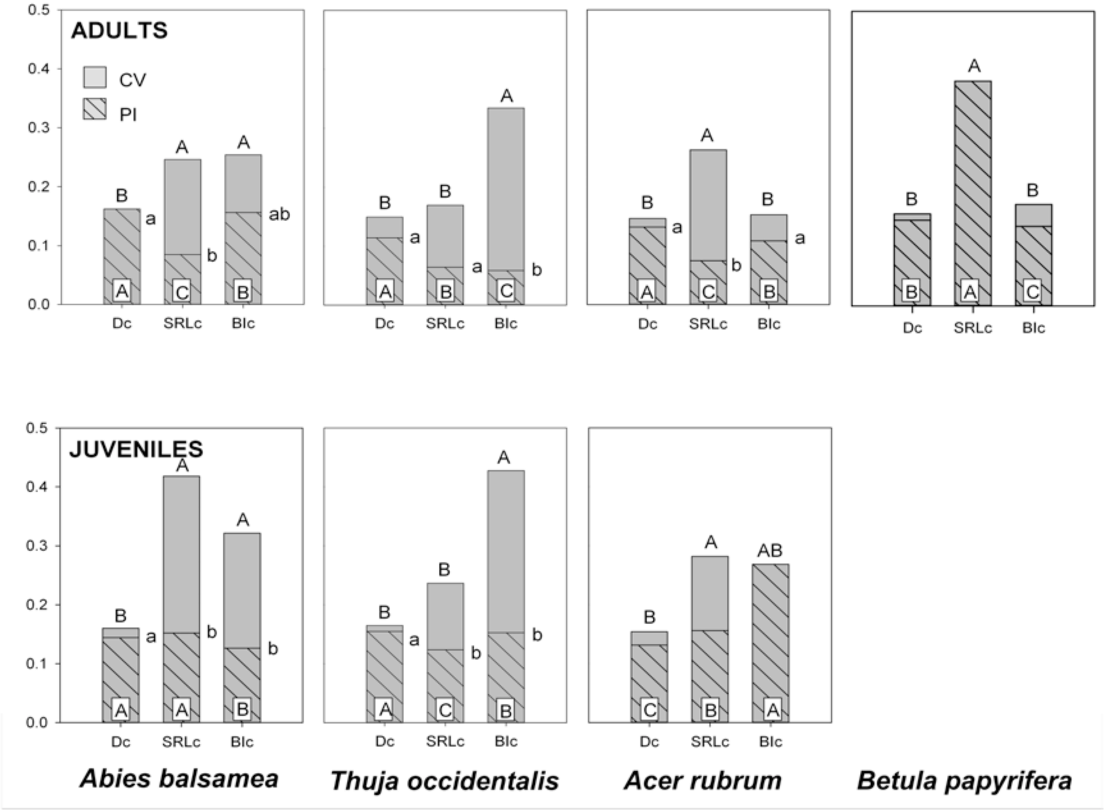

Figure 2. Coefficient of variation (CV, grey) and the phenotypic plasticity index (PI, grey hatched) for fine root traits of four North-American temperate forest species (NF dataset). Different letters indicate significant differences between traits (capital letters for CV, capital letters on white inset for PI and small letters for PI:CV). Traits include specific root length (SRLc), branching intensity (BIc) and fine root diameter (Dc) and were measured on roots < 2mm (subscript 'c'). Trait effects for CV and PI:CV were computed using the asymptotic interference test (Miller and Feltz, 1997). Trait effects for PI were computed on resampled populations and consecutive ANOVA models.

Fine root morphological traits were found to be strongly coordinated across species, but further work is needed to test for general patterns across ecosystems and biomes. Above- and belowground traits and whole-plant-strategies may not be as coordinated as previously thought once other factors such as site productivity are accounted for or controlled as we have done in this study for the common garden experiment. For the natural forest experiment, fine root traits responded differently to soil conditions within species, with fine root diameter being the most responsive. Diameter showed the least total variation yet much of it was explained by changes in the environment. Consequently, D may be the most suitable trait for evaluating plasticity to soil nutrition for the rhizosphere.

Lastly, the present study underscores the need for a unified framework of fine root classification and stronger control for the many possible confounding factors in root studies. Although a functional classification of fine roots managed to reduce variance in a limited number of cases, it improved estimator evaluation in at least one species. Most importantly, a unified framework would greatly facilitate the comparison of studies and therefore increase current understanding of the functional ecology of roots.

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CHAPTER II

ADVANCING BIODIVERSITY – ECOSYSTEM FUNCTIONING SCIENCE USING HIGH-DENSITY TREE-BASED EXPERIMENTS OVER FUNCTIONAL DIVERSITY GRADIENTS

Abstract

Increasing concern about loss of biodiversity and its effects on ecosystem functioning has triggered a series of manipulative experiments worldwide, which have demonstrated a general trend for ecosystem functioning to increase with diversity. General mechanisms proposed to explain diversity effects include complementary resource use and invoke a key role for species' functional traits. The actual mechanisms by which complementary resource use occurs remain, however poorly understood, as well as whether they apply to tree-dominated ecosystems. Here we present an experimental approach offering multiple innovative aspects to the field of biodiversity – ecosystem functioning (BEF) research. The International Diversity Experiment Network with Trees (IDENT) allows research to be conducted at several hierarchical levels within individuals, neighborhoods, and communities. The network investigates questions related to intraspecific trait variation, complementarity, and environmental stress. The goal of IDENT is to identify some of the mechanisms through which individuals and species interact to promote coexistence and the complementary use of resources. IDENT includes several implemented and planned sites in North America and Europe, and uses a replicated design of high-density tree plots of fixed species richness levels varying in functional diversity (FD). The design reduces the space and time needed for trees to interact allowing a thorough set of mixtures varying over different diversity gradients (specific, functional, phylogenetic) and environmental conditions (e.g. water stress) to be tested in the field. The intention of this paper is to share the experience in designing FD-focused BEF experiments with trees, to favor collaborations and expand the network to different conditions.

Key words : Experimental design; tree-dominated ecosystems; complementarity; functional diversity; functional traits, IDENT

Introduction

Over two decades of research have documented a positive relationship between ecosystem functioning and biodiversity for a multitude of systems, including grasslands, aquatic systems, bacterial microcosms and soil communities (Cardinale *et al.*, 2011 ; Hooper *et al.*, 2012 ; Reich *et al.*, 2012). However, most of the biodiversity-ecosystem functioning (BEF) research on plants to date has been conducted on experimentally grown grasslands (Caliman *et al.*, 2010), while studies on forests and tree-dominated ecosystems are more recent and scarce (Nadrowski, Wirth et Scherer-Lorenzen, 2010). The ability to determine what mixture of species could provide for better productivity and resilience, and how this may change with environmental conditions, is crucial for management strategies, even more so in the face of global change.

Since the size and longevity of trees make them inherently difficult to study, the bulk of studies have been observational, using forest inventory data. Most of these studies have reported positive relationships between diversity and productivity (Lei, Wang et Peng, 2009 ; Paquette et Messier, 2011 ; Vilà *et al.*, 2013 ; Vilà *et al.*, 2007 ; Zhang, Chen et Reich, 2012) or carbon stocks (Ruiz-Benito *et al.*, 2013) , but some have reported conflicting results (Jiang, Wan et Li, 2009) or even negative relationships (Thompson *et al.*, 2005 ; Vilà *et al.*, 2003). Although much welcomed for reasons of generality and applicability in the "real world" (Reiss *et al.*, 2009 ; Symstad *et al.*, 2003), observational studies may be limited in their abilities to investigate underlying mechanisms of BEF relationships, as well as other ecosystem functions than productivity (resource uptake, resilience, belowground and trophic interactions) not typically evaluated during forest surveys. Several mechanisms have been proposed to explain BEF relationships, with the main candidates including complementarity (CE) and selection effects (SE) (Loreau et Hector, 2001) (see Discussion for details on the mechanisms). Complementarity has been shown to be the dominant mechanism at work in grasslands and other ecosystems (Marquard *et al.*, 2009 ; Montès *et al.*, 2008 ; Spehn *et al.*, 2005). Furthermore, recent studies have suggested an increasing importance and dominance of complementarity with time (Allan *et al.*, 2011 ; Reich *et al.*, 2012). In trees however, the experimental isolation of CE has so far only been attempted in one tropical experiment (Sapijanskas, Potvin et Loreau, 2013 ; Zeugin *et al.*, 2010).

Functional traits are at the core of a mechanistic understanding of biodiversity effects (Reiss *et al.*, 2009). Functional traits link species to the roles they play in the ecosystem as "*morpho-physio-phenological traits which impact fitness via their effects on growth, reproduction and survival, ...*" (Violle *et al.*, 2007)as well as influence processes at higher organizational levels, and thus are key agents driving ecosystem processes (Díaz *et al.*, 2004). Species richness (SR) however has been the measure of biodiversity most often used in BEF research (Duffy, 2009), although evidence is accumulating that it may not be the most efficient predictor of EF and that other metrics such as functional diversity (FD - the diversity of traits in a community) are needed to quantify BEF mechanisms (Hooper *et al.*, 2005). Nonetheless, SR and FD, as well as phylogenetic diversity (PD), are unarguably linked in the natural realm and their covariance challenges our ability to unravel their respective effects on ecosystem functioning (Naeem, 2002b ; Paquette et Messier, 2011 ; Srivastava *et al.*, 2012).

Species complementarity may also operate at other trophic levels via shared enemies or mutualists, or from diversity effects that confer protection from disease or herbivory (Poisot, Mouquet et Gravel, 2013 ; Reiss *et al.*, 2009). Additionally, it was also proposed that biodiversity effects may be shaped by environmental conditions (Steudel *et al.*, 2012), with more diverse communities being more tolerant of environmental change, and CE being stronger under more stressful conditions. At the individual scale, within-species phenotypic plasticity with neighborhood composition may also enhance resource use efficiency and coexistence (Ashton *et al.*, 2010 ; Reiss *et al.*, 2009).

The use of large and long-lived models such as trees poses undeniable challenges, but also has benefits. In contrast to other plant-based models (e.g. grassland experiments), the position of individual trees and their respective count is invariable throughout the duration of the experiment (unless manipulated or if mortality occurs). A tree-based model offers the unique possibility to account for individual's contribution to the overall community-based functioning and to analyze the importance of spatial arrangements within and across species, as well as changes in those relations with time. Mixtures of trees thus make an excellent model for the next generation BEF research, by moving further from apparent overyielding to actual physiological and morphological adaptations of species that promote the complementary use of resources.

We report here the methodology of the International Diversity Experiment Network with Trees (IDENT), a set of replicated and coordinated BEF experiments testing a wide variety of tree mixtures and environmental conditions, as well as a variety of hypotheses on multiple trophic levels. The experimental approach allows separating the effects of FD and SR through a plot-based, replicated random design including tree species mixtures varying in FD independent of SR. This variation of continuous indices of FD within levels of constant SR also allows testing for underlying mechanisms such as CE and SE. The experimental approach used within the network is based on high-density tree plots and focuses on the early years of tree development, reducing space, time and effort of implementation and maintenance. In addition, the experimental approach offers great flexibility with little changes in the design allowing for individual sets of questions to each experimental site while sharing the core hypotheses with all other sites. This flexibility promotes international collaborations and new experiments to be established over a large gradient of conditions (e.g. soil, climate) and species pools, as proposed recently for testing global hypotheses in ecology (Fraser *et al.*, 2012). The network will help assess and quantify the direction, strength and shape of BEF relationships in early tree communities. In the following sections, we present the conceptual background that led to some of the specific research questions and challenges tackled by IDENT, as well as the design implemented to address them. We then present those research questions in more detail, and discuss how IDENT will address them. The main four research foci tackled by IDENT are relevant measures of diversity, underlying mechanisms and scale-dependency, importance of trophic interactions; and BEF effects over environmental gradients. IDENT aims to answer the following questions:

1. What is the contribution of the different components of diversity to ecosystem functioning?
2. How to choose species and traits to create the desired FD gradient?
3. Is complementarity the driving mechanism producing overyielding in early tree communities?
4. How does neighborhood diversity influences trait character displacement, thus the realized trait value and consequently realized functional diversity?
5. At what spatial and temporal scales do complementarity effects occur?
6. How to test for trophic-mediated complementarity?
7. How do environmental conditions influence species interactions?

Experimental approach

The common hypothesis underlying all IDENT experiments is that FD is a more mechanistic explanation and thus a better predictor of ecosystem functioning than SR. The separation of those diversity aspects is achieved through the establishment of two gradients. The first gradient consists of manipulations of SR (e.g. 1, 2, 4 and 12 species, Fig 1a). The second gradient consists of species combinations of constant SR over which FD is varied continuously. To better isolate the effect of FD (over that due to the presence/absence of a specific species or trait), FD levels are repeated using different species compositions and pooled in groups of similar value (Fig. 1a).

The sampling unit for system-scale metrics is the plot (7 x 7 or 8 x 8 assemblages of planted seedlings at regular intervals) and the design is replicated four times. Further replication allows additional treatments, such as irrigation, at some sites. Tree seedlings are planted at regular close intervals (40 or 50 cm depending on site productivity; Table 1). Although the relatively small individual plot size used will never allow a true forest ecosystem to develop, IDENT also has provisions to address the problem of scale as trees grow (see Q5). Focus in IDENT is clearly on the early successional stage of stand development, at the onset of competition that will determine later community composition (i.e. dominance, abundance, trait expression) and structure. Although interactions among juvenile trees will not match those of larger, mature trees that have developed over a long period of time, this difference should not be a barrier to the testing of general theory. Furthermore, it is well established that some crucial forest ecosystem parameters are less dependent on age as they occur at similar rates or levels in young and mature stands, such as leaf area index (Lieffers, Pinno et Stadt, 2002 ; Messier et Kimmins, 1991), fine root biomass (Claus et George, 2005 ; Lei, Scherer-Lorenzen et Bauhus, 2012), soil water retention and nutrient availability (Martin *et al.*, 2000). Given their cost and complexity, long-term full-scale experiments of forest BEF covering the whole range of forest dynamics are likely to be rare.

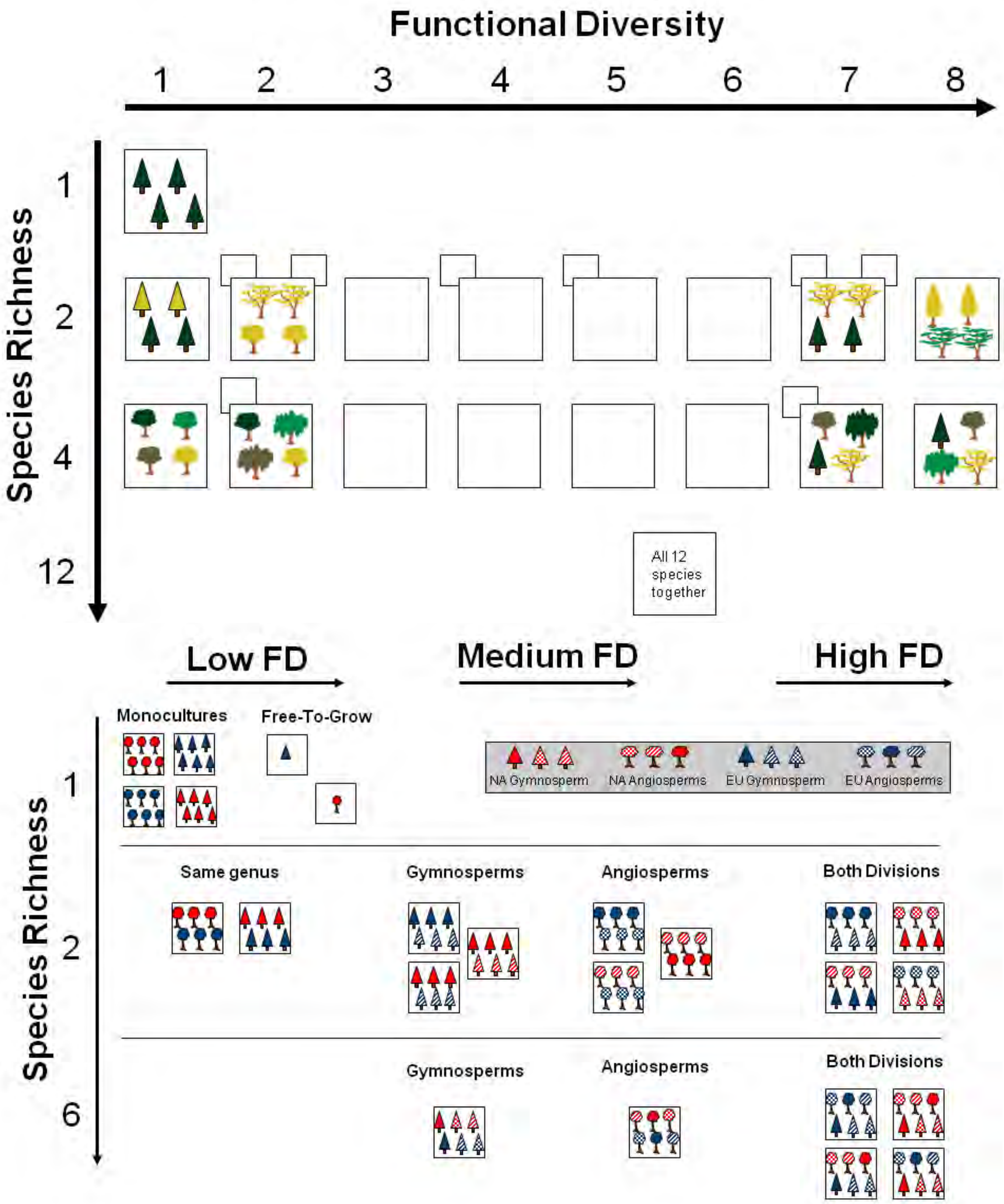

Figure 1. Schematic representations of the IDENT experimental design, showing manipulations of gradients of SR and FD. Monocultures of all species are always present. Upper panel: Design of the Montreal experiment with SR = 1, 2, 4 or 12 species and a FD gradient of 8 levels. Smaller squares behind larger ones indicate replications of the same FD level with different species combinations. Lower panel: Design established at the Auclair and Cloquet experiment. SR = 1, 2 or 6 species, and three FD groups (low, medium, high). Lowest FD values were achieved using pairs of similar species taken from the two continents; medium FD from mixtures of two species within the same division, and high FD from mixtures that include both gymnosperm and angiosperms

Specific design layouts

At present, two experiments within IDENT have been implemented (Table 1) at three sites, with more planned for 2013. The first experiment (Montreal; MTL) was established in spring 2009 near Montreal (Québec, Canada), where ~0.6 ha of a former high-input agricultural site was fenced to protect trees from herbivory. Nearly 10,000 individuals belonging to 12 North American temperate forest species (Table 2) were planted at 50 cm intervals on plots of 64 individuals (8 x 8 rows). SR varies from one, two, four to 12 species (Fig. 1a). In each replication block, 12 monocultures, 14 two-species, ten four-species, and one 12-species mixtures were implemented. The two- and four-species mixtures were established over a FD gradient of eight levels, plus added replication at some levels (Fig. 1a). These mixtures were chosen in a stratified random fashion in two steps. First, all possible mixtures of two and four species were arranged along a continuous FD gradient (Tables 2 and 3, also see Discussion for more on FD computation). Then mixtures were placed into eight FD classes, from which one or more were drawn at random (Fig. 1a).

A second experiment (AuCl) was established in 2010 at two sites, one near Auclair (Québec, Canada) and the other in Cloquet (Minnesota, USA), to tackle similar questions from a different angle. They were established on low-input abandoned pasture (Auclair) or previously forested (Cloquet) sites and are about 0.5 ha each with ~10 000 seedlings planted (Fig. 1b). Since both sites are less fertile and colder than MTL, trees were planted at slightly closer 40 cm intervals to accelerate interactions, in plots of 7 x 7 trees. The AuCl experiment is different from the MTL one as communities were chosen not at random, but manipulated to maximize FD gradients within a balanced design. AuCl includes six congeneric pairs of temperate tree species with each pair made up of a North American and a European species. Implemented species mixtures include plots with one, two or six species with low, medium and high replicated FD levels in the two-species mixtures (Fig. 1b). These two-species mixtures were specifically chosen to balance the number of angiosperms and gymnosperms, and the three genera within each division. Thus AuCl varies both FD and PD independently over a fixed number of species, as suggested by Srivastava et al. (2012) and implemented by Gravel et al. (2012) for marine bacteria communities. Low-diversity mixtures are composed of pairs of species from the same genus, medium-level uses species from the same division, while high diversity is realized when species are chosen from across divisions. However a central part of AuCl is the native vs. exotic contrast to study trophic complementarity (e.g. complementarity that may operate at other trophic levels via shared enemies or mutualists - see Discussion). Thus the design also balances the use of North American and European species in mixtures of both, and within each provenance (Fig. 1b).

Table 1. Characteristics of the two International Diversity Experiments implemented at three sites in Canada and the USA

	Montreal	Auclair / Cloquet
Location	Ste-Anne-de-Bellevue, Qc,	Auclair, Qc, Canada
Lat ; Long ; Elevation (m)	45.4247 ; -073.9390 ; 39	47.6969 ; -068.6551 ; 333
Year of establishment	2009	2010
Size of experiment (ha)	0.6	0.5
Number of replicate blocks	4	4
Number of plots (tree communities) per	37	48
Number of trees per plot	64 (8x8)	49 (7x7)
Number of trees total	9472	9408
Species richness treatments	1, 2, 4, 12	1, 2, 6
Planting distance (cm)	50	40
Number of species planted	12	12
Site history	high-input agricultural	low-input abandoned pasture /
Gradients implemented intentionally	FD over SR (2 and 4)	FD and PD over SR (2)

Notes: Size of experiments include corridors around plots and a planted buffer around the experiment, trees planted for destructive sampling and for Auclair / Cloquet, free to grow trees. FD gradients were implemented using two- and four-species mixtures at Montreal, and two-species mixtures at Auclair and Cloquet.

Planned sites for 2013 will be located in Sault-Saint-Marie (ON, Canada), Solsona (Catalonia, Spain), Sardinia (Italy) and Freiburg (Germany). The first three are located in dry to very dry climates (Solsona and Sardinia) or poor soils (Sault-Ste-Marie) and will include manipulated environmental gradients (through irrigation or partial removal of rainfall). Those will be implemented simply by doubling (or more) the replication of a given FD gradient over a constant SR level (any line in Fig. 1a or b) to accommodate both a control and a manipulated treatment. The Freiburg site is intended as a European counterpart to the AuCl experiment, with exotic and native species reversed (see question 6). IDENT is also part of a larger network of diversity experiments with trees, TreeDivNet, which includes mostly longer term experiments planted at larger spacings, such as BIOTREE (Scherer-Lorenzen *et al.*, 2007).

IDENT is a coordinated effort (Fraser *et al.*, 2012) and common sampling protocols, such as yearly growth measurements (diameter and height), are mandatory to all experiments. Generalization will be achieved using a multi-site approach such as in BIODEPTH (Hector *et al.*, 1999), especially for those experiments intentionally linked (e.g. AuCl). However, given that most sites also have particularities matching local issues (e.g. species pool, SR and FD gradient), over-arching analyses will be achieved in a meta-analyses framework using effect size (e.g. overyielding) as response variable, with sample sizes and variances to control for site-specific contributions to the overall trend, as well as a number of covariables depending on the function being analyzed (e.g. mean temperature).

Table 2. Tree species planted on experiments established near Montreal (MTL) and Auclair/Cloquet (AuCl) and functional traits used to compute functional diversity indices for analyses (see Table 3)

Species	Code	MTL	AuCl	Geographic	Wood density	Seed mass	Leaf N (%)
Abies balsamea	ABBA	x		NA	0.34	7.6	1.66
Acer platanoides	ACPL		x	EU	0.5165	139	1.99
Acer rubrum	ACRU	x		NA	0.49	26.5	1.91
Acer saccharum	ACSA	x	x	NA	0.56	55.2	1.83
Betula alleghaniensis	BEAL	x		NA	0.55	0.9	2.20
Betula papyrifera	BEPA	x	x	NA	0.48	0.4	2.31
Betula pendula	BEPE		x	EU	0.5125	0.29	2.33
Larix decidua	LADE		x	EU	0.474	7.1	2.05
Larix laricina	LALA	x	x	NA	0.49	2	1.36
Picea abies	PIAB		x	EU	0.37	7	1.19
Picea glauca	PIGL	x	x	NA	0.33	2.4	1.28
Picea rubens	PIRU	x		NA	0.38	3.3	1.15
Pinus resinosa	PIRE	x		NA	0.39	8	1.17
Pinus strobus	PIST	x	x	NA	0.34	17	1.42
Pinus sylvestris	PISY		x	EU	0.422	6	1.33
Quercus robur	QURO		x	EU	0.56	3378	2.37
Quercus rubra	QURU	x	x	NA	0.56	3143	2.06
Thuja occidentalis	THOC	x		NA	0.3	1.4	1.02

Notes: NA – North America, EU – Europe. Trait data compiled from published sources (Royal Botanic Gardens Kew, 2008 ; Wright *et al.*, 2004 ; Zanne *et al.*, 2009).

Discussion

Here we present the main research questions (1-7) that will be addressed within IDENT, articulated along four main themes: relevant measures of diversity; underlying mechanisms and scale-dependency; importance of trophic interactions; and BEF effects over environmental gradients. The objective is to share our experience in designing BEF experiments with respect to these, and to favor collaborations and expand the network to include different questions.

Measures of biodiversity

Biodiversity can be measured on various biotic scales, ranging from genetic variation within a species, to variation among species and finally, biomes. For the purpose of IDENT, we focus on individual and species-based measures at the community scale. Here, the components of diversity can include taxonomic diversity (SR and related measures of species relative abundances) and FD as well as PD. FD focuses on traits that relate the species to the function being measured (i.e. physiological, morphological and ecological traits) (Petchey et Gaston, 2006 ; Reich *et al.*, 2004). FD measures the extent of functional differences (distance) among species in a community (Laliberté et Legendre, 2010), and can be computed based on single or multiple traits. The functional identity of a community on the other hand is not given by the diversity of a trait among component species, but rather by its mean value weighted by abundances (community weighted mean value of traits, CWM) (Roscher *et al.*, 2012). Phylogenetic measures of diversity focus on distances between species based on evolutionary history (i.e. time since last common ancestors), and may use branch lengths between species on a phylogenetic dendrogram (Clarke et Warwick, 2001 ; Faith, 1992). Following the recent democratization of phylogenetics, PD has been proposed as an alternative to FD measures that rely on scarce and difficult to measure functional traits, as traits are the results of the evolutionary history inherited from ancestors (Cadotte *et al.*, 2009 ; Cavender-Bares, Ackerly et Kozak, 2012 ; Gravel *et al.*, 2012).

Strong correlation between those diversity components has rendered it difficult to unravel their respective effects on EF and only few experiments so far have attempted this, none with trees (Reich *et al.*, 2004 ; Scherber *et al.*, 2006). In an observational study of temperate and boreal North American forests, an index of FD best explained tree productivity, although both SR and PD also performed well (Paquette et Messier, 2011). Following recent shifts in the assessment of biodiversity in conservation science (Devictor *et al.*, 2010), biodiversity experiments are much needed to disentangle the respective contributions of biodiversity components to ecosystem functioning. In contrast to most prior BEF studies, our experimental design is explicitly built to do exactly that.

Question 1: What is the contribution of the different components of diversity to ecosystem functioning?

If the addition of any one species to a community contributes some unique functions to EF (i.e. species do not overlap in function), then the effect of FD on EF should not be different from the effect of SR on EF. However, more likely FD does not increase linearly with increasing SR but shows a saturating relationship due to functional redundancy (Loreau et Hector, 2001) (Fig. 2). A positive and more linear relationship between FD and EF (than of SR to EF) would be the result. IDENT experiments are aimed at orthogonally separating the respective effects of FD and SR on EF. This is achieved primarily by varying FD within communities of fixed number of species (Fig. 1).

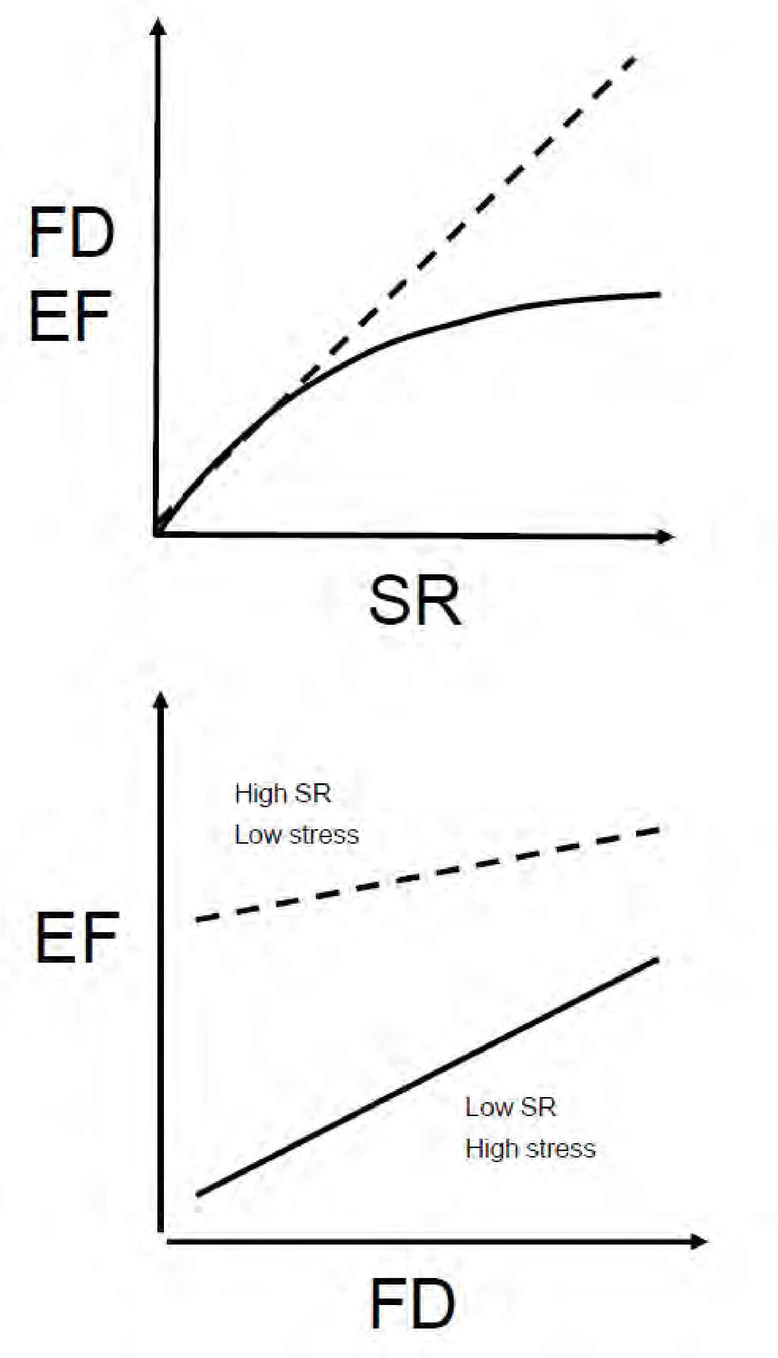

Figure 2. Upper panel: Expected relationships between species richness (SR) and functional diversity (FD) or ecosystem functioning (EF), assuming a linear or saturating relationship. The difference between the two lines is due to functional redundancy between species. A linear relationship is not expected as it would require all species to be functionally singular (no overlap). Lower panel: A positive and mostly linear relationship between EF and FD. Hypotheses to be tested in IDENT are presented as differences in either slopes or EF level (see Table 4). Illustrated here are differences in EF that may be due to an added effect of species richness (SR) or exposition to stress, resulting in different relationships with FD.

However, feedbacks that occur over time could result in a different pattern over longer periods, where EF becomes increasingly linearly related to SR due to all or most species having significant effects at some point in time (Reich *et al.*, 2012). This might be especially important in forest systems undergoing succession, even over relatively short periods. With time, relationships between species that promote coexistence may change, and accordingly the relative importance of a given set of traits and the corresponding FD metric's performance at predicting functions (see also question 2). PD could be a useful complementary measure for the longer term study of BEF experiments as by design it is less affected by shifts in the relative importance of a given set of traits over time. Alternatively, PD could also be used in place of traits in new BEF experiments established in little understood ecosystems with poor functional trait coverage.

An important yet often neglected issue to allow for the partition of the different components of diversity is the use of FD and PD indices that are computationally free of SR (Helmus *et al.*, 2007 ; Laliberté et Legendre, 2010). But more generally, choosing species and functional traits *a priori* to build the experimental layout poses its own challenges.

Question 2: How to choose species and traits to create the desired FD gradient?

Within IDENT, one of the first challenges was calculating FD indices to guide the choice of species representing the traits anticipated to play important roles in the function(s) targeted, choices that directly influence the species pool and the achievable FD gradient. At the MTL site the aim was to create a wide range of FD within mostly two SR levels. The trait matrix used to compute the FD index for all possible combinations of two and four species (from which mixtures were assigned to eight bins and then chosen at random to be planted - see “Specific design layouts” included a wide range of above- and belowground traits to capture species’ relations in trait space associated with multiple ecosystem processes. This approach did create the desired "general" spectrum of FD, but also has two potential drawbacks: i) the FD index is based on traits measured elsewhere, and ii) the included traits are not profoundly implied in all ecosystem processes under investigation.

Therefore, for the second experiment (AuCl) we chose a different, complementary approach. Despite modern FD metrics that make use of multi-dimensional trait space to compute distances between species (Laliberté et Legendre, 2010), it remains especially challenging for the establishment of biodiversity experiments to create mixtures of very low FD. This is however crucial to partition FD from SR. Low FD values can be achieved with the inclusion of congeneric species that share similar traits. At MTL these naturally co-occur (e.g. *Acer saccharum* and *Acer rubrum*) but are few. In the case of the AuCl experiments, pairs of functionally similar species were chosen *a priori* for that purpose. The pairs make up planted communities of congenerics including a North American and a European taxa of otherwise physiologically similar species (e.g. *Acer saccharum* and *Acer platanoides*).

The identity of traits with explanatory power is likely to change with the ecosystem process under investigation, and with time as species interactions change, both of which have great scientific interest. One method to identify relevant traits is the calculation of FD indices for each individual trait and assessment of their explanatory power in multiple regressions (Roscher *et al.*, 2012). Through the calculation of community-weighted means (Diaz *et al.*, 2007), the effect of functional identity can be compared to that of FD. Table 3 presents an example of FD indices computed for species combinations at AuCl for three of the most often reported traits relevant for the productivity of forests (Paquette et Messier, 2011 ; Ruiz-Benito *et al.*, 2013). In general the values match the three FD classes (low to high) used to pool communities in our design (Fig. 1b), with e.g. lowest values found in same-genus communities. However, one can also perceive the effect of trait choice, such as seed mass, that largely explains why highest FD values are obtained in the presence of either *Quercus* species. Whether that relates to a true diversity effect will depend on the process being analyzed.

Table 3. Functional diversity matrix for Auclair and Cloquet based on wood density, seed mass, and leaf nitrogen content (Table 2) for two- and six-species combinations (FDis index; Laliberté et Legendre, 2010).

	ACPL	ACSA	BEPA	BEPE	LADE	LALA	PIAB	PIGL	PIST	PISY	QURO
ACPL											
ACSA	0.36 [a]										
BEPA	*0.95* [b]	*0.99* [b]									
BEPE	*0.94* [b]	*0.93* [b]	0.20 [a]								
LADE	0.59 [c]	0.67 [c]	0.44 [c]	0.51 [c]							
LALA	1.01 [c]	0.86 [c]	1.07 [c]	1.10 [c]	0.79 [a]						
PIAB	1.35 [c]	1.38 [c]	1.44 [c]	1.56 [c]	*1.14* [b]	*0.76* [b]					
PIGL	1.52 [c]	1.59 [c]	1.46 [c]	1.60 [c]	*1.22* [b]	*0.96* [b]	0.30 [a]				
PIST	1.28 [c]	1.40 [c]	1.38 [c]	1.52 [c]	*1.07* [b]	*0.95* [b]	*0.35* [b]	*0.35* [b]			
PISY	1.08 [c]	1.06 [c]	1.18 [c]	1.27 [c]	*0.86* [b]	*0.44* [b]	*0.35* [b]	*0.57* [b]	0.53 [a]		
QURO	*0.77* [b]	*0.96* [b]	*1.52* [b]	*1.48* [b]	1.28 [c]	1.76 [c]	2.06 [c]	2.23 [c]	1.94 [c]	1.82 [c]	
QURU	*0.63* [b]	*0.78* [b]	*1.53* [b]	*1.50* [b]	1.21 [c]	1.56 [c]	1.85 [c]	2.05 [c]	1.77 [c]	1.61 [c]	0.34 [a]
6 Angiosperms	*1.23* [b]										
6 Gymnosperms	*0.92* [b]										
NA Angios + EU Gymnos	1.43 [c]										
NA Gymnos + EU Angios	1.71 [c]										
6 NA	1.65 [c]										
6 EU	1.46 [c]										

Not all species combinations represented here were established in the experiment. Traits are standardized prior to distance computations; seed mass was log-transformed. angiosp. Angiosperms, gymnosp. gymnosperms; for other abbreviations, see Tables 1 and 2. [a]Low FD (same genus); see Fig. 1b, [b]Medium FD (same division); see Fig. 1b, [c]High FD (between divisions); see Fig. 1b

Complementarity effects

Niche complementarity or complementary resource use hinges on the idea of niche partitioning through differences in functional traits between species. To quantitatively detect a positive mixture effect, the rate of the ecosystem function under examination (most commonly yield) in mixtures has traditionally been compared to expectations from monocultures of the same species (Loreau et Hector, 2001). For a positive mixture effect, the EF rate per area in mixtures divided by the mean EF rate per area of the constituent species in monocultures must exceed one (“overyielding”). The concept of overyielding is strongly rooted in the ratio of inter- to intraspecific competition (Loreau, 2004), which also happens to be a criterion for stable coexistence. In agriculture, this method is known as the ‘land equivalent ratio’ (LER) (Vandermeer, 1989). A positive mixture effect could have different underlying resource-related mechanisms, as previously identified: the SE and CE. Our experimental design, by focusing on monocultures and two or more species mixtures will enable us to compute interaction coefficients, investigate their relation to functional proximity and therefore mechanisms underlying the BEF.

Question 3: Which mechanisms underlie BEF relationships?

It is expected that with increasing FD, net biodiversity effects increase due to increasing CE (as well as reduced disease or pest damage, which we minimally address herein for brevity). *A priori* manipulation (i.e. species mixtures of constant SR varying in FD) will allow testing for the relationship between FD and EF, independent of SR (Fig. 2). Response EF will be analyzed in IDENT within a framework composed of two main steps in a similar fashion as employed by Roscher et al. 2012 (2012). Firstly, the net biodiversity effect (NE) will be explicitly partitioned into CE and selection (identity) effects through additive partitioning of the observed and expected (from monocultures) yields following Loreau and Hector (2001):

$$NE = \Delta Y = CE + SE = N * \overline{\Delta RYM} + N * cov(\Delta RY, M) \qquad (1)$$

where Y is the response being analyzed (e.g. growth), N the number of species present (i.e. SR), RY the relative yield of a species in mixtures, and M the yield in monocultures. Secondly, the following general equation (restricted maximum likelihood mixed model) will then be used to further investigate the nature of the above biodiversity effects and links to FD and identity (see a detailed example in Table 4):

$$Y' = block(R) + SR + block * SR(R) + FD + SR * FD + covar_1 + \cdots + covar_{\,n} + \varepsilon \qquad (2)$$

where Y' is the biodiversity effect being investigated (e.g. CE or SE, but could also be applied to raw responses such height growth; Table 4), block and its interaction with SR are random factors (R), SR is a multi-level factor excluding monocultures (and e.g. in MTL the 12-species plots). Covariables are added to control for the effect of e.g. microtopographic differences in soils. In this example FD, a FD index (continuous), would be used to explain the nature of an observed CE. To control for the effect of species composition (i.e. species functional identity), CWM may be added in an overarching model tested against the net effect (NE), or used instead of FD to explain a SE. At MTL, thanks to the replicated SR levels, differences in slopes (i.e. significant SR x FD effect; Table 4) will be used to test for the additional contribution to EF attributed to increased species numbers (Fig. 2), which would in part reflect the imperfection of our measure of FD. We used data for tree height at the end of the first growing season (2009) to validate the model with real data (Table 4). As expected, no significant effect was found given the short duration. The driving forces behind complementarity are likely to be manifold, but space limitations preclude their treatment here.

Table 4. Sample results of fixed and random (*R*) effects of an exemplary mixed model (REML) used for analyzing results within IDENT sites for a given diversity effect or response function. Shown are results for first year tree height at the Montreal site tested against species richness (SR), functional diversity (FD), community weighted mean (CWM), and a randomly generated co-variable.

Effect	DF	F-ratio	p-value
Block(*R*)	3		
SR	1	0.51	0.51
Block*SR(*R*)	3		
FD	1	1.38	0.24
SR*FD	1	0.29	0.59
CWM	1	2.36	0.13
SR*CWM	1	0.37	0.55
FD*CWM	1	0.62	0.43
Co-variable	1	0.11	0.74

Question 4: How does neighborhood diversity influence intraspecific trait variation and consequently FD?

BEF experiments with trees, such as IDENT, have advantages for investigating trait plasticity and its consequences on FD and functioning. Having many non-moving individuals (trees) over a relatively small area facilitates quantification of changes in traits in relation to neighborhood composition and time (growth), and how they contribute to ecosystem functioning. One view to complementarity is that species differ in their fundamental niches (i.e. without competitors). But complementary resource use may also result from differences in realized niches due to intraspecific trait plasticity (i.e. character displacement) (Ashton *et al.*, 2010). Empirical studies as well as growth models provide indications that intraspecific trait plasticity can indeed reduce competition and improve performance in a competitive context (Callaway, Pennings et Richards, 2003). Traits measured on an individual plant basis will allow the computation of "realized-FD" metrics (i.e. the FD achieved in a community through individual's plasticity), and the assessment of contributions of intra- and interspecific trait variation to biodiversity effects. Specifically, we expect to find a stronger realized-FD to EF relationship (i.e. better predictability) than the fundamental FD-EF (no plasticity), due to character displacement (measured as an individual’s trait value deviation from that in monocultures).

Question 5: At what spatial and temporal scales do CE occur?

The IDENT design will also be useful to investigate BEF across scales. Indeed, little is known about the scale at which competition (but see Boivin *et al.*, 2010 ; Boyden *et al.*, 2009 ; Kennedy *et al.*, 2002) and complementarity occur, especially for trees, and few experiments were designed with that in mind (Scherer-Lorenzen *et al.*, 2007). Planted trees do not move, become large and live long enough to make it possible to follow each individual through time. Character displacement, for example, can be tracked for each individual with respect to immediate neighborhoods of variable size (such as within a moving-window approach). Interestingly, such change in scale can also be used to keep experiments going longer even as trees outgrow their initial plot-based communities. With the growing evidence from grassland experiments of the increasing importance of CE over time (Reich *et al.*, 2012), we intend to shift our definition of the IDENT design from the original plot-based to a ‘neighborhood-focused’ experiment. Accordingly, hypotheses will shift from plot-based responses to individual-based responses.

Trees in IDENT experiments will eventually reach sizes at which the present plots are no longer relevant regarding processes and interactions (each site varying in time required to reach that point depending on species used, planted density and plot size, and fertility). From that point and into the future, analyses will be carried out using circular neighborhoods around focus individuals or groups, the appropriate size of which will be derived from the data themselves.

Trophic-mediated complementarity

The concept of functional complementarity (Loreau, 1998) was primarily derived for plants competing for a single resource. Functional traits determine how plants exploit limiting resources (e.g. different rooting depths for water uptake) and thus interspecific competitive interactions. Although exploitative competition is common among plants, numerous indirect interactions via shared enemies or mutualists can result in indirect interactions that reduce or enhance performance. There is strong evidence that complementarity can also arise from density-dependent diversity effects that confer protection from disease or herbivory (Maron *et al.*, 2011 ; Schnitzer *et al.*, 2011) and this mechanism is not mutually exclusive from resource-based mechanisms. For instance, when two plant species share a common herbivore, they interact via “apparent” competition (Holt, 1977) because an increasing population size of one species will translate into higher herbivory pressure for the other species. Similarly, plants could interact by “apparent” mutualism via shared mutualists such as mycorrhizae. Recent theoretical developments on BEF generalized the concept of complementarity to all types of indirect interactions and suggest that traditional analyses of resource acquisition-related traits might provide only a partial understanding of complementarity (Poisot, Mouquet et Gravel, 2013).

Question 6: How to test for trophic-mediated complementarity?

We expect that native and exotic species are not functionally equivalent, even when they share very similar life history strategies. A key feature of some IDENT experiments is the combination of native and exotic species with similar traits from North America and Europe (Table 2). Consequently we hypothesize that unexplained variation in tree productivity after accounting for resource-related FD will be related to trophic and mutualistic complementarity. Complementarity should thus decrease with overlap in major enemies and increase with overlap in mutualists (Maron *et al.*, 2011 ; Schnitzer *et al.*, 2011). Trophic and mutualistic interactions will be documented in monocultures and mixtures at the different sites of the network. Trophic-mediated complementarity will be estimated in IDENT in the field in a similar fashion to FD using matrices of interactions with soil and aboveground organisms and network theory tools to estimate niche overlap (Poisot, Mouquet et Gravel, 2013). Finally, the addition of a third site to the AuCl pair, in Freiburg in 2013, will allow us to confirm these hypotheses by running the same analyses with the same experimental design, species and therefore FD, but with the reversal of their native-exotic status.

Complementarity along environmental gradients

As shown empirically, the balance between positive and negative plant interactions may be dependent on the abiotic environment such as individual resource availability (Brooker *et al.*, 2008). Elucidating the effects of environmental stressors on BEF relations is of critical importance in the face of global change. Global increases in temperatures, changes in precipitation regimes and eutrophication are just a few phenomena related to global change that will inevitably affect species interactions and hence BEF relationships (Reich *et al.*, 2001).

The frequency of positive plant interactions (i.e. facilitation) has been shown to increase with environmental stress (Brooker *et al.*, 2008). However, most studies have been conducted on pairs of species and it remains contentious how the effects of greater plant diversity on ecosystem functioning interplay with environmental stress. Model predictions, for example, suggest a greater importance of complementarity in less productive (Warren, Topping et James, 2009), which has been documented in a few, contrasted systems (Li *et al.*, 2010 ; Paquette et Messier, 2011 ; Steudel *et al.*, 2012 ; Wacker *et al.*, 2009).

Question 7: How do environmental conditions influence species interactions?

Answers to many if not all of the above-mentioned research questions are likely to change with varying environmental conditions as the relationship between functional traits and the fundamental niche is dependent on the environment (McGill *et al.*, 2006). In IDENT, environmental differences among sites, as well as within-site treatments (e.g. irrigation) will be used to examine changes in species interactions and to test whether the frequency and importance of complementarity increase with environmental stress. Within upcoming sites (2013), two replicated sets of identical species mixtures of constant SR and varying FD will be implemented (as well as corresponding monocultures). Exposing one of those sets to differences in one environmental condition (e.g. irrigation on dry sites or rainfall exclusion on wetter sites - Sánchez-Humanes et Espelta, 2011) will create environmentally more stressful conditions for one set of mixtures. We expect that whereas total EF rates will be reduced with environmental stress, this reduction will be lessened in more diverse communities (Fig. 2), thus showing greater tolerance to stress with increased diversity.

Conclusion

Although great advances in the understanding of the effects of biodiversity on ecosystem functioning have been achieved, many crucial links and aspects have yet to be examined, especially for tree-dominated ecosystems. Despite the growing acknowledgment and understanding of the importance of FD in explaining BEF relations, only few experiments actually manipulate FD in tree communities. In addition to the realized and expected FD gradients within IDENT, to our knowledge no other study has been set up to successfully separate FD from SR in trees, and we argue that knowing more about this will be particularly important for managing and assessing the functioning of tree-dominated ecosystems facing global changes. The research questions presented in this paper are only a selection of potentially interesting ones that could be addressed within IDENT or other studies with similar approaches. Future research will foster investigations of the role of tree diversity, complementarity, facilitation, competition and spatial complexity in maintaining functional ecosystems in the face of global changes.

In this paper we have attempted to convince readers that trees and related arboreal systems are not only a necessary next step in BEF research, but equally important, they may be an excellent model for the next generation of BEF experiments. Trees are large organisms that can be easily accessed and followed through time on an individual basis, thus allowing for a number of new questions to be asked, bringing the science closer to a more detailed understanding of how individuals regulate the way in which species interact to form both positive and negative outcomes. But working with trees does have its challenges. Trees indeed become large, and need time to establish and interact, thus imposing a larger price tag with respect to comparable research carried out with smaller organisms with faster turnover. Therefore, while changes in FD and feedbacks of FD on ecosystem processes could lead to shifts in the form of the BEF relationship over ecologically realistic time frames (Reich *et al.*, 2012), some IDENT experiments may have to be terminated before large-scale competitive exclusions take place, and also before some potentially important functional traits such as seed production have been expressed in their true function. IDENT, therefore is most focused on the early interactions between trees, which in turn are fundamental in determining the later dynamics and compositions of forests. Naturally, large temporal and spatial scale experiments like BIOTREE (Scherer-Lorenzen *et al.*, 2007) are needed to complement experiments like IDENT and look at the longer term impacts of varying species and FD on EF.

Our intention in this article was to share our experience in designing BEF experiments with trees, the questions we faced and the “solutions” we applied. The objective was to favor exchange with other researchers who may offer different solutions or research questions, or be interested in carrying out research within IDENT or establishing new sites in different environments. We also hope that our experience may be helpful to other groups planning BEF experiments within other ecosystems heretofore unstudied in these respects.

Acknowledgments

A large number of researchers are already conducting experiments on existing IDENT sites, or are in the process of establishing new ones. The authors wish to thank them for stimulating exchanges of ideas. A. Stefanski's help with setting up the AuCl experiment was much appreciated, as well as the everlasting support of the Quebec provincial nurseries. Also, we wish to express our deepest gratitude to the numerous people that have helped establish and maintain the present sites. IDENT is part of the TreeDivNet, an international platform for research on the relation between tree species diversity and ecosystem functioning, which helped foster yet more exchange of ideas and new partnerships at the last meeting in Florence, Italy (February 2013). Two anonymous reviewers contributed constructive ideas to help improve this article. This work complies with the current laws of Canada and the USA, in which the experiments were established.

CHAPTER III

FUNCTIONAL IDENTITY DRIVES OVERYIELDING IN EARLY TREE COMMUNITIES

Abstract

After more than two decades of biodiversity and ecosystem functioning (BEF) research, general consensus leans toward a general increase of producer growth with producer diversity. One of the main candidate mechanisms proposed to underlie this positive relationship is niche complementarity that is conceptually based on functional trait variation (i.e. functional diversity, FD). However, few studies to date specifically manipulated and tested for effects of FD on ecosystem functioning, especially in trees.

Here we present results of a common garden experiment where high-density tree communities were varied along a gradient of continuous FD, independent of species richness (one-, two-, four- and twelve-species mixtures). We specifically tested for the effect of FD on productivity and its link to complementarity. After four years of growth, no transgressive overyielding was detected but positive mixture effects (overyielding) were confirmed for the majority of tree communities. However, these were largely due to selection effects driven by some fast-growing deciduous species and the competitive exclusion of many evergreen species. Consequently, functional identity based on leaf longevity, seed mass and root traits had greater explanatory power on productivity than functional diversity.

We conclude that in young tree communities, functional identity drives ecosystem functioning in favor of what was formerly described as *r* - strategists. The importance of root traits in explaining tree productivity and diversity effects may reflect adaptations to the experimental conditions (rich sandy soils, young trees) where light was not limiting, especially in the first two years.

Key words : biodiversity and ecosystem functioning, overyielding, tree root traits, complementarity, functional diversity, functional identity, IDENT

Introduction

The idea of increasing producer diversity leading to increased growth is known at least since the 19th century. European Forester von Cotta proposed in 1828 that "*Since not all tree species utilize resources in the same manner, growth is more lively in mixed stands…*" (in Pretzsch, 2005). Three decades later, Darwin enunciated in his seminal work that a "divergence of character" would reduce interspecific competition and likely yield greater productivity (Darwin, 1859). However, it is not until the late 20th century with the considerable and accelerating change in the earth's biota that a systematic and concerted search for the effects of biodiversity on ecosystem functioning (BEF) began. After more than two decades of BEF research, the hypothesis that increased producer diversity leads to increased producer productivity has been accepted with high confidence for a variety of systems but still based mostly on herbaceous experiments (Balvanera *et al.*, 2013 ; Cardinale *et al.*, 2012 ; Hooper *et al.*, 2012).

Although mixture trials with trees date back several centuries, experiments with adequate controls are rare and our understanding of BEF in tree systems lags behind herbaceous (mostly grassland) systems. Recent meta-analyses (Zhang, Chen et Reich, 2012) and reviews (Nadrowski, Wirth et Scherer-Lorenzen, 2010 ; Thompson *et al.*, 2009) bring together close to 100 experimental and observational studies covering more than 30 years. From these studies, a general trend of increased tree productivity with tree diversity was concluded. Interestingly, this trend was not dependent on biomes or stand origin (plantation versus natural forest) indicating a more general phenomenon than previously assumed (Zhang, Chen et Reich, 2012). At the same time, strong effects of evenness (Zhang, Chen et Reich, 2012) and functional identity (Nadrowski, Wirth et Scherer-Lorenzen, 2010) indicated that species richness (SR) alone may not be the best measure of biodiversity.

To explain positive BEF relations, two main mechanisms have been proposed. Complementarity effects include niche partitioning and positive interactions (i.e. facilitation) due to increased trait diversity, whereas selection effects are due to dominant species with particular traits driving ecosystem functioning (Roscher *et al.*, 2012). Both mechanisms are not mutually exclusive and have been shown to be at work in creating positive BEF relationships in a variety of systems

(Cardinale *et al.*, 2011) with evidence suggesting shifts between them and increasing importance, and in fact dominance of complementarity with time (Allan *et al.*, 2011 ; Cardinale *et al.*, 2007 ; Fargione *et al.*, 2007 ; Reich *et al.*, 2012). Both mechanisms hinge on the pivotal role of functional traits and indeed, functional aspects of diversity have been shown to have greater explanatory power on ecosystem functioning than SR alone (Díaz et Cabido, 2001 ; Mokany, Ash et Roxburgh, 2008). Two main approaches to calculate functional aspects of diversity have been used. On the one hand, continuous functional diversity indices estimate the distance between species in a multidimensional trait space (Laliberté et Legendre, 2010 ; Mouchet *et al.*, 2010). Theory predicts that functional diversity should be linked to complementarity, as the diversity in traits of the community should be an expression of niche overlap. In this way, increased functional diversity should result in greater ecosystem functioning through enhanced resource use complementarity (Hooper, 1998 ; Petchey, 2003). On the other hand, community weighed means (CWM) have been used as a way to assess the mean trait value of all species present in a mixture weighed by their abundance. Conceptually, CWM are based on the ‘mass ratio hypothesis’ stating that the functional traits of the dominating species in a community drive ecosystem functioning (Grime, 1998). In consequence, CWM are closely linked to selection effects (SE) (Mokany, Ash et Roxburgh, 2008 ; Roscher *et al.*, 2012). De facto, both approaches have been shown to exhibit explanatory power on ecosystem functioning in herbaceous (Mokany, Ash et Roxburgh, 2008 ; Roscher *et al.*, 2012) and tree systems (Nadrowski, Wirth et Scherer-Lorenzen, 2010).

Species richness and functional aspects of diversity are inevitably linked making it difficult to disentangle their respective influence on ecosystem functioning (Naeem, 2002b). In addition, their relationship is more likely to be non-linear. While at low SR, each species addition may linearly increase FD, the relationship may truncate at higher levels of SR due to functional redundancy. In consequence, the relationship between FD and EF would be positive and more linear than between SR and EF (Tobner *et al.*, 2013). However, only few studies so far manipulated continuous FD metrics and tested for the effect of FD on EF independently of SR, even more so with trees (see www.treedivnet.ugent.be for a summary of current biodiversity experiment with trees).

We conducted a common garden experiment of high-density tree communities near Montreal, Canada (Tobner *et al.*, 2013). The core of this experiment consists of species mixtures varying in FD, independent of SR, including ten two-species and 14 four-species mixtures. This experiment aimed to specifically test for the effect of FD on tree productivity, independently of SR. The implementation of monocultures of all species present in mixtures allowed calculations of net biodiversity effect and its components complementarity and selection effect (following the additive partioning approach of Loreau et Hector, 2001). Here, we present the effects of tree diversity on tree productivity, four years after experiment establishment. We specifically tested the hypotheses that:

1. Tree mixtures perform better than expected with respect to their respective monocultures (positive net biodiversity effect, overyielding),
2. Increases in productivity are due largely to complementarity effects,
3. Hence, FD is a better predictor of tree mixture productivity than CWM,
4. Complementarity increases over time, and
5. There is no significant difference between two-and four-species mixtures (i.e. no significant effect of SR).

Methodology

Site description

The study site is located in Ste-Anne-de-Bellevue, near Montreal, Québec, Canada (45˚26’N, Long 73˚56’W, 39 m.s.l). Mean annual temperature is 6.2 ºC with a mean annual precipitation of 963 mm (climate.weatheroffice.gc.ca). The study site is a former agricultural field that has been intensively managed for several decades. The soil consists of a 20 to 70 cm sandy layer followed by clay. In spring 2009, an area of about 0.6 ha was cleared of corn debris before tree communities were planted with seedlings of one (broadleaf) or two (conifer) years of age (Tobner *et al.*, 2013).

The species pool comprised 12 North American temperate forest species covering a wide range of functional traits including five broadleaf species: *Acer saccharum* Marsh., *Acer rubrum* L., *Betula alleghaniensis* Britton, *Betula papyrifera* Marsh. and *Quercus rubra* L. as well as seven conifers: *Abies balsamea* (L.) Mill., *Larix laricina* (Du Roi) K. Koch, *Pinus strobus* L., *Pinus resinosa* Aiton, *Picea glauca* (Moench) Voss, *Picea rubens* Sarg. and *Thuja occidentalis* L. (Table 1).

The Montreal experiment is part of the “International Diversity Experiment Network with Trees” (IDENT) that includes several sites in North America and Europe (Tobner *et al.*, 2013). Common to all IDENT sites are gradients of FD to specifically test for the effect of FD on EF. The experiment described here was the first to be established and its focus was on a comprehensive gradient of FD, independent of SR.

Experimental design

Trees were planted in square plots of 8x8 individuals, with 50 cm planting distance. Tree-free buffer zones of 1.25 m around the plots were used for circulation within the site and to minimize inter-plot interactions. For the latter reason, tree roots were also sliced 30 cm deep around each plot in those buffers in 2011 and 2012. Plots included monocultures of all 12 species, 14 combinations of two-species mixtures, ten combinations of four-species mixtures and one mixture including all 12 species (Fig 1) (Tobner *et al.*, 2013). Each community was replicated four times adding up to a total of 148 plots and 9472 individual trees. Within plots, trees in mixture were planted at random with restrictions. In two species mixtures, at least two of the eight neighbors had to be different species from any tree. In four species mixtures, at least two of the eight neighbors had to be from two different species. Planting patterns within plots were repeated in all four blocks. Within each block however, plots were randomly distributed. Around the outermost rows of the experiment, three rows of trees at 50 cm distance were planted to serve as a buffer to the experiment and to replace dead trees after the first year of the experiment. In total, 52 trees were replaced after the first year. A fence to protect against herbivory surrounded the experiment and all plots were regularly weeded manually to keep them free of any herbaceous competition.

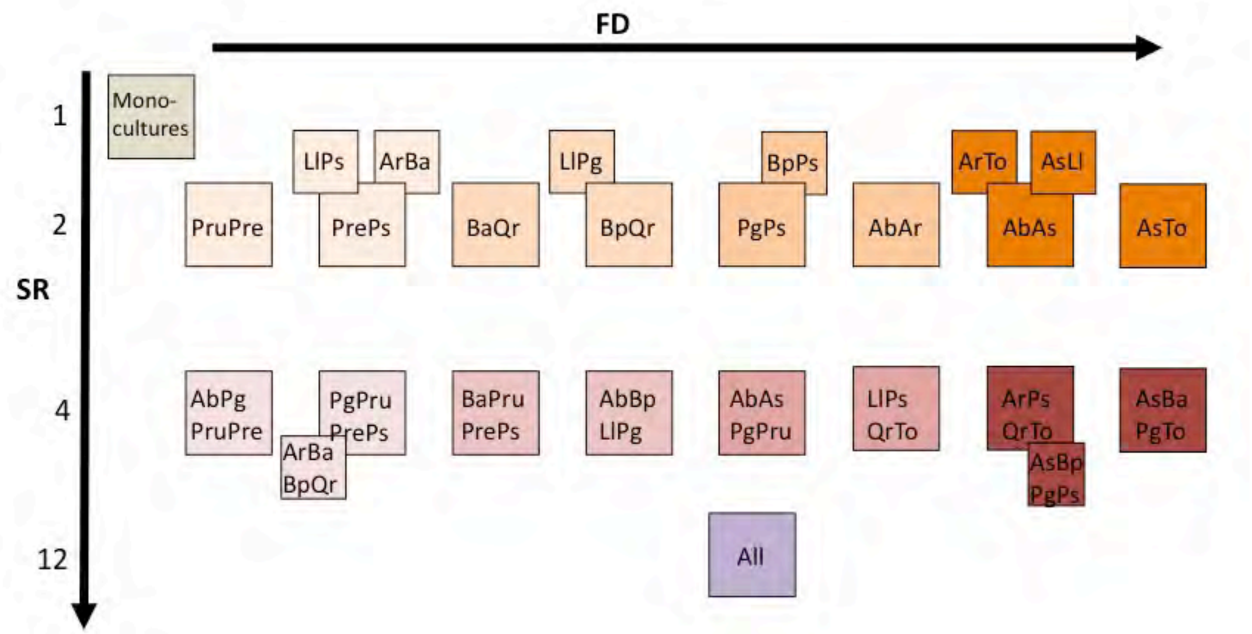

Figure 1. Schematic of the experimental design (replicated four times). Communities are implemented along a gradient of species richness (SR) and functional diversity (FD). Smaller superposed squares indicate the replication of different communities with similar FD resulting in a total of 14 two-species mixtures and ten four-species mixtures. 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* and To – *Thuja occidentalis*.

FD calculation

The experiment aimed specifically at testing for the effect of FD on EF and the existence of complementarity, two concepts closely related. Niche complementarity or complementary resource use hinges on the idea of niche partitioning through differences in functional traits. Hence, the two- and four-species mixtures in the experiment were selected along a gradient of continuous FD (Fig 1). To establish these gradients, FD indices had to be calculated prior to planting. The index used to calculate FD throughout this paper was functional dispersion (FDis, Laliberté et Legendre, 2010). FDis produces indices similar to Rao's quadratic entropy but offers several advantages. FDis is the mean distance of each species to the center of mass of all species in a multidimensional trait space. Species' abundances can be used to weigh distances. In addition to accepting any number and type of trait (i.e. continuous to qualitative), FDis is mathematically independent of SR, resolves for communities of two (or more) species contrary to other indices, and allows weighing of individual traits (Laliberté et Legendre, 2010), all of which are needed to test our hypotheses (for example to distinguish SR from FD).

Although only productivity is presented here, a variety of ecosystem processes on multiple trophic levels have been and will be assessed at the Montreal experiment, which is expected to last several years still. Hence, initial FD indices included 12 above- and belowground traits to ensure the inclusion of traits linked to many different of ecosystem processes. These traits included maximal tree height, growth rate, wood density, seed mass, wood decomposition rate, rooting depth, fine root diameter, mycorrhization, specific leaf area, leaf longevity, mass-based leaf nitrogen and leaf size.

However, this approach has also drawbacks. First, the availability of trait data on certain species and especially belowground traits in the literature is limited. Second, traits derived from the literature may vary substantially for the same species, depending on the study. In those cases, we chose trait values from studies encompassing biotic and abiotic conditions closest to our experiment. However, it remains uncertain how those literature values vary from local (in the Montreal experiment) ones. Lastly, initial FD indices may include traits not linked to ecosystem processes under study. Careful choice of number and identity of traits is however vital to reflect ecosystem processes and must correspond to hypotheses linked thereto (Petchey et Gaston, 2006).

To create the initial FD gradient, FDis was calculated for all possible assemblages of two and four species mixtures (i.e. 66 two-species mixtures and 495 four-species mixtures), using traits mentioned above. After ranking the assemblages according to their FD index, the assemblages were divided into eight classes of equal size. From the middle of each class, one species assemblage was chosen to be planted in the field. To control for species composition and add replication (same FD achieved with different species combinations), some classes were resampled, resulting in 14 two-species and ten four-species mixtures (Fig 1). During this process, it was assured that species were distributed as evenly as possible over the gradients.

In the third and fourth year of the experiment (i.e. 2011 and 2012), local traits were measured in monocultures to substitute missing or most variable literature values in final analyses. Specific root length, fine root diameter and branching intensity (i.e. number of tips per cm length) were measured on first to third order roots in 2011 (for methodology and results see Tobner, Paquette et Messier, 2013). Leaf area (cm^2) and leaf mass per area ($mg\ mm^{-2}$) were measured on sun leaves in 2012. We also updated the original trait table with new or improved values from the literature for those traits we did not measure *in situ*.

In analyses, we applied univariate (single trait) FDis as multivariate FD indices do not permit to directly identify the contribution of each trait to a particular ecosystem process (Roscher *et al.*, 2012). In addition, multivariate indices were shown to mask signals when traits with opposing effects were included (Spasojevic et Suding, 2012). In addition, multivariate indices never increased model fit when tested in the present study (data not shown).

Aboveground stem productivity

In general, diversity indices were calculated over the entire plot (8 x 8 individuals) whereas ecosystem responses (i.e. productivity) were assessed over the inner 6 x 6 individuals to exclude buffer effects. To assess productivity in a non-destructive fashion, tree height and diameter (at 5 cm tree height) were measured at the end of each vegetation period from 2009 to 2012. An approximation of biomass was calculated for each year as diameter^2 x height x wood density.

Mortality over the four years was negligible. In 2012, out of the 5328 trees of the inner 6 x 6, 39 were dead and 122 showed signs of crown damage, mostly due to herbivory or snow. In 2011, wasp nests impeded the measurement of certain trees. To accommodate for these missing values, biomass per plot was calculated as the mean tree biomass per species multiplied by the number of individuals present in the plot. Net diversity effects (NE), complementarity effects (CE) and selection effects (SE) were calculated on these values.

Diversity indices (i.e. CWM and FDis) were weighed by species' relative dominance measured as volume, as this generally increased explanatory power (data not shown). In this case, the mean tree volume (diameter^2 x height) per plot and species was calculated including all 8 x 8 individuals.

Biodiversity effects

One fundamental approach to assess the scale of diversity (mixture) effects is the relative yield (RY) approach (de Wit, 1960). In its essence, the relative yield approach compares the yield of any given species in mixture to its relative (i.e. same individual numbers) yield in monoculture. For any given species A in mixture with B, RY is calculated as $RY_A = Y_{AB} /(p_A Y_A)$, where Y_{AB} is the yield of species A in mixture with B and $p_A Y_A$ its proportion in monoculture (Williams et McCarthy, 2001). A RY = 0 would thus indicate no mixture effect, a RY > 1 a positive and a RY

< 1 a negative mixture effect. To assess the effect of diversity on a community level, species' RY can be averaged ($\overline{RY}$) or summed (relative yield total, RYT) over all species within a given community.

A more recent approach to assess diversity effects is based on a partitioning of net biodiversity effects (NE) into complementarity (CE) and selection effects (SE) (Loreau et Hector, 2001). Both constituent effects (CE and SE) hinge on the calculation of RY. SE is simply the covariance between species' relative (ΔRY) and monoculture yields (M) multiplied by the number of species present in the community (N, equation 1). CE is the mean of species' relative yield ($\overline{\Delta RY}$) multiplied by the mean of species' monoculture yields ($\overline{M}$) and the number of species (N) (equation 1, Loreau et Hector, 2001).

$$NE = CE + SE = N\overline{\Delta RY}\,\overline{M} + N\,cov(\Delta RY, M) \qquad \text{[Eq. 1]}$$

In summary, the relative yield approach allows assessing the effects of diversity on a species-specific level while NE and its components operate at a community level. In this sense, RY averaged $\overline{RY}$ or summed (RYT) over all species in a community is similar to a relative NE, which is simply the percent increase in yield in mixture compared to the average monoculture (Fig. 2). The latter approach clearly offers the unique advantage to link diversity effects to underlying mechanisms by assessing the contribution of single species effects (SE) and hence functional identity as well as multiple species effects (CE) and consequently functional diversity. However, this approach has its limitations, especially when being applied to tree-dominated systems. First, through the inclusion of monoculture yields in both components, these measures are sensitive to absolute yields and may overweigh the contribution of higher-yielding species (Fridley, 2003). Second, perennial plants such as trees increase in biomass every year (or season) and consequently in NE. The partitioning approach is thus not suited to test for the effect of time in those systems. In addition, NE and its components are calculated based on the absolute increase in yield. However, increasing the same amount of yield units in mixture compared to monoculture constitutes a relatively greater effect on smaller trees compared to bigger trees (Fig. 2).

In the present study, we applied the additive partitioning method to assess general diversity effects for each community and the respective contribution of single (SE) and multiple species effects (CE). To test for effects of diversity over time and on a species-specific level however, the RY approach was applied.

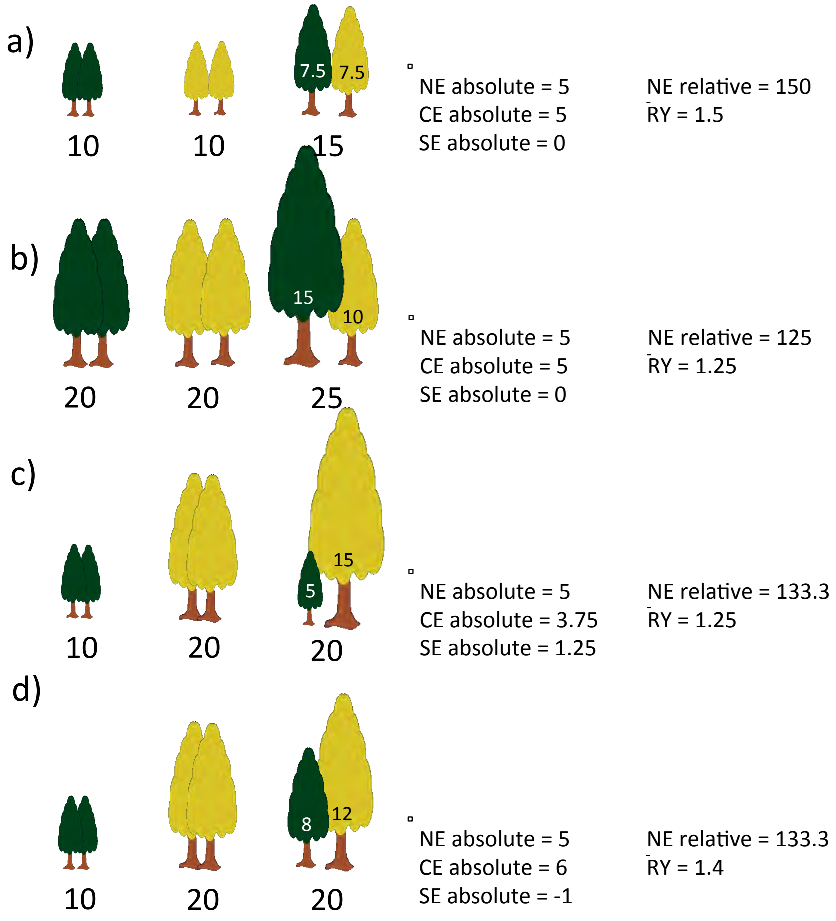

Figure 2. Schematic for different calculations of net diversity effects (NE), complementarity (CE) and selection effects (SE) following additive partitioning (Loreau and Hector 2001) as well as relative yields (RY, deWit, 1960). Absolute NE in all examples equals 5: all mixtures produced 5 units of yield more than expected from their average monoculture. In relative terms however, the increase in yield in mixture compared to the monoculture is higher in a) than in b), similarly to RY. In other words, compared to the smaller monocultures in a), an absolute increase in 5 units of yield is relatively greater in b) (150% versus 125%). In c) and d) absolute and relative NE are equal but SE range from positive (c) to negative (d).

Data analysis

To test for effects of functional diversity and identity on response variables (i.e. biomass and diversity effects), a restricted maximum likelihood model (REML) was applied using the following general structure:

$$Y' = microtopography + block(random) + FD_1 + \cdots + FD_n + CWM_1 + \cdots + CWM_n + \varepsilon,$$

where the co-variable microtopography is the difference in elevation between plot centers measured on site to account for slight differences in soil humidity, ‘FD’ functional diversity indices (FDis), ‘CWM’ community weighed means and ‘ε’ an error term. Models included two- and four-species mixtures, only. Data were checked for heteroscedasticity and log transformed, were necessary.

To start, all (single trait) FD indices and CWMs were entered into this model. Stepwise regression methods were applied to identify diversity indices that had a significant effect on the response variable. To control for possible multicollinearity, constraints were added to this stepwise regression process. CWM of wood density was omitted from analyses since that information was used in biomass calculations. From suites of traits with known correlations in leaves (e.g. LMA, leaf are, leaf nitrogen) or roots (SRL, fine root diameter, branching intensity) only one trait per suite was permitted in final model fits (see Fig. 5 for complete list of FD indices). However, the latter constraints did not have to be applied. Biomass and net diversity effects were tested against FD and CWM, CE only against FD and SE only against CWM as conceptually suggested. The residuals of the final model fit were tested against species richness (two- versus four species-mixtures).

To test if diversity effects changed over the four years, repeated measures ANOVA were applied including microtopography, year and species richness as well as the interaction term between year and SR (never significant). In cases of significant effects of year on diversity effects, differences in RY between years were tested against zero in a one-sample t-test. A correction for multiple comparisons similar to the one used in Tukey HSD tests was applied.

Results

In the fourth year of the experiment, aboveground stem biomass ranged from 14.5 kg to 98.1 kg per plot. The highest biomass was achieved in *L. laricina* monocultures, followed by a four species mixture (AsBpPgPs) and two two-species mixtures (BpQr and BpPs) that all include *B. papyrifera* (Fig 3).

Although no transgressive overyielding was observed, positive net biodiversity effects (NE) occurred in 19 out of 25 mixtures (Fig 4). NE ranged from -3.6 kg for the *A. rubrum* and *B. alleghaniensis* mixture (ArBa) to +44 kg for a four species mixture including *A. saccharum, B. papyrifera*, *P. glauca* and *P. strobus* (AsBpPgPs, Fig. 4). Positive mixture effects were largely due to selection effects (SE). Whereas SE had negative values in only three communities (PruPs, ArBa, BpQr), more than half (i.e. fourteen) of the communities had negative values for CE (Fig 4). If only positive values are considered, a total of 197 kg was overyielded in the two-and four-species mixtures (NE) out of which 70% (137 kg) were due to SE and another 30% (60 kg) were due to CE. More than 90% of the 197 kg were overyielded in seven mixtures, including three two-species and four four-species mixtures. All but one (BqQr) are mixtures of deciduous and evergreen species and they all contain *B. papyrifera* and/or *L. laricina* (except BaPruPrePs).

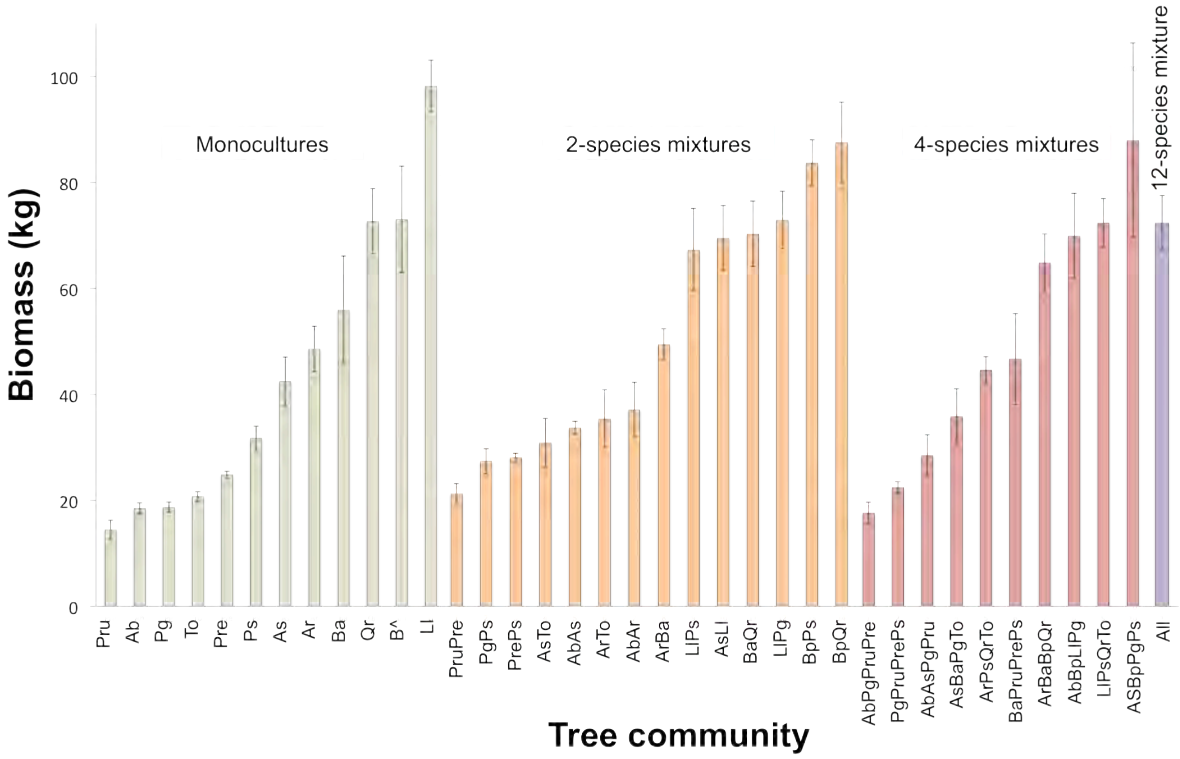

Figure 3. Stem biomass (calculated on the inner 6 x 6 trees) by tree community (means ± standard error for the four blocks). Ab – *Abies balsamea*, Ar – *Acer rubrum*, As – *Acer saccharum*, Ba – *Betula alleghaniensis*, Bp – *Betula papyrifera*, Ll – *Larix laricina*, Pg – *Picea glauca*, Pru – *Picea rubens*, Pre – *Pinus resinosa*, Ps – *Pinus strobus*, Qr – *Quercus rubra* and To – *Thuja occidentalis*.

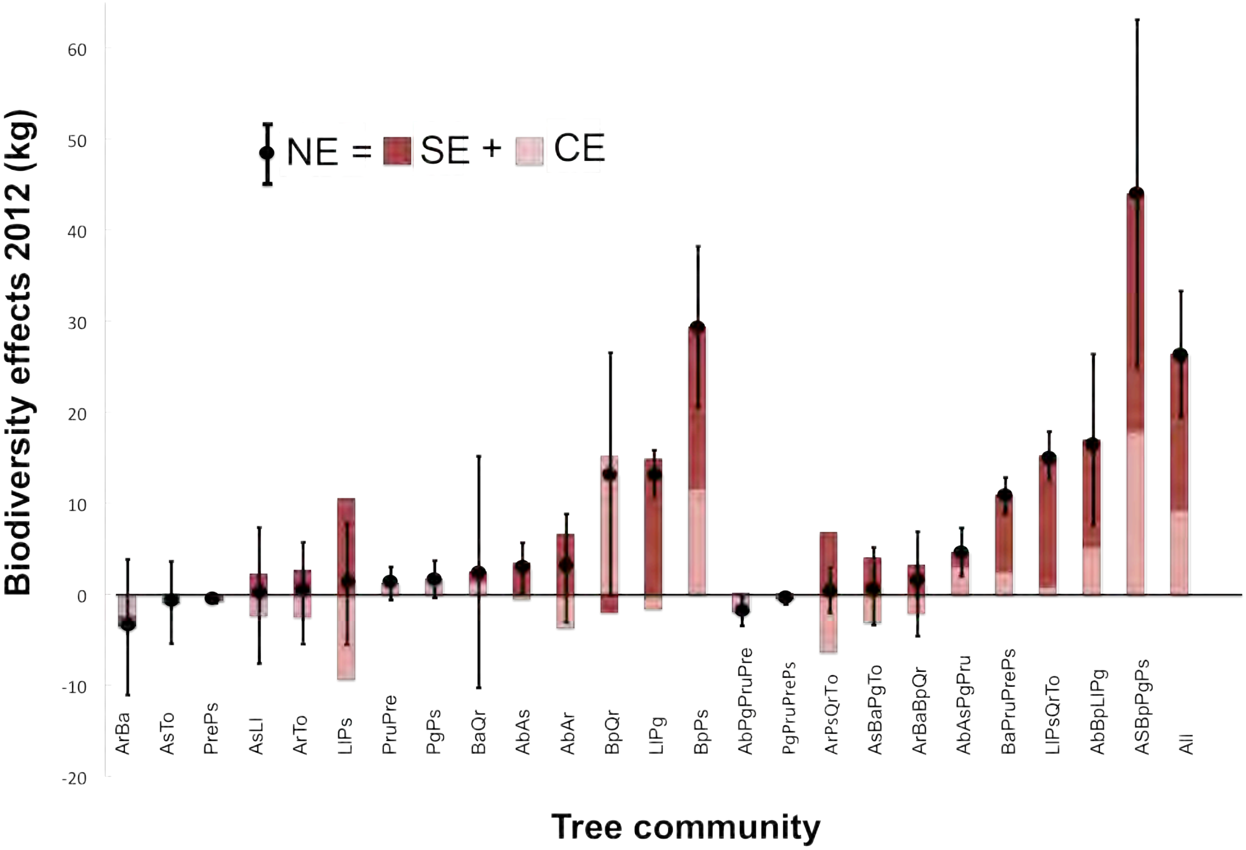

Figure 4. Biodiversity effects by tree community.Given are net biodiversity effect (NE, filled circles) ± standard error (for the four blocks) and its two components complementarity effects (CE, light red bars) and selection effects (SE, dark red bars). Biodiversity effects were calculated on mean species biomass in each mixture in the fourth year of the experiment, 2012. 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*.

In general, community weighed means (CWM) were more strongly correlated to aboveground stem biomass and NE than FDis. In addition, most of FDis indices were negatively related to those two response variables (Fig. 5). Through stepwise regression methods, six functional diversity indices were identified that together with microtopography explained more than 90% of variation in aboveground stem biomass. The majority of these indices were community weighed means (i.e. leaf longevity, rooting depth, branching intensity, seed mass and leaf nitrogen), only FDis of seed mass significantly contributed to biomass (Table 1). Functional diversity indices identified with significant explanatory power on NE largely overlap those identified for biomass. Together, CWM of leaf longevity, rooting depth, branching intensity, seed mass and FDis of seed mass and leaf nitrogen explain around 50% of variation in NE (Table 1).

Around 30% of variation in SE was explained by microtopography and CWM. Similar to biomass and NE, branching intensity and leaf nitrogen significantly explained variation in SE. The strongest effect in SE however was related to shade tolerance (Table 1). Complementarity effects on the contrary could not be significantly explained by any of the FDis calculated in the present study. Microtopography alone however explained roughly 25% of variation in CE (Table 1).

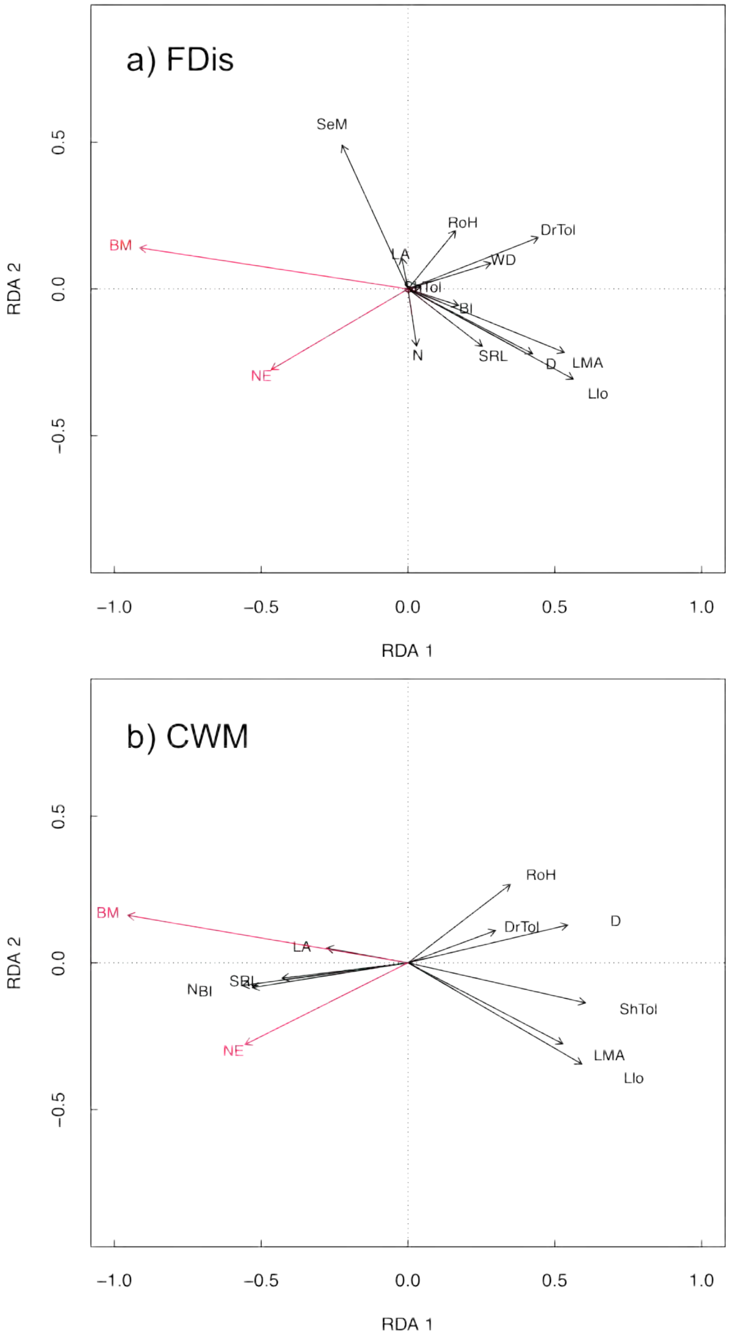

Figure 5. Redundancy analysis of functional diversity indices (black arrows) and biomass (BM) and (NE) (red arrows). Traits used to calculate a) functional dispersion (FDis) and b) community weighed means include: seed mass (SeM, g 1000 seeds^{-1}), wood density (WD, g cm^{-3}), rooting depth (RoH, shallow, medium deep rooted), fine root diameter (D, mm), specific root length (SRL, m g^{-1}), branching intensity (BI, number of root tips per length), leaf longevity (Llo, months), leaf area (LA, cm), leaf nitrogen (N, % per unit mass), leaf mass per area (LMA, g m^{-2}), drought and shade tolerance (DrTol and ShTol, 1 – intolerant to 5 – tolerant). Note that wood density was not included in CWM indices due to its use in biomass calculation.

Table 1 Summary of mixed model (REML). Degrees of freedom (DF), F-ratios, p-values and the coefficient of determination for the whole model (R^2) including fixed effects (functional diversity – FD and community weighed means – CWM) on biomass (BM), net diversity effects (NE), complementarity effects (CE) and selection effects (SE). Given are effects after stepwise regressions (see Fig. 5 for full array of diversity indices). Microtopography was measured as the elevation of each plot center. Only significant effects are shown; see text for complete list of effects tested. Difference between highest and lowest plot was 36 cm.

	Effect	Sign	DF	F-ratio	p-value	R^2
BM	Microtopography	-	1	30.7	<.001	0.91
	CWM leaf longevity	-	1	351.3	<.001	
	CWM rooting depth	-	1	113.1	<.001	
	CWM branching intensity	+	1	92.6	<.001	
	CWM seed mass	-	1	34.8	<.001	
	CWM leaf nitrogen	+	1	8.9	0.004	
	FD seed mass	+	1	6.0	0.016	
NE	Microtopography	-	1	14.2	<.001	0.47
	CWM branching intensity	+	1	26.2	<.001	
	CWM rooting depth	-	1	13.5	<.001	
	CWM leaf longevity	-	1	7.5	<.001	
	CWM seed mass	-	1	5.9	0.017	
	FD seed mass	+	1	15.2	<.001	
	FD leaf nitrogen	+	1	7.3	0.008	
CE	Microtopography	-	1	11.4	0.0011	0.24
SE	Microtopography	-	1	12.2	0.04	0.31
	CWM Shade Tolerance	-	1	16.5	<.001	
	CWM leaf nitrogen	+	1	6.6	0.012	
	CWM branching intensity	+	1	5.9	0.017	

Although calculating diversity effects following Loreau and Hector (2001) offers the advantage of being able to separate SE and CE, values are sensitive to changes in absolute yield. To compare diversity effects over time (independent on absolute stem biomass), we calculated relative yield (RY). Averaged over all mixtures, RY increased significantly from 2009 to 2010 but decreased in 2011 and 2012 to levels similar to 2009, with no significant difference between species richness two and four (Fig. 6).

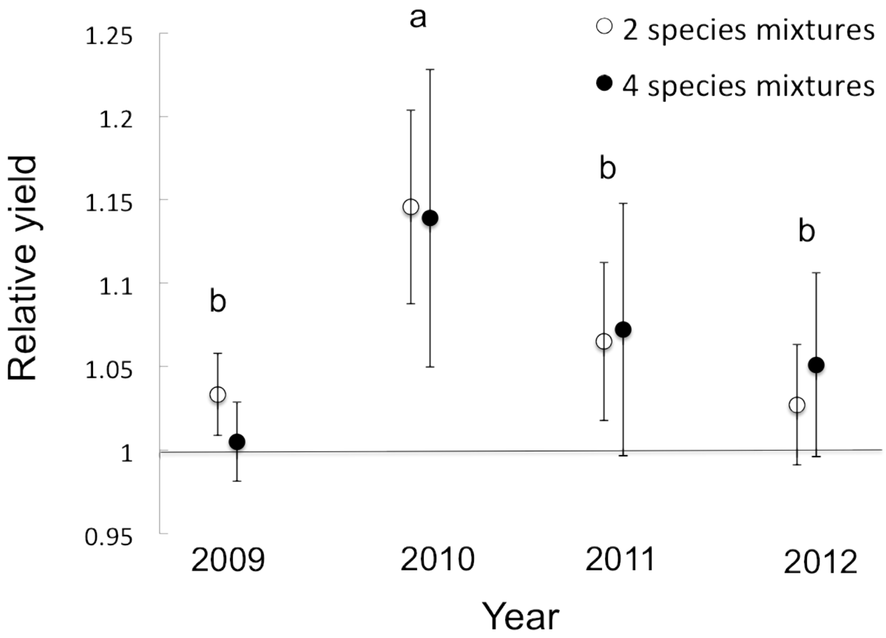

Figure 6. Relative yield (RY) of two- (empty circle) and four-species mixtures (filled circle) by year. Symbols are slightly offset to improve readability. Given are means ± standard error across mixtures and blocks (N = 56 for 2-species and 40 for 4-species mixtures). Different letters indicate significant differences between years for all mixtures, as there was no significant difference between 2- and 4-species mixtures. RY >1 indicate positive mixture effects, RY< 1 indicate negative mixture effects.

On a species-specific level, RY in 2012 varied between 0.54 for *P. strobus* and 2.74 for *B. papyrifera* when averaged over all mixtures. Within individual mixtures, relative yield ranged from 0.3 (i.e. 70% less biomass than expected) to around 5.0 (i.e. 500% more biomass than expected) (Fig. 7). In general, RY was lower for evergreen compared to deciduous species (Fig. 7). About half of the species showed RY values significantly different from one, indicating significant mixture effects (Fig. 7). Among the seven species significantly affected by mixtures, four evergreen coniferous species underyielded while *B. papyrifera*, *L. laricina* and *Q. rubra* significantly overyielded in mixtures.

Changes in RY over time were species specific. While RY for *B. papyrifera* and *L. laricina* significantly increased, RY for *A. balsamea, P. glauca, P. strobus* and *T. occidentalis* significantly decreased from 2009 to 2012 (Fig. 7). RY for all other species did not change significantly over time.

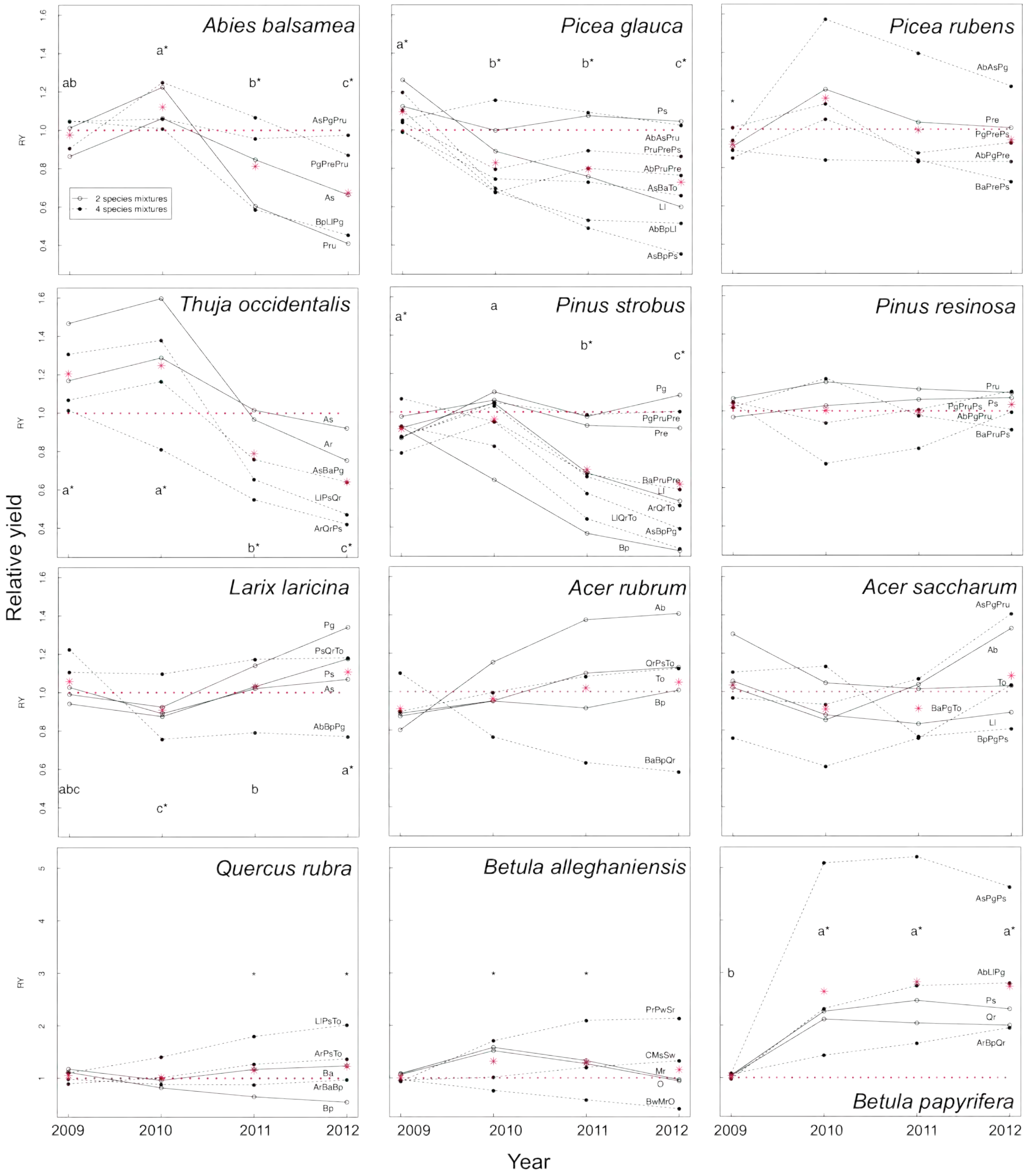

Figure 7. Relative yield (RY) of each species in two (solid lines) and four species mixtures (dotted lines) from 2009 to 2012. Given is also the mean per species (red asterisk, effect of species richness was never significant). Different letters indicate significant differences between years for the species mean. RY >1 indicate positive mixture effects, RY< 1 indicate negative mixture effects. 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*.

Discussion

The present study confirms the general positive mixture effect that was documented for systems as different as forests (Zhang, Chen et Reich, 2012), grasslands (Cardinale *et al.*, 2011) and aquatic (Cardinale *et al.*, 2012 ; Mora *et al.*, 2011) environments on different trophic levels such as producers, herbivores, predators and detrivors (Cardinale *et al.*, 2006). There was no transgressive overyielding in our experiment so far. The highest biomass after four years of the experiment was achieved in monocultures of *L. laricina*. Although transgressive overyielding is often seen as the ultimate demonstration of niche complementarity, such overyielding has been documented in but a few cases and remains a rare phenomenon (Cardinale *et al.*, 2011 ; Loreau et Hector, 2001 ; Schmid *et al.*, 2008).

The present study is one of the first to test for underlying mechanisms of diversity effects in trees. Here, positive diversity effects were largely driven by selection (around 70%). In other words, some species that did well in monoculture profited from reduced interspecific competition compared to intraspecific competition and came to dominate mixtures. Across a variety of BEF studies, complementarity and selection effects were found to contribute around 50% each to positive net biodiversity effects (Cardinale *et al.*, 2011). In contrast to grassland systems were all species are more or less equally shade-intolerant, trees exhibit considerable variation in shade-tolerance (Humbert *et al.*, 2007). In the present study, the species that significantly enhanced biomass in mixture compared to monocultures included four deciduous, shade-intolerant species (*B. papyrifera, L. laricina, Q. rubra* and *B. alleghaniensis*). It is thus those four species that were most likely best adapted to the open conditions during the first years of the experiment and their accrued growth led to intraspecific competition clearly exceeding interspecific competition.

Following the stress gradient hypothesis (Bertness et Callaway, 1994), positive plant interactions have been hypothesized to gain importance in stressful environments and it has often been assumed that the diversity productivity relation as well as the contribution of complementarity and selection effects depend on site conditions (Reich *et al.*, 2001 ; Warren, Topping et James, 2009). Studies examining BEF along environmental gradients are scarce and the few results controversial (Steudel *et al.*, 2012 ; Wacker *et al.*, 2009). Evidence for reduced competition and increased complementarity (at least in relative importance) in environmentally challenging conditions has been documented in herbaceous (Jarchow et Liebman, 2012 ; Wacker et al., 2008), microalgae (Steudel *et al.*, 2012) and tree systems (Paquette et Messier, 2011 ; Pretzsch *et al.*, 2013). Here, the high intensity agricultural input over decades on the study site resulted in nutrient-abundant conditions possibly favoring single species effects (i.e. selection). This is consistent with theoretical considerations that the coexistence of functionally divergent species increases productivity in less productive and more stressful environments, while dominant and highly productive species are able to competitively dominate in more productive habitats (Bertness et Callaway, 1994 ; Gause, 1934a).

Similarly, effects of biodiversity in general (species richness) were less pronounced on more fertile sites (Potter et Woodall) and in less stressful (i.e. temperate compared to boreal) environments (Paquette et Messier, 2011). Corroborating these observations, on the rather nutrient rich study site described here, no significant differences between two- and four-species mixtures were found in productivity and diversity effect.

Diversity indices

Consistent with the large contribution of selection effects to net biodiversity effects, community weighed means (CWM) had greater explanatory power on variation in biomass and diversity effects. This corroborates studies in herbaceous (Díaz et Cabido, 2001 ; Mokany, Ash et Roxburgh, 2008 ; Roscher *et al.*, 2012) and tree systems (Nadrowski, Wirth et Scherer-Lorenzen, 2010) where functional identity rather than diversity better explained productivity.

Although around 30% of net biodiversity effects were attributed to complementarity in the present study, none of the measured FDis significantly explained complementarity effects. In addition, microtopography alone explained around 25% of variation in CE. In fact all measures of diversity (including RY) as well as productivity significantly decreased with increasing plot center elevation indicating that in lower elevation plots higher biomass and hence increased species interactions lead to increased diversity effects.

Only little is known about which traits are involved in tree productivity and its diversity effects. In forests, positive mixture effects appear most common in stands of species with vertical stratification (Garber et Maguire, 2004 ; Kelty, 1992) and/or contrasting traits such as shade tolerance (Zhang, Chen et Reich, 2012), wood density (Swenson et Enquist, 2007), seed mass (Ben-Hur *et al.*, 2012) and maximum height (Paquette et Messier, 2011 ; Ruiz-Benito *et al.*, 2013). Due to large ontogenetic shifts in trees, it can be expected, that traits linked to productivity change with tree age. It would thus appear logic that maximum height may not be of importance in young tree communities. In the present study, community weighed means of leaf longevity, seed mass and two root traits showed strongest explanatory power on productivity and net diversity effects (NE). In other words, communities of increased biomass were dominated by species with the following functional characteristics: a reduced leaf life span (i.e. deciduous), smaller seeds (early successional species), shallower root systems and highly branched fine roots. The significant positive effect of FDis of seed mass implies that a certain trait variation in seed mass contributed to increased biomass. All of those traits show some correlation (Fig. 5) and can be grouped along the same life-history axes, formerly described as *r*-strategists (Reznick, Bryant et Bashey, 2002). In fact, deciduous, rapidly developing, shade-intolerant species in their identity or diversity have thus been crucial in explaining overyielding in all cases.

Interesting to note in the present study is the importance of root traits in explaining productivity and diversity effects. The significant effect of rooting depth and branching intensity may reflect increased belowground compared to aboveground competition in those young tree communities. Especially in the first two years of the experiment, light was not a limiting resource. The lack of mature shade-casting trees and ample space between planted seedlings may have emphasized belowground competition and favored species with shallow, highly branched roots. As most plant nutrients are situated in the upper layers of the soil, shallower, increasingly branched fine roots may reflect an increased capacity to access resources. This corroborates results from natural forests where mixed species showed increased fine root productivity through increased soil volume filling, especially in the upper soil layers (Brassard *et al.*, 2011).

Consequently, it could be expected that with increasing growth and accrued species interactions, diversity effects increase, at lest in relative importance. It could be expected that with increasing canopy closure, aboveground traits increase in respective importance (Ishii, Azuma et Nabeshima, 2013). However, one could also expect increased belowground niche partitioning due to the increased uptake and depletion of nutrients. Accumulating evidence from the longest-running (grassland) BEF experiments do point to increased complementarity with time (Reich *et al.*, 2012).

Diversity effects over time

Over a large number of studies, net diversity effects have been found to increase with time (Cardinale *et al.*, 2012). Although two distinct ecological mechanisms were proposed to underlie positive mixture effects, both (complementarity and selection) have been shown to be mutually at work in creating positive net biodiversity effects. Their relative contribution over time however has been shown to shift towards increasing importance, and in fact dominance of complementarity with time in many cases (Allan *et al.*, 2011 ; Cardinale *et al.*, 2007 ; Fargione *et al.*, 2007 ; Reich *et al.*, 2012).

In the present study, overyielding (mean RY for all plots) was significantly higher in the second year of the experiment, compared to all other years (Fig. 6). This was independent of species richness. While the first year of the experiment was characterized by an establishment phase with moderate growth, trees profited from the unoccupied space around them in the second year and showed highest relative growth rates (data not shown) and highest relative yields. This corroborates with first evidence from experiments where diversity effects increased with biotope space (Dimitrakopoulos et Schmid, 2004). In the following years, reduced diversity effects could be linked to the start of physical tree interactions and thus reduced biotope space. When calculated per species, RY did not generally decrease over time but was rather species-specific. While *L. laricina* and *B. papyrifera* could significantly increase their RY from 2009 to 2012, several evergreen species significantly decreased in RY. After four years of tree interactions, two competitive species came to dominate ecosystem functioning due to competitive exclusion of several evergreen species.

Interestingly, in grasslands (Cardinale *et al.*, 2007) and tropical tree plantations (Sapijanskas, Potvin et Loreau, 2013) it took five years to detect a significant signal of complementarity / overyielding. Increasing complementarity over time was shown due to increasing functional divergence of species (Sapijanskas, Potvin et Loreau, 2013) and/or functional turnover in species (Reich *et al.*, 2012). In contrast to herbaceous species, trees accumulate large amounts of carbon and nutrients. Here, it may thus be expected that species with greater investment in belowground structures or reserves catch up in aboveground investment in future years resulting in increased tree interactions. It has been shown that traits are plastic in response to neighbor diversity and identity possibly promoting complementary resource use (Ashton *et al.*, 2010 ; Messier *et al.*, 2009). Hence, in the present study, increased interactions and possible phenotypic plasticity could create stronger positive mixture effects in the future due to functional divergence. Long-term experiments however are necessary to test for temporal complementarity through species turnover in trees.

Conclusion

These are the first results from experimental tree communities that specifically tested for the effects of functional diversity and the existence of complementarity in tree communities, independent of species richness. We demonstrated general positive mixture effects for most polycultures. After four years of growth, those mixture effects were driven primarily by selection (70%) compared to complementarity effects (30%). In consequence, functional identity better explained productivity and diversity effects than functional diversity, attesting the dominance of few deciduous species and the competitive exclusion of most evergreen species. The strong effects of root traits emphasize the need to better investigate and understand belowground interactions. Following natural succession patterns of those species, changes in dominance are to be expected (in favor of evergreen species) and consequently, possible shifts in diversity effects. Evidence is emerging, that complementarity may be a mechanism gaining importance in the long-term, assuring spatial and temporal stability (Cardinale *et al.*, 2012).

Studying BEF relations in tree-dominated systems bears undeniable advantages as well as caveats. Traditional approaches to assess diversity effects as done in herbaceous systems are limited in tree systems. In contrast to herbaceous plant species, trees have secondary growth and through reserves and different allocation strategies, responses assessed over several years may bear signals from previous years. In the present study, trees are still closing the canopy and increasing interactions. Consequently, diversity effects of the last years could differ from the early years of the experiment (less interactions). Assessing diversity effects on the last years growth (biomass 2012 – biomass 2011) instead of the total aboveground biomass accumulated over four years may avoid a dilution of the diversity signal and give a clearer idea of the underlying BEF mechanisms in the future. In addition, the additive partitioning method should not be used to test for effects of time on diversity effects. Here, we presented a mixed approach using the additive partitioning approach and the relative yield approach.

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Coté, John Watson and Marc Samoisette provided valuable information on the study site, advice and support with site maintenance. Laura Williams kindly provided *in situ* leaf traits.

CONCLUSION

The aim of this thesis was to fill crucial gaps in knowledge surrounding plant functional traits in tree-dominated systems. Specifically, the objectives were to improve our understanding of fine root trait variation within and across tree species, to design and implement an experimental design, to test for the effects of trait diversity (functional diversity) on productivity as well as the existence of complementarity in tree communities, and to evaluate how functional diversity affects aboveground productivity in trees.

The hidden half

Despite the vital role of roots for plant performance, little is known about root trait variation, especially in trees. This finding confirms emerging evidence for a root trait syndrome – similar to the well established “leaf economics spectrum” that links several leaf traits – that may be due to physiological-economic trade-offs. In contrast to expectations based on earlier studies, no relationship was found between these belowground traits and whole-plant strategies (relative growth rate), indicating a possible link to site fertility.

Chapter I also showed that despite strong correlations between root traits across species, responses to changes in the environment within species were trait specific. A novel approach presented in chapter I provided indications for underlying mechanisms of these trait-specific responses. Through the combination of a trait’s total variation and its phenotypic plasticity (i.e. variation due to the environment), environmental indicator traits can be identified. Fine root diameter for example proved to be the best environmental indicator among the three fine root traits studied with low total variation and almost all due to phenotypic plasticity. In the quest for a mechanistic framework linking functional traits to environmental drivers, identifying indicator traits may greatly enhance our ability to extrapolate from traits to plant communities and ameliorate our capacity to monitor and predict (e.g. the effect of global change drivers).

Chapter III provided further strength to the importance of roots for the performance of trees and the functioning of tree dominated systems. In this chapter the relation between trait diversity and tree productivity as well as diversity effects was tested. Out of all 12 traits included in analyses, four traits significantly explained productivity and net diversity effects, two of which were belowground traits. In the first years of the experiment described in chapter III, light was not a limiting resource. The importance of root traits likely reflects the belowground species interactions and competition for nutrients and / or water. Of the three root traits studied in chapter I and III, community weighed means of branching intensity was significantly correlated to growth and overyielding. Community weighed means assess the functional identity of communities. The low plasticity in regard to ontogeny and environmental changes may make branching intensity a more reliable trait to characterize a species' functional identity.

Together, these results suggest that understanding the rhizosphere and more specifically root trait variation is crucial for understanding the underlying mechanisms of ecosystem functioning. As highlighted in chapter I, one of the most important things to advance root trait research is a unifying framework to assess fine roots. Although often criticized, fine roots are still defined by arbitrary size classes (most often <2 mm) in many places. A functional approach, based on root orders has been proposed. However, studies applying this functional approach use different numbers of root orders rendering a broader understanding (across studies) difficult. Advances in technology are also needed. Even with image analyzing software, time and effort to study fine roots greatly exceed those for aboveground traits. Improved precision in wave reflectance instruments like ground-penetrating radar could provide valuable tools to access the rhizosphere more easily.

Biodiversity and Ecosystem Functioning

Based on the synthesis and the identification of open research questions surrounding BEF in chapter II, it is clear that the question "whether" biodiversity influences EF has long been answered. However, much uncertainty remains about "how" biodiversity influences EF. The IDENT framework proposed in chapter II was developed in response to this knowledge gap. IDENT is a unique network of tree functional diversity experiments designed to be both flexible and easy to implement. As a result, IDENT serves as an effective tool to tackle several open research questions.

The Montreal site of IDENT presented in chapter III is the first study to test the effect of continuous functional diversity on tree productivity, independent on species richness. In addition, diversity effects were separated into complementarity and selection effects in tree communities for the first time, stressing the importance of the latter in young tree communities. In other words, species that did well in monocultures profited from lesser intraspecific competition compared to intraspecific competition. Consequently, indices of functional identity (community weighed means) had greater explanatory power on productivity and diversity effects than indices of functional diversity. Traits linked to productivity and overyielding included community weighed means of leaf life span, seed mass, rooting depth and root branching intensity. In other words, species that profited from lesser interspecific compared to intraspecific competition included early successional species with shallow and finely branched root systems and can be grouped along the same life-history strategies formerly known as *r*-strategists. This demonstrates the adaptation of early successional species to the open experimental conditions and resembles the patterns of natural succession.

Following the concept of natural succession, it could be expected that late-successional species will increase in relative abundance (as expressed by biomass) with time. In addition, all species are still in a period of fast growth likely resulting in increased interspecific interactions in the following years. Undoubtedly, this will influence the absolute and relative contribution of complementarity and selection to net diversity effects. Diversity effects did not increase over time in the Montreal site. These findings contrast many others in the literature where diversity effects tend to increase with time, generally in favor of complementarity effects (Cardinale *et al.*, 2011). However, most of these studies were conducted in grasslands and increased complementarity was attributed to species turnover with different species dominating and driving ecosystem functioning over the years thus maintaining high biomass (Allan *et al.*, 2011). The experimental design presented here is limited in its spatial and temporal extents to test for increased complementarity due to species turnover considering that the average life span of the present species is well beyond 100 years. The only other experiment to date that tested for diversity effects over time in trees found that increasing overyielding was due to functional divergence of species (Sapijanskas, Potvin et Loreau, 2013). In the present experiment, trees are still developing rapidly and species interactions increasing. Taking advantage of the nature of the experimental organisms, in particular their size, one could follow individual trees, organs or even extremities (a root or branch) and observe changes in trait values depending on the neighbor identity. I would thus expect increasing complementarity effects with time due to functional divergence in the present experiment.

However, chapter III also showed that traditional approaches to assessing mixture effects are limited in tree dominated systems. In contrast to annual species, trees accumulate tissue and reserves and biomass. Calculating mixture effects (complementarity and selection) is based on biomass. Hence, mixture effects of any given year in tree communities will always include signals of previous years of tree growth. One way to avoid including information from previous years in assessing productivity would be to calculate annual increment ([biomass year x+1] – [biomass year x]). In a second step, diversity effects could be calculated on these increments and allow contribution of diversity effects in the early years to be separated from the contributions of later years.

Biodiversity and ecosystem functioning research with trees is only just beginning. It will be indispensable to study the effect of functional diversity on ecosystem functioning over time, as this collection of recently established experiments mature. After four years, trees have only started to interact and it will be most interesting to see how the contribution of selection and complementarity effects change in absolute and relative importance over the next years. However, this thesis showed that short-term studies such as within IDENT are a valuable tool to identify mixture effects and functional identities of tree communities overyielding in early years.

Long-term studies are nonetheless vital to complement these findings and examine for example the effect of natural disturbances or resilience to pathogens.

Plant functional traits

My quest for the Holy Grail in plant functional traits certainly lost some of the initial enthusiasm. While understanding on the variation and role of functional traits in ecosystem functioning in trees grew, a general application and extrapolation to ecosystem functioning however seems still far. For one, the ecological significance of many traits (especially belowground ones) lacks consensus in the literature. Specific root length for example is certainly the root trait most employed in root research and has been proposed as environmental indicator trait (Ostonen *et al.*, 2007). In chapter I, this trait was shown less responsive to changes in soil conditions in natural forests than the until now less employed fine root diameter. In fact, due to the divergent responses of specific root length in the literature, this trait was labeled “mysterious” (Ryser, 2006). Another example is the role of functional traits in chapter III. Although almost 30% of net diversity effects were attributed to complementarity, none of the 12 functional diversity indices assessed were significantly correlated to complementarity effects.

Assuming that traits respond differently to neighborhood diversity as they do to ontogeny and age (in chapter I), the specific trait value could potentially be different in each mixture (depending on neighborhood identity and diversity). However, most functional diversity indices do not take this intraspecific variation into consideration. This may explain why none of the FD indices used in chapter III contributed significantly to productivity and overyielding. It is likely that trait plasticity plays a bigger role than often accounted for and the approach proposed in chapter I of comparing total variation to variation due to plasticity might offer possibilities to identify traits that show greater plasticity in response to neighborhood and thus offer greater inside into how complementary resource use may be facilitated.

As proposed in chapter II, assessing ‘realized’ niches through integration of intraspecific variability (plasticity) will likely yield better predictability and finally increase our understanding of underlying mechanisms in creating positive diversity effects. I propose that one way of assessing realized niches could be expressed as the deviation of trait values in mixture from those in monoculture. This surely implies a greater amount of investment, in terms of time, effort and financial resources. The approach used in chapter I that compares total variation of a trait to its phenotypic plasticity may help identifying traits with greater explanatory potential for functional identity (low plasticity) or functional diversity (high plasticity with neighborhood diversity) and thus help direct resources.

In short, this body of work presents progress toward the Holy Grail of linking plant traits with community composition and ecosystem functioning, highlighted the importance of belowground traits and developed a novel experimental approach toward understanding the roles of traits in tree-dominated systems. In addition, the existence of complementarity and selection effects in tree systems was documented for the first time underlining the dominance of the latter and consequently the pivotal role of functional identity in young tree communities.

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