LETTER

Functional identity is the main driver of diversity effects in young tree communities

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Abstract

Two main effects are proposed to explain biodiversity–ecosystem functioning relationships: niche complementarity and selection effects. Both can be functionally defined using the functional diversity (FD) and functional identity (FI) of the community respectively. Herein, we present results from the first tree diversity experiment that separated the effect of selection from that of complementarity by varying community composition in high-density plots along a gradient of FD, independent of species richness and testing for the effects of FD and community weighted means of traits (a proxy for FI) on stem biomass increment (a proxy for productivity). After 4 years of growth, most mixtures did not differ in productivity from the averages of their respective monocultures, but some did overyield significantly. Those positive diversity effects resulted mostly from selection effects, primarily driven by fast-growing deciduous species and associated traits. Net diversity effect did not increase with time over 4 years.

Keywords

Biodiversity and ecosystem functioning, biodiversity experiment, complementarity, functional diversity, functional identity, functional traits of trees, IDENT, overyielding.

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INTRODUCTION

The idea that increasing diversity leads to increased ecosystem functioning has been proposed at least since the 19th century. However, it was 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 (Cardinale *et al.* 2012; Balvanera *et al.* 2014).

To explain positive BEF relations, two main effects have been proposed: complementarity and selection. Complementarity effects include niche partitioning, positive interactions (i.e. facilitation) and positive feedbacks on resource supply, whereas selection effects are due to dominant species driving ecosystem functioning (Roscher *et al.* 2012). These mechanisms have been shown to work together in a variety of systems, with complementarity often explaining more of the variance (Reich *et al.* 2001; Cardinale *et al.* 2007; Fargione *et al.* 2007; Cardinale *et al.* 2011), especially with the advance of time (Cardinale *et al.* 2007; Fargione *et al.* 2007; Allan *et al.* 2011; Reich *et al.* 2012). Both mechanisms hinge on the role of functional traits. Indeed, functional aspects of diversity

have been shown to have greater explanatory power on ecosystem functioning than SR (species richness) alone (Díaz & Cabido 2001; Mokany *et al.* 2008; Gravel *et al.* 2011), although recent work highlights that the approach taken in such analyses can lead to the opposite conclusion (Venail *et al.* 2015).

Two main approaches to measure functional aspects of a community have been used. One approach measures distances among species in a multidimensional trait space (Laliberté & Legendre 2010; Mouchet *et al.* 2010) to characterise functional trait diversity (FD). Since functional traits should be related to a species' resource-based niche, greater differentiation among species in functional traits ought to reflect greater resource-use complementarity and reduced competition (Hooper 1998; Petchey 2003). Another approach assesses the community weighted mean trait value of all species present in a mixture (CWM, Mokany *et al.* 2008; Roscher *et al.* 2012). Conceptually, CWMs are based on the 'mass ratio hypothesis' stating that the functional traits of the dominating species in a community drive ecosystem functioning (Grime 1998). As a consequence, CWMs are closely linked to the selection effect (SE) and are a direct measure of the functional identity (FI) of a species assemblage (Mokany *et al.* 2008; Roscher *et al.* 2012). In mature forests, CWM canopy traits explained a large majority of the variance in productivity across > 100

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sites (Reich 2012). De facto, both approaches have been shown to be good predictors of ecosystem functioning in herbaceous (Mokany *et al*. 2008; Roscher *et al*. 2012) and tree systems (Nadrowski *et al*. 2010).

Among natural assemblages, SR and FD are inevitably linked, which makes it difficult to disentangle their respective influence on ecosystem functioning (Naeem 2002). In addition, the relationship between SR and FD is likely to be nonlinear. While at low SR, each species addition may linearly increase FD, the relationship may plateau at higher levels of SR due to functional redundancy. As a consequence, it has been hypothesised that the relationship between FD and ecosystem functions ought to be positive and more linear than between SR and ecosystem functions (Tobner *et al*. 2014). However, very few published studies so far have manipulated FD variation and tested for its effect on ecosystem functioning independently of SR (Reich *et al*. 2004), and even fewer have done so with trees (but see www.treedivnet.ugent.be).

We conducted a common garden experiment using high-density tree communities to assess the relationship between FD and stem biomass increment (a proxy for productivity; hence this term is used thereafter), independently of SR (Tobner *et al*. 2014). The core of this experiment consists of species mixtures of identical SR varying in FD. Here, we present the first results of this experiment, 4 years after its establishment. We investigated the following hypotheses:

(1) FD and CWMs both explain tree mixture productivity, but with the former being a stronger predictor, and
(2) Net diversity effects increase over time (i.e. 4 years), driven primarily by increases in complementarity.

METHODS

Site description

The study site is located at Ste-Anne-de-Bellevue, near Montreal, Québec, Canada (45°26′ N, Long 73°56′W, 39 m.a.s.l.). Mean annual temperature is 6.2 °C with a mean annual precipitation of 963 mm (climate.weatheroffice.gc.ca). The study site is a flat former agricultural field that has been intensively managed for decades. The soil consists of a 20–70 cm deep sandy layer (91 ± 3.7% sand, 6 ± 3.0% clay, 3 ± 2.1% silt, mean ± standard deviation) overtopping clay.

In spring 2009, an area of 0.6 ha was cleared of corn debris before trees were planted with seedlings 1 or 2 years old (Tobner *et al*. 2014) (Appendix S1). The species pool comprised of 12 North American temperate forest species, namely five broad-leaf species and seven conifers (Appendix S1). This experiment is part of the 'International Diversity Experiment Network with Trees' (IDENT) that includes several sites in North America and Europe (Tobner *et al*. 2014).

Experimental design

Trees were planted in square plots of 8×8 individuals, with 50 cm spacing among trees and 1.25 m between plots to allow movement and minimise interplot interactions. For the latter reason, tree roots were also sliced vertically 30 cm deep

around each plot in the third and fourth growing seasons (2011 and 2012). Plot types were monocultures of all 12 species, 14 combinations of two-species mixtures, 10 combinations of four-species mixtures and one mixture including all 12 species (Tobner *et al*. 2014). Each community was replicated four times in a randomised block design for a total of 148 plots and 9472 trees. Within plots, species were planted at random and equal proportions with some restrictions: in two-species mixtures, at least two of the eight neighbours had to be different species. In four-species mixtures, at least two of the eight neighbours had to be from two different species. In the 12 species mixture, all species had at least five individuals, and four had six (for a total of 64).

The distribution of trees within plots was identical in all four blocks. However, the distribution of plots was randomised for each block. Around the outermost rows of the experiment, three rows of trees at 50 cm distance were planted to minimise edge effects and a resource for replacing dead trees – 52 trees died and were replaced after the first year. A fence to protect against herbivory surrounded the experiment and all plots were regularly weeded manually to minimise herbaceous competition.

Calculation of functional identity and diversity

The effects of FD and identity (CWMs) on productivity were tested. To calculate FD, we chose functional dispersion (FDis, Laliberté & Legendre 2010; Tobner *et al*. 2014). FDis is the mean distance of each species to the centre of mass of all species in a multidimensional trait space and produces indices similar to Rao's quadratic entropy but offers advantages pertinent to this study: species' abundances can be used to weight distances; in addition to accepting any number and type of trait (i.e. continuous to qualitative), FDis resolves for communities with as few as two species, and allows weighting of individual traits (Laliberté & Legendre 2010).

Functional dispersion was calculated twice: once prior to planting only for constructing the initial FD gradient (Fig. 1), and once more for post-planting data analyses with updated trait data from the literature and *in situ* measurements. Prior to planting, FDis were therefore calculated for all possible combinations of two and four species from the 12 species pool and 14 two-species and 10 four-species mixtures were chosen to comprise the initial FD gradient (Fig. 1) (Tobner *et al*. 2014). Those initial FDis indices were computed using 12 above- and belowground traits to capture plant resource-use strategies linked to a wide range of ecosystem processes, and weighted simply using planted abundances. For post-planting analyses FDis were weighted by species' relative importance measured using stem volume (diameter^2 × height) (Appendices S2 and S3 for details).

Community weighted means of trait values (CWM) were computed for each trait following Lavorel *et al*. (2008) as the mean trait value of all species present weighted by their relative importance (Appendices S2 and S3). Stem volume per plot and species, FDis and CWM were calculated including all 8×8 individuals in a plot as they impact on the inner 6×6 trees used for computing response variables, whereas plot-level productivity (response variable) was assessed for the
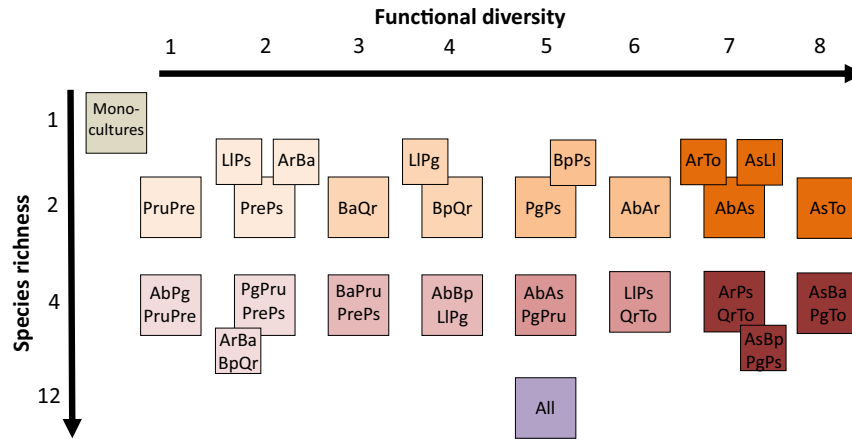
Functional diversity

Figure 1 Schematic representation of the experimental design (replicated four times). Communities are implemented along a gradient of species richness (SR) and functional diversity (FD). FD was calculated as functional dispersion (FDis) (Laliberté & Legendre 2010) based on 12 above- and belowground traits (see section FD calculation). Smaller superposed squares indicate the replication of different communities with similar FD resulting in a total of 14 two-species mixtures and 10 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*; To, *Thuja occidentalis*.

inner 6 × 6 only to minimise edge effects from neighbouring plots.

Aboveground stem productivity

Tree height (*H*) and diameter (*D*, at 5 cm from ground) were measured at the end of each growing season from 2009 to 2012. An approximation of stem biomass was calculated for each year as $D^2 \times H \times$ wood density. Mortality was negligible over the first 4 years. In 2012, 39 out of the 5328 trees of the inner 6 × 6 had died and 122 showed signs of crown damage, mostly due to insect herbivory or snow. In 2011, wasp nests prevented the measurement of 35 trees. To accommodate for these missing values, biomass per plot was calculated as the species mean biomass of measured trees multiplied by the number of planted individuals of each species, summed for all species, all within the same 6 × 6 subplot. Net diversity effects (NE), complementarity effects (CE) and selection effects (SE) were calculated with these values.

Biodiversity effects

Several metrics are used to partition the effects of diversity on ecosystem functioning (most often yield). The common aspect to all of those metrics is the comparison between a species' yield in mixture and its yield in monoculture, also called relative yield (RY, De Wit 1960). Relative yield can be calculated for each component species or for the whole community (relative yield total, RYT, Vandermeer & Goldberg 2003). For a two-species mixture of species A and B, RYT is calculated as follows (dimensionless):

$$RYT = \frac{yield_A \ (mixture)}{yield_A \ (monoculture)} + \frac{yield_B \ (mixture)}{yield_B \ (monoculture)} \quad (1)$$

where yield is expressed as unit per area (e.g. ton biomass per hectare). RYT = 1 indicates no diversity effect (i.e. the performance of species in mixture is equal to their performance in

monoculture). RYT < 1 indicates a negative and RYT > 1 a positive mixture effect.

However, the RY approach does not allow distinguishing the mechanisms underlying diversity effects. A related approach is also based on the calculation of a general deviation of yield in mixture (observed yield, Y_O) from that in monoculture (expected yield, Y_E). This (net) diversity effect (NE - dimensionless) can be partitioned into complementarity (CE) and selection effects (SE) (Loreau & Hector 2001, eqn 2).

$$NE = Y_O - Y_E = CE + SE$$
$$= N \times \overline{\Delta RY} \ \overline{M} + N \times cov(\Delta RY, M) \quad (2)$$

Both constituent effects (CE and SE) hinge on the calculation of RY, in this case expressed as ΔRY:

$$\Delta RY_A = \frac{yield_A \ (mixture)}{yield_A \ (monoculture)} - P_A \quad (3)$$

where *P* is the proportion of the species in mixture (i.e. in terms of density).

CE is the mean of the change in species' relative yields ($\overline{\Delta RY}$) multiplied by the mean of species' monoculture yields ($\overline{M}$) times the number of species (*N*) (eqn 2, Loreau & Hector 2001). CE averages positive and negative diversity effects of all species present in the mixture. SE is calculated as the covariance between species' relative (ΔRY) and monoculture yields (*M*) multiplied by the number of species present in the community (*N*, eqn 2). SE is positive when more productive species in monoculture perform better in mixture than in monoculture, and alternatively negative when less productive species perform better in mixtures than in monoculture. In case of overyielding of both high and low productive monoculture species, SE can be positive or negative, depending on the stronger effect (see Appendix S4 for illustrations).

Using NE, CE and SE offers the advantage of linking diversity effects to underlying mechanisms. However, some caveats have to be kept in mind, especially when working with

trees. NE, CE and SE are sensitive to absolute values (i.e. monoculture yields) and strongly weight the contribution of higher yielding species (Fridley 2003, Appendix S4 for illustration). To assess the relative importance of the diversity effect, we also calculated RYT at the plot level and RY for each species.

Data analysis

We first used a simple random effect model with REML estimation to test for the effects of species richness (SR; 1, 2, 4 and 12) on aboveground stem biomass accumulated after 4 years, with block and plot[SR] as random factors (noted R), and an error term ε:

$$logBiomass = block(R) + SR + SR \times block(R) \\ + plot[SR](R) + \varepsilon \tag{4}$$

Plot[SR] (i.e. the different assemblages of species within a SR level), was added to account for the large differences in the sources of variations between the four different SR levels. We calculated NE (i.e. positive NE equalling overyielding) to test whether mixtures performed better than expected compared with their respective monocultures. NE, CE and SE were calculated for each plot. Two-tailed t-tests were applied ($n = 4$ blocks) to test when diversity effects were significantly different from zero.

A second model was applied to test for the relationships of functional diversity (FDis) and identity (CWM) on response variables (i.e. biomass and diversity effects, Y') including two- and four-species mixtures only, and microtopography (the difference in elevation between plot centres measured on site; range = 36 cm) to account for slight differences in drainage:

$$Y' = microtopography + block(R) + FDis_1 + \cdots + FDis_n \\ + CWM_1 + \cdots + CWM_n + \varepsilon \tag{5}$$

where 'FDis' is functional dispersion, and 'CWM' community weighed means. Models included two- and four-species mixtures only. Residuals were checked for heteroscedasticity and the data were log transformed in one case (CWM of leaf longevity). FDis and CWMs to include into the model were chosen using visual estimation of relatedness to Y' through redundancy analyses (see Appendix S3 for full list of traits), as follows. Stepwise regression was applied to select FDis and CWMs with significant effects (p < 0.05) on the response variable. Constraints were added to the stepwise selection: i) CWM of wood density was omitted from analyses since that information was used in biomass calculations and ii) only one trait from suites of traits with known correlations in leaves (e.g. LMA, leaf area, leaf nitrogen) or roots (SRL, fine root diameter, branching intensity) was used. CE was tested against FDis and SE against CWMs only, as conceptually suggested. We also tested if there was a relationship between the residuals of the model and SR but no significant results were found.

We tested if the effect of diversity changed over the 4 years with repeated measures ANOVA including microtopography, year and SR as treatments and relative yield totals as response variable. In case of significant effect of year, differences in RYT 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

Averaged over blocks, aboveground stem biomass ranged from 14.5 kg to 98.1 kg per plot (11.8 and 80.1 Mg ha^{-1}) after the fourth year of the experiment (Appendix S5 and S8) but did not show significant variation among species richness levels (Fig. 2). Monocultures of *L. laricina* produced the highest biomass, followed by mixtures that included *B. papyrifera* (Appendix S5). Although biomass was highest in the 12 species plots in absolute values, and lowest in monocultures, sources of variations were large by design in two- and four-species plots (where composition varied over a FD gradient), which is illustrated by the large coefficient of determination ($R^2 = 0.93$) obtained by accounting for plot identity (eqn 4). In other words, the observed variation in productivity was due for the most part to species composition, not their number.

Transgressive overyielding (i.e. where mixture yield exceeds the highest monoculture yield) was not observed. NE were mostly not significantly different from zero but included some significant positive mixture effects. Positive NE occurred in two two-species mixtures, two four-species mixtures and in the 12-species mixture (Fig. 3, Appendix S8). NE ranged from −3.6 kg (−2.9 Mg ha^{-1}) for the *A. rubrum* and *B. alleghaniensis* mixture to +44 kg (35.9 Mg ha^{-1}) for the *A. saccharum, B. papyrifera, P. glauca* and *P. strobus* mixture (Fig. 3).

Positive mixture effects, when present, were largely due to significant selection effects (SE) (Appendix S8). Although SE had no significant negative values and many positive (9), more than half (i.e. 14) of the communities had negative absolute values for CE, however, none were significant
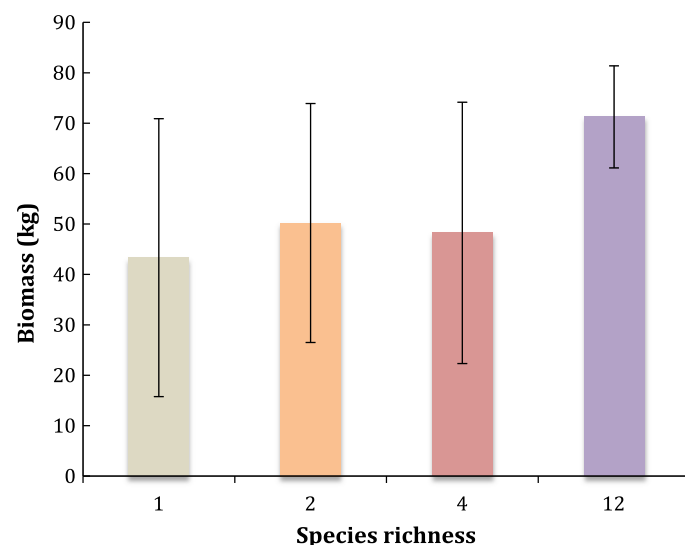

Figure 2 Stem biomass measured in 2012 by species richness (means and standard deviation, across all blocks and plots). Random effect model (eqn 4) did not find a significant effect of species richness ($P < 0.001$) ($P = 0.56$; $R^2 = 0.93$).
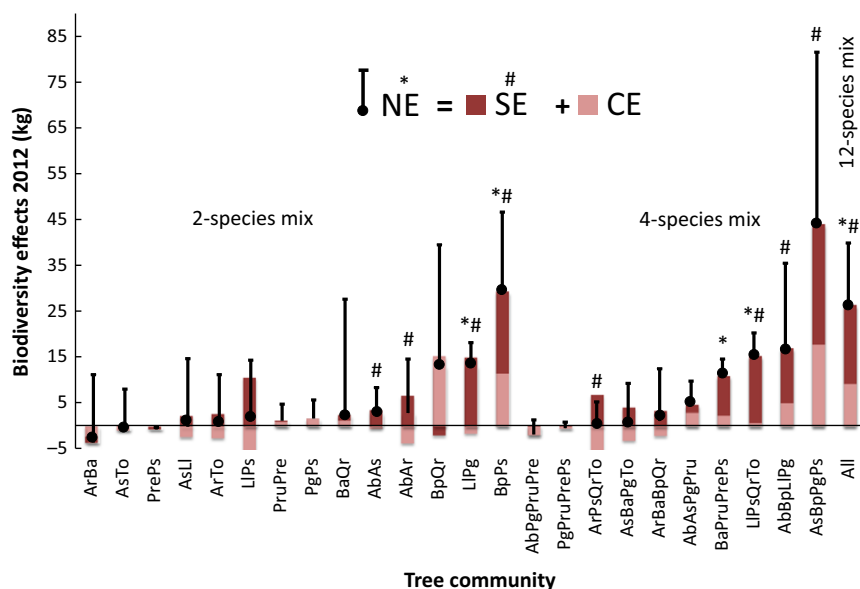
Figure 3 Biodiversity effects by tree community. Net biodiversity effect (NE, filled circles) + standard deviation (for the four blocks) and its two components: complementarity effects (CE, light red bars) and selection effects (SE, dark red bars). Biodiversity effects were calculated on mean species biomass in each mixture in the fourth year of the experiment, 2012. Communities with significant NE are annotated with *, whereas significant selection effects are noted using # ($P < 0.05$). See Fig. 1 for species codes.

(Fig. 3; Appendix S8). SE was larger than CE in seven of the eight mixtures with greatest overyielding (including the 12-species plots). A total of 190 kg (155 Mg ha^{-1}) were overyielded in the two-and four-species mixtures with significant positive effects, of which 79% (123 Mg ha^{-1}) was due to SE and the other 21% (32 Mg ha^{-1}) to CE. Almost 90% of the overyielding occurred in eight mixtures, including three two-species and four four-species mixtures, as well as the one with all 12-species (Fig. 3). All were mixtures of deciduous and evergreen species (except *B. papyrifera*, *Q. rubra*) and all but one contained either or both *B. papyrifera* and *L. laricina*.

Diversity indices

In general, mean trait values (CWMs) explained a larger proportion of variance of stem biomass and NE than trait variation (FDis). Six indices were selected by the stepwise method that together with microtopography explain more than 90% of variation in aboveground stem biomass. The diversity indices with the greatest F-ratios include CWMs of leaf longevity, rooting depth and fine root branching intensity (Fig. 4). The sign for the first two indices is negative, indicating that greater aboveground biomass was achieved in communities with shorter leaf life spans and shallower root systems. The positive sign for branching intensity indicates that greater aboveground stem biomass was achieved in communities with dominance of highly branched fine roots (Fig. 4). Other significant predictors of aboveground stem biomass included CWMs of seed mass and leaf nitrogen and a small but significant effect of variation in seed mass (Fig. 4).

Indices selected to predict NE largely overlap those for aboveground stem biomass. Those with greatest explanatory power on NE were CWMs of fine root branching intensity (positive sign) and rooting depth (negative sign) as well as trait variation (FDis) in seed mass (positive sign). Together with CWM of leaf longevity and seed mass, FDis of leaf nitrogen and microtopography, 47% of variation in NE was explained (Fig. 4). Looking at the two aspects of NE separately, CWMs of shade tolerance, leaf nitrogen and branching intensity together with microtopography explained 31% of variation in SE. The strongest effect on SE was related to community trait means of shade tolerance followed by CWMs of leaf nitrogen and fine root branching intensity (Fig. 4). However, no FDis index had a significant effect on CE. Microtopography alone explained 24% of variation in CE (Fig. 4).

Diversity indices (RY) over time

RYT was greater or equal to one in all years when averaged over all mixtures (i.e. 2009 through 2012). RYT increased significantly from 2009 to 2010 but decreased in 2011 and 2012 to levels similar to 2009, with no significant difference between SR two and four (Fig. 5). Relative yield for a given species varied from 0.5 for *T. occidentalis* to 3.1 for *B. papyrifera* (both in four-species mixtures). Diversity had a significant effect on most species, which was mostly negative to no effect (RY ≤ 1) for coniferous species and no effect to positive (RY ≥ 1) for broad-leaved species (Fig. 6, Appendix S6). 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 (Appendix S6). RY for all the other species did not change significantly over time.
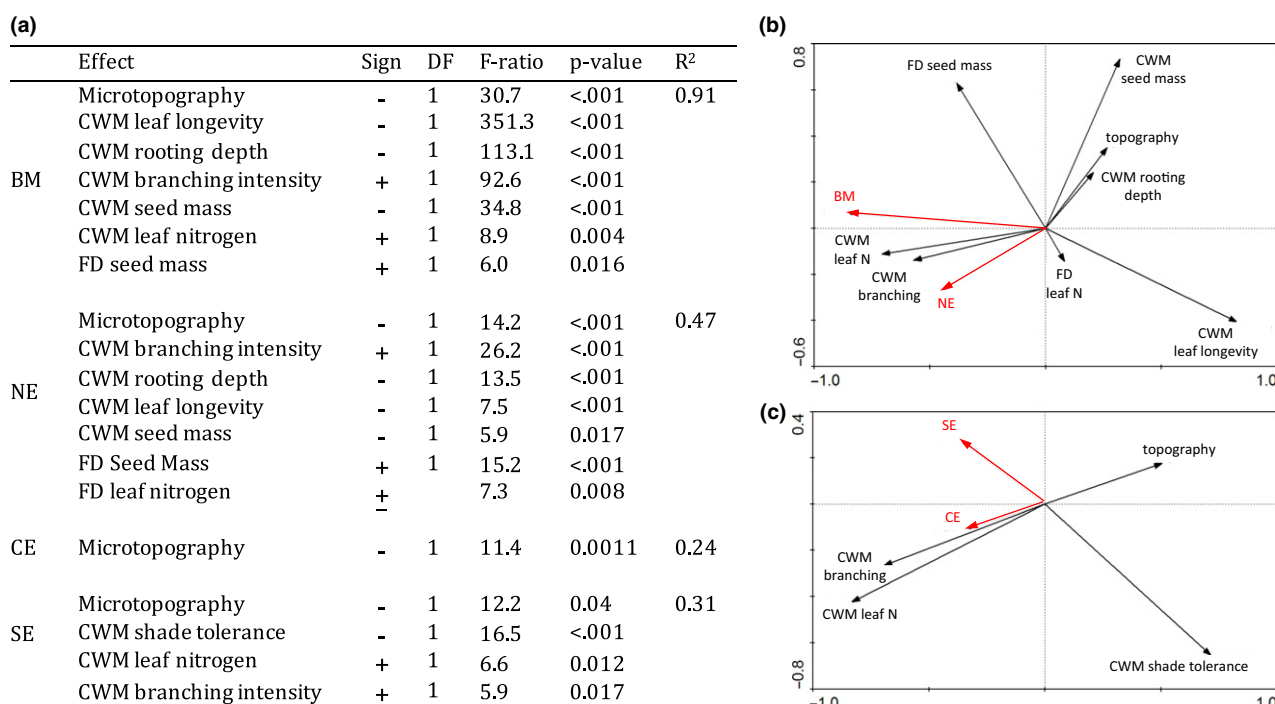
(a)

	Effect	Sign	DF	F-ratio	p-value	R²
	Microtopography	-	1	30.7	<.001	0.91
	CWM leaf longevity	-	1	351.3	<.001	
	CWM rooting depth	-	1	113.1	<.001	
BM	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	
	Microtopography	-	1	14.2	<.001	0.47
	CWM branching intensity	+	1	26.2	<.001	
NE	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	+		7.3	0.008	
CE	Microtopography	-	1	11.4	0.0011	0.24
	Microtopography	-	1	12.2	0.04	0.31
SE	CWM shade tolerance	-	1	16.5	<.001	
	CWM leaf nitrogen	+	1	6.6	0.012	
	CWM branching intensity	+	1	5.9	0.017	

Figure 4 (a) Summary of random effect model (REML estimation) and redundancy analyses of significant diversity indices on (b) biomass (BM) and net diversity effects (NE), as well as c) complementarity (CE) and selection effects (SE). Summary includes degrees of freedom (DF), F-ratios, *P*-values and the coefficient of determination for the whole model (*R²*). Given are significant effects after stepwise regressions. Microtopography (topo) was measured as the elevation of each plot centre (maximum difference 36 cm). Only significant effects are shown, including functional dispersion indices (FDis) and community weighed means (CWM) of seed mass (SeM), leaf nitrogen content (N), leaf longevity (Llo), fine root branching intensity (BI), rooting depth (RoD) and shade tolerance (see Appendix S8 for complete list of tested effects).
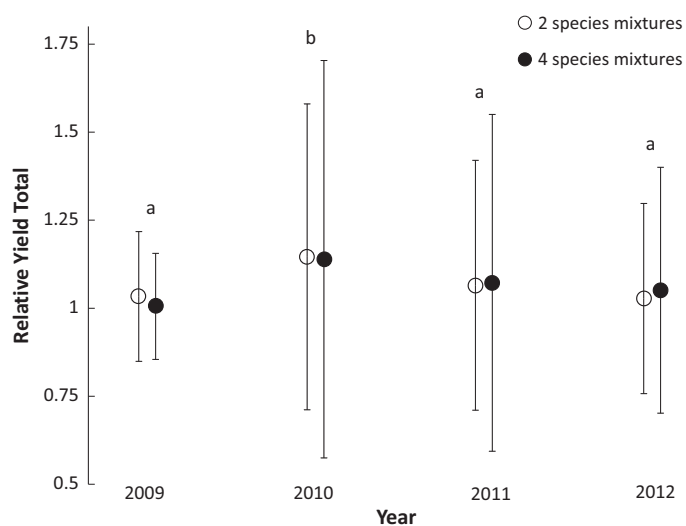
Figure 5 Relative yield (RYT) of two- (empty circle) and four-species mixtures (filled circle) by year. Symbols are slightly offset to improve readability. Given are means ± standard deviation across mixtures and blocks (*N* = 56 for two-species and 40 for four-species mixtures). Different letters indicate significant differences between years for all mixtures, as there was no significant difference between two- and four-species mixtures. RYT > 1 indicate positive diversity effects

DISCUSSION

This study provided weak support for the long-running hypothesis that mixtures on average are more productive than their monoculture counterparts, as all mixtures showed non-significant to positive net diversity effects, with five of them overyielding significantly. It concurs with other studies that have documented positive effects of mixtures for a variety of ecosystems such as forests (Zhang *et al.* 2012), grasslands (Cardinale *et al.* 2011), lakes and streams (Mora *et al.* 2011; Cardinale *et al.* 2012), and at different trophic levels (Cardinale *et al.* 2006). Transgressive overyielding, viewed by some as the ultimate demonstration of a biodiversity effect, was not observed in our study. However, it has been documented in only a few cases and remains a rare phenomenon (Loreau & Hector 2001; Schmid *et al.* 2008; Cardinale *et al.* 2011).

Tree mixtures, functional diversity and complementarity effects

This study is one of the first to test mechanisms underlying diversity effects with trees. Contrary to generally stronger effects of complementarity in prior studies, we found that significant net diversity effects (NE) were roughly driven 80% by selection (SE) and 20% by complementarity effects (CE). In other words, some species that grew well in monoculture benefited from reduced competition when growing in mixtures, dominating them and overyielding. Species that significantly enhanced biomass in mixture compared to monocultures (i.e. species responsible for SE) were four deciduous shade-intolerant (*B. papyrifera*, *L. laricina*) and mid-tolerant species (*Q. rubra* and *B. alleghaniensis*).
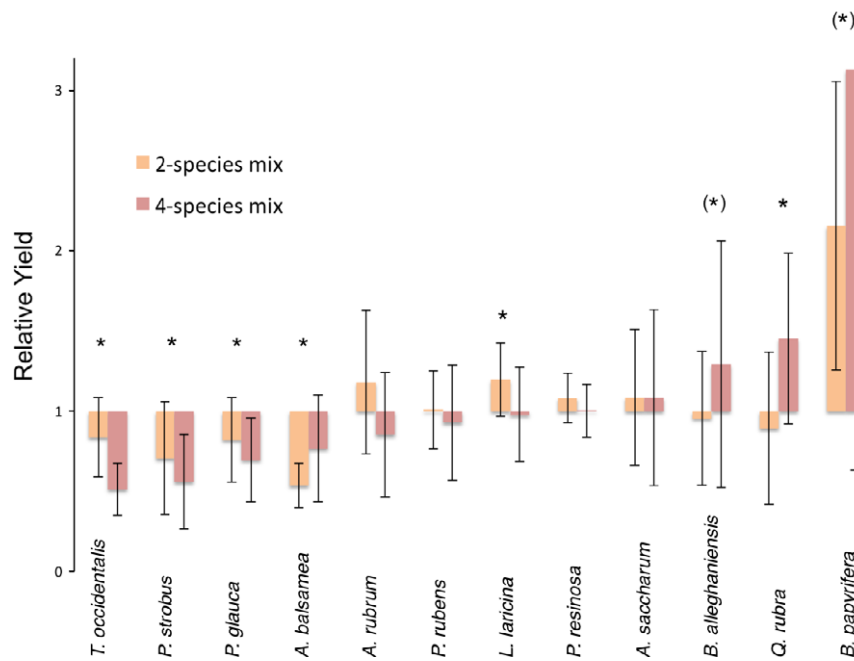
Figure 6 Diversity effects (here measured as relative yield, RY) ± standard deviation (error bar for *B. papyrifera* cut for better resolution) by species, in two- (pale red) and four-species mixtures (dark red) in 2012. RY > 1 indicate positive mixture effects, RY < 1 indicate negative mixture effects. Note that individual species RY were scaled back to 1 (rather than 0.5 or 0.25 depending on SR levels) for ease of comparison. Significant species RY mean (in all mixtures) annotated with asterisks (* for *P* < 0.05, (*) for *P* < 0.1).

By comparison, complementarity and selection effects were found to contribute around 50% each to positive net biodiversity effects across a variety of BEF studies (Cardinale *et al.* 2011), with selection becoming less influential with time (Reich *et al.* 2012). In contrast to grassland ecosystems, where species differ less in shade tolerance and none are strongly tolerant, trees exhibit considerable variation in shade tolerance. This may be important to their interactions in mixtures, as light is a much more directional resource than soil resources, which are typically more important in grasslands. In this study, the shade-intolerant species were well-adapted to the high light conditions of the establishing phases of the experiment and had better growth in monocultures than shade-tolerant species (Appendix S6). Thus, it is possible that the nature of light competition reduces the value of niche complementarity, contributing to stronger selection effects in this forest than in grassland experiments (Zhang *et al.* 2014). Alternatively, as complementarity grew over time (decadal scale) in grassland mixtures (Reich *et al.* 2012), apparently due to time-sensitive biogeochemical feedbacks as well as growing niche differentiation, the early stage of ecosystem development of our mixed communities may in part be responsible for the relatively greater importance of selection effects.

It has been proposed that the strength of the diversity–productivity relationship as well as the relative contribution of complementarity and selection effects depend on site conditions (Reich *et al.* 2001). Positive interactions among plants for instance have been hypothesised to gain importance in stressful environments (the stress gradient hypothesis, Bertness & Callaway 1994). Evidence for reduced competition and increased complementarity for mixtures in environmentally challenging conditions (i.e. lower resources) has been documented in herbaceous communities (Wacker *et al.* 2008; Jarchow & Liebman 2012), microalgae (Steudel *et al.* 2012) and forests (Paquette & Messier 2011). In this study, the agricultural input at the study site prior to the setup of the experiment resulted in nutrient-abundant conditions, possibly favouring single species effects (i.e. selection). This is consistent with theoretical considerations (Gause 1934; Bertness & Callaway 1994) and empirical evidence 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 dominate in more productive habitats (Reich 2009).

Out of the 12 species present in the experiment, four species significantly increased and four significantly decreased aboveground stem productivity in mixtures compared to their monocultures. The four species positively affected by mixture were the four most productive species, all deciduous, including three broad-leaved species (*B. alleghaniensis*, *B. papyrifera*, *Q. rubra*) and larch (*L. laricina*; Fig. 6, Appendix S6). The four species negatively affected by mixture (*A. balsamea*, *P. glauca*, *P. strobus*, *T. occidentalis*) are all evergreen conifers that were among the less productive species overall.

Net diversity effects as explained by trait variation (FD) vs. trait means (CWMs)

Our analysis of functional diversity revealed which traits are responsible for the importance of the selection effect. Community weighted mean (CWM) indices had greater explanatory power than FDis on variation in biomass and NE, consistent with the dominance of selection effects.

Surprisingly CWMs and FDis have never before been interpreted in terms of selection and complementarity effects, to the best of our knowledge, although the idea was suggested by Roscher *et al.* (2012). CWMs allow the evaluation of the effect of a dominant trait on productivity, while FDis quantifies the effect of the variability in this trait on productivity. Our findings corroborate studies in herbaceous (Díaz & Cabido 2001; Mokany *et al.* 2008; Roscher *et al.* 2012) and tree systems (Nadrowski *et al.* 2010) where functional identity rather than diversity better explained productivity. Although around 20% of net biodiversity effects were attributed to complementarity in this study, none of the measured FDis significantly explained complementarity effects (and no single CE effect was significant). Microtopography alone explained around 25% of variation in complementarity. All measures of diversity effects (including RY), as well as productivity, significantly decreased with increasing plot elevation, indicating that in lower elevation plots higher biomass and hence increased species interactions led to increased diversity effects. This could be due to the combined effect of the distance to the richer underlying clay layer and local drainage conditions (water availability), given the absence of a general slope.

Little is known about which traits are involved in diversity effects that increase tree productivity. In forests, positive mixture effects appear most common in stands of species with vertical stratification (Kelty 1992; Garber & Maguire 2004) and/or contrasting traits such as shade tolerance (Zhang *et al.* 2012), wood density (Swenson & Enquist 2007), seed mass (Ben-Hur *et al.* 2012) and maximum height (Paquette & Messier 2011; Ruiz-Benito *et al.* 2014). These results are consistent with evidence that increasing functional group diversity results in higher biomass even at a constant SR, as found in grasslands (Reich *et al.* 2004). Due to large ontogenetic shifts in trees, it can be expected that traits linked to productivity change with tree age. It would thus appear logical that maximum height may not be of importance in young tree communities, particularly since the fastest growing species in these early tree communities do not tend to be the tallest at maturity. In this 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, domination by species with the following functional characteristics increased mixture aboveground stem productivity: short leaf life span (i.e. deciduous), smaller seeds (early successional species), shallower root systems and highly branched fine roots (Fig. 4). Shallow rooted species may produce even shallower roots in mixtures compared to monocultures, lowering their root/shoot ratio and thus increasing competitiveness for light and consequently productivity (Zhang *et al.* 2014).

All of those traits show some correlation (Fig. 4, Appendices S7 and S9) and can be grouped along the same life history axes, and together are possessed by species that have been alternatively described as *r*-strategists (Reznick *et al.* 2002) or as having a fast (resource acquisition) whole-plant economic strategy (Reich 2014). Congruently, deciduous, rapidly developing, shade-intolerant species were crucial in explaining overyielding in all cases in this study.

Net diversity effect over time

Net diversity effects and the relative importance of CE vs. SE have been found to increase with time over a large number of studies (Allan *et al.* 2011; Cardinale *et al.* 2012), including the small number of long-term studies (Reich *et al.* 2012). This was not clearly seen in our study. Increasing net diversity effect through complementarity over time has been related to functional divergence (Reich *et al.* 2012; Sapijanskas *et al.* 2013) and/or turnover (Reich *et al.* 2012). Interestingly, in some grasslands (Cardinale *et al.* 2007) and tropical tree plantations (Sapijanskas *et al.* 2013) it took 5 years to detect a significant signal of complementarity. It has been shown that traits are plastic in response to neighbour diversity and identity, thereby promoting complementary resource use (Messier *et al.* 2009; Ashton *et al.* 2010; Reich *et al.* 2012). In this study, interactions and phenotypic plasticity could create stronger positive mixture effects in the future due to functional divergence, highlighting the need for longer lasting experiments with trees.

CONCLUSION

We presented results of what is to the best of our knowledge the first experiment with tree communities testing for the effects of functional diversity on productivity, and the existence of complementarity in tree communities, independently of species richness. Most net biodiversity effects were positive, but statistically significant in only one-fifth of the cases with no significant negative effects. The positive mixture effects were driven mostly by selection effects (~ 80%). Congruently, functional identity better explained productivity and diversity effects than functional diversity, due to the dominance of some deciduous species and the competitive suppression of most evergreen species in mixtures. The significance of both leaf longevity and root traits, especially for identity effects, may signal their importance to both negative and positive interactions in young tree mixtures. We present herein what is an early snapshot (prior to mortality or reproduction) in the long-term ontogeny of a tree community.

More research is needed to document whether diversity effects in trees are largely limited to specific combinations of species that are perhaps favoured in natural settings but not in a manipulated experiment context, or whether they need more time to develop. Indeed, following natural succession, changes in dominance (towards evergreen and/or shade-tolerant species) are to be expected given more time and consequently, shifts in diversity effects may occur, possibly towards increased complementarity as documented in other systems. Understanding the role of diversity in plant–plant interactions in a young developing community provides new insight, but better understanding of how it influences such interactions throughout stand development remains an important unmet goal for the scientific community.

AUTHOR CONTRIBUTIONS

AP and CM coordinate the IDENT network; CMT, AP, CM, DG and PBR designed the study; CMT, AP and LJW collected and contributed data; CMT and AP analysed the data; all authors participated in the writing of the manuscript (CMT wrote first draft).

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