

Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients

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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.

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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 et al. 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 on trees have been observational, using forest inventory data. Most of these studies have reported positive relationships between diversity and productivity (Lei et al. 2009; Paquette and Messier 2011; Vilà et al. 2007, 2013; Zhang et al. 2012) or C stocks (Ruiz-Benito et al. 2013), but some have reported conflicting results (Jiang et al. 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 positive BEF relationships, with the main candidates including complementarity (CE) and selection effects (SE) (Loreau and 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 et al. 2012; 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 (Naem 2002; Paquette and 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 et al. 2013; Reiss et al. 2009). Additionally, it was also proposed that biodiversity effects may be shaped by environmental conditions (Stuedel 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 an 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 influence trait character displacement, thus the realized trait value and consequently realized FD?
5. At what spatial and temporal scales do CE 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 (7×7 or 8×8 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 question 5). 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 et al. 2002; Messier and Kimmins 1991), fine root biomass (Claus and George 2005; Lei et al. 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.

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 (8×8 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, 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 7×7 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

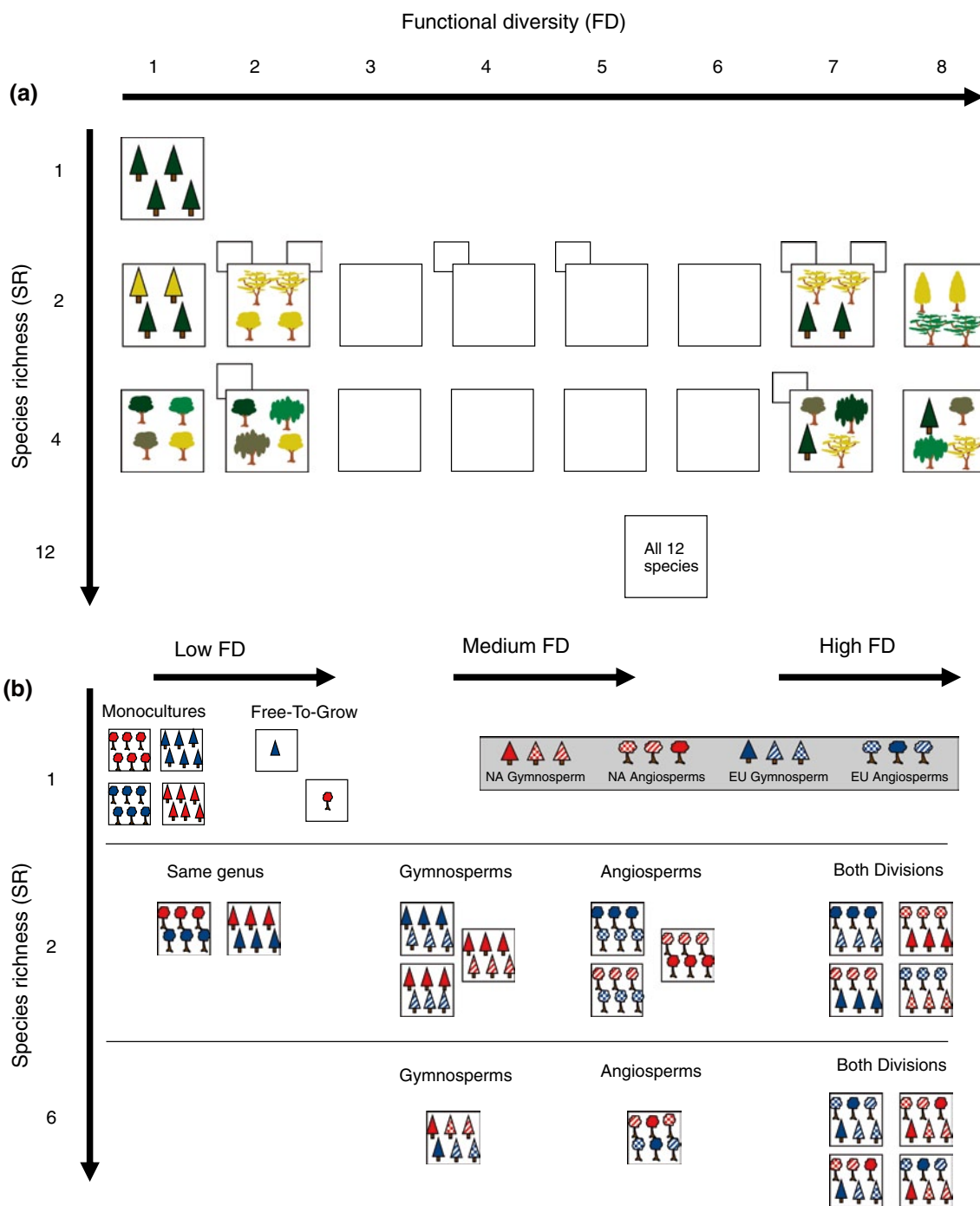


Fig. 1 Schematic representations of the International Diversity Experiment Network with Trees (IDENT) experimental design, showing manipulations of gradients of species richness (SR) and functional diversity (FD). Monocultures of all species are always present. **a** Design of the Montreal (MTL) experiment with SR = 1, 2, 4 or 12 species and a FD gradient of eight levels. *Smaller squares* behind larger ones indicate replications of the same FD level with different

species combinations. **b** 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 was from mixtures of two species within the same division, and high FD from mixtures that include both a gymnosperm and an angiosperm

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

Table 1 Characteristics of the two international diversity experiments implemented at three sites in Canada and the USA

	MTL	AuCl
Location	Ste-Anne-de-Bellevue, QC	Auclair, QC; Cloquet, MN
Latitude, longitude, elevation (m)	45.4247, -073.9390, 39	47.6969, -068.6551, 333; 46.6792, -092.5192, 383
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 block	37	48
Number of trees per plot	64 (8 × 8)	49 (7 × 7)
Number of trees total	9,472	9,408
SR 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/forested
Gradients implemented intentionally	FD over SR (2 and 4)	FD and PD over SR (2) native vs exotics

Size of experiments include corridors around plots and a planted buffer around the experiment, trees planted for destructive sampling and for Auclair/Cloquet (*AuCl*), free to grow trees. Functional diversity (*FD*) gradients were implemented using two- and four-species mixtures (species richness; *SR*) at Montreal (*MTL*), and two species mixtures at AuCl

Table 2 Tree species planted on experiments established near MTL and AuCl and functional traits used to compute FD indices for analyses (see Table 3)

Species	Code	MTL	AuCl	Geographic origin	Wood density (g cm ⁻³)	Seed mass (g 1,000 seeds ⁻¹)	Leaf N (%) (mass based)
<i>Abies balsamea</i>	ABBA	×		NA	0.34	7.6	1.66
<i>Acer platanoides</i>	ACPL		×	EU	0.5165	139	1.99
<i>Acer rubrum</i>	ACRU	×		NA	0.49	26.5	1.91
<i>Acer saccharum</i>	ACSA	×	×	NA	0.56	55.2	1.83
<i>Betula alleghaniensis</i>	BEAL	×		NA	0.55	0.9	2.20
<i>Betula papyrifera</i>	BEPA	×	×	NA	0.48	0.4	2.31
<i>Betula pendula</i>	BEPE		×	EU	0.5125	0.29	2.33
<i>Larix decidua</i>	LADE		×	EU	0.474	7.1	2.05
<i>Larix laricina</i>	LALA	×	×	NA	0.49	2	1.36
<i>Picea abies</i>	PIAB		×	EU	0.37	7	1.19
<i>Picea glauca</i>	PIGL	×	×	NA	0.33	2.4	1.28
<i>Picea rubens</i>	PIRU	×		NA	0.38	3.3	1.15
<i>Pinus resinosa</i>	PIRE	×		NA	0.39	8	1.17
<i>Pinus strobus</i>	PIST	×	×	NA	0.34	17	1.42
<i>Pinus sylvestris</i>	PISY		×	EU	0.422	6	1.33
<i>Quercus robur</i>	QURO		×	EU	0.56	3,378	2.37
<i>Quercus rubra</i>	QURU	×	×	NA	0.56	3,143	2.06
<i>Thuja occidentalis</i>	THOC	×		NA	0.3	1.4	1.02

Trait data compiled from Royal Botanic Gardens Kew (2008), Wright et al. (2004), and Zanne et al. (2009)

NA North America, EU Europe; for other abbreviations, see Table 1

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 diversity 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

Table 3 FD matrix for AuCI based on wood density, seed mass, and leaf N content (Table 2) for two- and six-species combinations [FD index (Laliberté and Legendre 2010)]

	ACPL	ACSA	BEPA	BEPE	LADE	LALA	PIAB	PIGL	PIST	PISY	QURO	QURU
ACPL												
ACSA	0.36											
BEPA	<i>0.95</i>	<i>0.99</i>										
BEPE	<i>0.94</i>	<i>0.93</i>	0.20									
LADE	0.59	0.67	0.44	0.51								
LALA	1.01	0.86	1.07	1.10	0.79							
PIAB	1.35	1.38	1.44	1.56	<i>1.14</i>	<i>0.76</i>						
PIGL	1.52	1.59	1.46	1.60	<i>1.22</i>	<i>0.96</i>	0.30					
PIST	1.28	1.40	1.38	1.52	<i>1.07</i>	<i>0.95</i>	<i>0.35</i>	<i>0.35</i>				
PISY	1.08	1.06	1.18	1.27	<i>0.86</i>	<i>0.44</i>	<i>0.35</i>	<i>0.57</i>	0.5			
QURO	<i>0.77</i>	<i>0.96</i>	<i>1.52</i>	<i>1.48</i>	1.28	1.76	2.06	2.23	1.94	1.82		
QURU	<i>0.63</i>	<i>0.78</i>	<i>1.53</i>	<i>1.50</i>	1.21	1.56	1.85	2.05	1.77	1.61	0.34	
Six Angios.	<i>1.23</i>											
Six Gymnos.	<i>0.92</i>											
NA Angios. + EU Gymnos.	1.43											
NA Gymnos. + EU Angios.	1.71											
Six NA	1.65											
Six EU	1.46											

Not all two-species combinations represented here were established in the experiment. Traits are standardized prior to distance computations; seed mass was log-transformed. *Angios.* Angiosperms, *Gymnos.* gymnosperms; for other abbreviations, see Tables 1 and 2

Values in roman indicate low FD (same genus); see Fig. 1b

Values in italics indicate medium FD (same division); see Fig. 1b

Values in bold indicate high FD (between divisions); see Fig. 1b

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).

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 AuCI 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 BIODDEPTH (Hector et al. 1999), especially for those experiments intentionally linked (e.g., AuCI). 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).

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 and Gaston 2006; Reich et al. 2004). FD measures the extent of functional differences (distance) among species in a community (Laliberté and 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 and 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 et al. 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 and 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

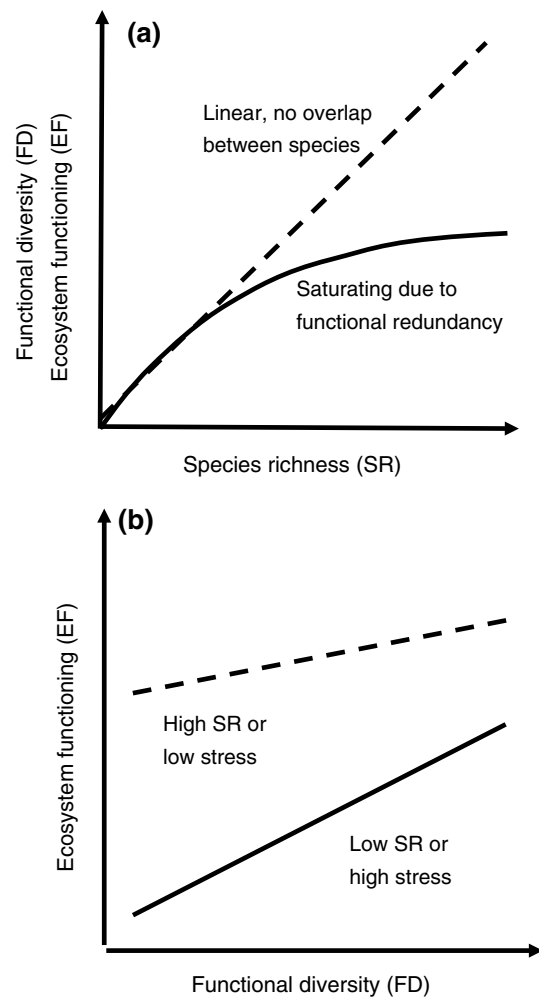


Fig. 2 **a** Expected relationships between SR and FD or ecosystem functioning (*EF*), assuming a linear or saturating relationship. The difference between the two lines is due to functional redundancy between species. A linear relationship is not expected as it would require all species to be functionally singular (no overlap). **b** 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 SR or exposition to stress, resulting in different relationships with FD. For other abbreviations, see Fig. 1

shows a saturating relationship due to functional redundancy (Loreau and 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).

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 and 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: the FD index is based on traits measured elsewhere, and the included traits are not profoundly implied in all ecosystem processes under investigation.

Therefore, for the second experiment (AuCI) we chose a different, complementary approach. Despite modern FD metrics that make use of multi-dimensional trait space to compute distances between species (Laliberté and 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 AuCI experiments, pairs of functionally similar species were chosen a priori for that purpose. The pairs make up planted communities of congenics 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 AuCI for three of the most often reported traits relevant for the productivity of forests (Paquette and 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.

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 and 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 intra-specific competition (Loreau 2004), which also happens to be a criterion for stable coexistence. In agriculture, this method is known as the land equivalent ratio (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). 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):

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

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):

$$Y' = \text{block}(R) + SR + \text{block} * SR(R) + FD + SR * FD + \text{covar}_1 + \dots + \text{covar}_n + \varepsilon \quad (2)$$

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 \times 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.

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

Table 4 Sample results of fixed and random (R) effects of an exemplary mixed model (restricted maximum likelihood) used for analyzing results within the International Diversity Experiment Network with Trees sites for a given diversity effect or response function

Effect	df	F -ratio	P -value
Block(R)	3		
SR	1	0.51	0.51
Block \times SR(R)	3		
FD	1	1.38	0.24
SR \times FD	1	0.29	0.59
CWM	1	2.36	0.13
SR \times CWM	1	0.37	0.55
FD \times CWM	1	0.62	0.43
Covariable	1	0.11	0.74

Shown are results for first-year tree height at the MTL site tested against SR, FD, community weighted mean (CWM), and a randomly generated covariable. For other abbreviations, see Table 1

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 et al. 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 an 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 will no longer be 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 et al. 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 et al. 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 environments (Warren et al. 2009), which has been documented in a few, contrasted systems (Li et al. 2010; Paquette and 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 and 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.

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