

Can niche plasticity promote biodiversity–productivity relationships through increased complementarity?

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Abstract. Most experimental biodiversity–ecosystem functioning research to date has addressed herbaceous plant communities. Comparably little is known about how forest communities will respond to species losses, despite their importance for global biogeochemical cycling. We studied tree species interactions in experimental subtropical tree communities with 33 distinct tree species mixtures and one, two, or four species. Plots were either exposed to natural light levels or shaded. Trees grew rapidly and were intensely competing above ground after 1.5 growing seasons when plots were thinned and the vertical distribution of leaves and wood determined by separating the biomass of harvested trees into 50 cm height increments. Our aim was to analyze effects of species richness in relation to the vertical allocation of leaf biomass and wood, with an emphasis on bipartite competitive interactions among species. Aboveground productivity increased with species richness. The community-level vertical leaf and wood distribution depended on the species composition of communities. Mean height and breadth of species-level vertical leaf and wood distributions did not change with species richness. However, the extra biomass produced by mixtures compared to monocultures of the component species increased when vertical leaf distributions of monocultures were more different. Decomposition of biodiversity effects with the additive partitioning scheme indicated positive complementarity effects that were higher in light than in shade. Selection effects did not deviate from zero, irrespective of light levels. Vertical leaf distributions shifted apart in mixed stands as consequence of competition-driven phenotypic plasticity, promoting realized complementarity. Structural equation models showed that this effect was larger for species that differed more in growth strategies that were characterized by functional traits. In 13 of the 18 investigated two-species mixtures, both species benefitted relative to intraspecific competition in monoculture. In the remaining five pairwise mixtures, the relative yield gain of one species exceeded the relative yield loss of the other species, resulting in a relative yield total (RYT) exceeding 1. Overall, our analysis indicates that richness–productivity relationships are promoted by interspecific niche complementarity at early stages of stand development, and that this effect is enhanced by architectural plasticity.

Key words: *additive partitioning; biodiversity–productivity relationships; canopy stratification; competition; complementarity; functional trait dissimilarity; niche overlap; niche plasticity; subtropical tree stands.*

INTRODUCTION

The questions of whether and through which mechanisms plant biodiversity promotes ecosystem functioning have motivated numerous investigations in the past decades (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2012). Most experimental studies to date have focused on herbaceous vegetation and found increased productivity with increased species richness (Hector et al. 1999, Tilman et al. 2001). A large amount of data about the relationship between productivity and species richness is also available from forest inventory

plots and tree plantations (Vila et al. 2007, Piotta 2008, Paquette and Messier 2011, Barrufol et al. 2013, Gamfeldt et al. 2013). However, with observational data it is difficult to separate effects of species richness from covarying environmental effects, in particular if these span large spatial gradients across different forest types and climatic and edaphic conditions. Experiments in which the diversity of tree species has been manipulated directly and systematically, while keeping other factors constant, have only been established relatively recently (e.g., Potvin and Gotelli 2008, Ewel et al. 2015). This underrepresentation of forest ecosystems in experimental biodiversity research appears critical in the light of their importance for global biogeochemical cycling and climate regulation (Dixon et al. 1994, Durieux et al. 2003) and the high species richness many of these ecosystems harbor

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TABLE 1. Glossary of terms related to the quantification and analysis of biodiversity effects.

Term	Description
Net biodiversity effect	The <i>net biodiversity effect</i> is the extra yield produced by mixed communities relative to the mean yield of the monocultures of the component species. It is synonymous with <i>overyielding</i> .
Overyielding	A mixture is <i>overyielding</i> when its <i>net biodiversity effect</i> is positive. Overyielding is <i>transgressive</i> when the yield of a mixture of species is higher than the yield of the most productive monoculture of its component species.
Selection probability effect	The <i>selection probability effect</i> (also called <i>sampling effect</i>) describes the phenomenon that more species-rich communities are more likely to comprise of species that perform well and thus promote community productivity. This effect is not to be confounded with a <i>selection effect</i> .
Relative yield (RY)	The <i>relative yield</i> is the yield of a species growing in a mixed community divided by its yield in monoculture. A null model of identical interspecific and intraspecific interactions results in an expected value $RY = 1/S$ in a community of S species when yield is quantified per area, or $RY = 1$ when referring to individual biomass (Fig. 3).
Relative yield total (RYT)	The sum of the <i>relative yields</i> (per area) of all species in a mixture. $RYT > 1$ indicates that species, on average, benefit from growing in mixed communities. $RY > 1$ (per area) for all species is clear evidence that interspecific niche complementarity drives <i>overyielding</i> .
Additive partitioning	A statistical scheme proposed by Loreau and Hector (2001) to decompose <i>net biodiversity effects</i> into a <i>complementarity effect</i> and a <i>selection effect</i> . It is based on ΔRY , which is the change in <i>relative yield</i> (per area) of species relative to the expected value of $1/S$ in an S -species community (null model).
Complementarity effect	A component of the <i>net biodiversity effect</i> determined using <i>additive partitioning</i> . It is proportional to the average ΔRY of the species growing in a mixture. Positive <i>complementarity effects</i> are typically interpreted as evidence that interspecific niche complementarity drives <i>overyielding</i> , although this only is certain when $\Delta RY > 0$ for all species.
Selection effect	A component of the <i>net biodiversity effect</i> determined using <i>additive partitioning</i> . It is proportional to the covariance of monoculture yields and ΔRY . Positive <i>selection effects</i> indicate that, on average, species with higher yield in monoculture also have larger <i>relative yields</i> in mixture. <i>Selection effects</i> typically occur when biomass gains of productive species occur at the expense of subordinate species

Notes: These analyses generally are applied to experiments in which the total density of individuals is independent of species richness, i.e., a diversity gradient is constructed by replacing individuals by individuals of other species.

particularly at low latitudes. Also, the longevity, large stature, and functional separation of persistent woody biomass and leaf biomass, which is less persistent but physiologically more active, may give rise to diversity–productivity relationships that differ from those found in herbaceous plant communities.

The net biodiversity effect, or overyielding (Table 1; Schmid et al. 2008), quantifies the extent to which the yield of a mixture exceeds the average yield of the monocultures of the species it contains. Two main hypotheses have been proposed to explain overyielding (Aarssen 1997, Tilman 1997). First, interspecific niche complementarity may result in a more complete capture of resources that limit plant growth and therefore lead to higher productivity. Second, communities with greater species richness are more likely to contain species that perform particularly well and thus promote community-level productivity, a mechanism that has been referred to as “sampling” effect. Loreau and Hector (2001) have proposed the “additive partitioning” scheme to break net biodiversity effects down into a “selection effect” and a “complementarity effect” based on the yields of species in mixtures relative to their yield in monoculture (Table 1). It is important to note that the complementarity effects obtained with this statistical approach do not necessarily correspond to yield gains from resource niche complementarity. Instead, they aggregate many ecological

interactions, including mutualism and facilitation, in addition to effects of reduced interspecific competition. Furthermore, selection effects ultimately also depend on niche differences. While the additive partitioning method has been successfully applied to the analysis of data from biodiversity–ecosystem functioning experiments (e.g., Fargione et al. 2007), it remains phenomenological in nature and leaves the mechanistic nature of complementarity elusive unless these effects can be linked to specific biological mechanisms.

The study of species interactions is more amenable in bipartite mixtures than in more complex communities. Such pairwise species interactions have traditionally been classified into positive (facilitation), negative (competition, parasitism), or neutral. Interactions in more diverse communities can involve more than two partners, but the properties of these communities can nevertheless be predicted to some extent from the pairwise interactions of the component species (Dormann and Roxburgh 2005, Carrara et al. 2015). Also, the largest yield increase in experimental biodiversity studies is generally found when moving from one to two species, indicating important contributions of two-species interactions to the overall biodiversity effect. This suggests that the analysis of bipartite interactions may pave the way to a better mechanistic understanding of biodiversity effects also in more complex mixtures of species.

Biodiversity–ecosystem functioning relationships are driven by direct or indirect interspecific interactions. Ultimately, these depend on functional trait differences among species. Several studies have aimed to identify the dimension in complementary niches that promotes positive biodiversity effects on community productivity (Hille Ris Lambers et al. 2004, von Felten et al. 2009). The decisive niche axes may be related to resources such as physical space, light, or nutrients, but causal relationships are difficult to identify (Flynn et al. 2011). Dimitrakopoulos and Schmid (2004) found increased complementarity effects with larger vertical soil “biotope” space available and concluded that some form of vertical space partitioning by species was at play. von Felten et al. (2012) traced differences in nitrogen (N) uptake from different soil layers using stable isotopes but did not find evidence for interspecific N partitioning by soil depth. More recently, studies have also focused on complementarity in trophic interactions, in particular pathogen niches (Callaway et al. 2011, Maron et al. 2011, Johnson et al. 2012).

In forests, light is an important resource that controls many processes including carbon acquisition through photosynthesis and demographic processes through gap dynamics. However, all tree species thrive on a similar set of resources and empirical evidence for resource partitioning among species is limited. Community-level light interception is often higher in species-rich communities, a fact that has been attributed to a more complete filling of light climate-related niches in vertical aboveground space (Hardiman et al. 2011, Morin et al. 2011). On the other hand, competition for light is strongly asymmetric (Hautier et al. 2009), and taller individuals are therefore able to pre-empt the use of this resource, which likely limits the potential for vertical niche partitioning. The light climate experienced in mixed stands also strongly depends on size such that individuals will experience vastly changing conditions throughout their ontogeny. Light partitioning might therefore be more important within than among species (Lichstein et al. 2007). These considerations, combined with available data, suggest that it remains currently unresolved whether higher biomass in mixed communities is attained through more complete light interception or whether light interception is merely the result of higher biomass due to complementarity in another domain, for example nutrient or hydrology-related niches or niches related to trophic interactions.

More diverse and more productive forests often allocate biomass more efficiently in canopy space, a phenomenon that has been referred to as packing of tree crowns. Canopy packing is promoted by architectural plasticity (Cianciaruso et al. 2009). Trees often shift their crowns laterally relative to their stem base to fill available gaps (Farrior et al. 2016). Jucker et al. (2015) have found that trees grew taller rather than growing laterally in monospecific stands, whereas crowns were wider in mixed communities in which they interfered less with their

neighbors. This resulted in greater canopy packing with respect to crown volumes. Other studies have found enhanced vertical canopy stratification in more diverse tree stands (e.g., secondary subtropical forest: Castro-Izaguirre et al. 2016). The relation of these processes to biodiversity–productivity relationships, however, is difficult to establish. First, virtually all studies so far were observational in nature, so an unequivocal causal link from species richness to canopy packing is difficult to establish. Second, effects on canopy structure do not necessarily translate into higher productivity; for example, Jucker et al. (2015) found more efficient canopy packing in diverse stands, but no corresponding increase in stem basal area, a commonly adopted proxy of forest aboveground biomass.

In summary, observational studies in natural forests indicate that architectural complementarity may promote biodiversity–productivity relationships in forests, either directly or indirectly through processes that may be as diverse as more complete light capture, hindered pathogen transmission, or altered microclimatic conditions. However, these mechanisms await verification and a more detailed analysis in a setting in which species richness unequivocally acts as causal driver.

We have set up a biodiversity experiment with stands of subtropical tree species. The focus of our study was on analyzing traceable competitive interactions between species, in particular species pairs. We therefore focused on high density stands with relatively low species numbers. Starting with three independent pools of four species each, we created all possible one, two, and four-species combinations within each pool and replicated these four-fold. A factorial shade house treatment altered the availability of light. Trees were harvested after 1.5 yr and their vertical allocation of leaves and wood quantified at the individual tree level in monocultures and mixtures. Our research was motivated by the following questions: (1) Do the vertical stratification of leaves and wood at the community level change with species richness? (2) Do average height and vertical extent of species-level leaf and wood distribution change with species richness? (3) Can the overyielding of a species mixture be predicted from vertical interspecific differences of leaf distributions found in the monocultures of the component species? (4) Do interspecific differences in leaf and wood distributions increase under interspecific competition, i.e., does phenotypic plasticity increase complementarity, and can this effect be related to growth-related functional traits of species? (5) Are the above effects modified by light availability?

MATERIALS AND METHODS

Study site and experimental design

In March 2009, a field experiment factorially combining a plant diversity and a light availability treatment was established in a river valley near Xingangshan,

TABLE 2. Overview of tree species used in the present study.

Abbreviation	Full species name and authors	Leaf habit
Pool 1		
ch	<i>Castanea henryi</i> Rehder & E.H.Wilson	d b
ed	<i>Elaeocarpus decipiens</i> Hemsley	e b
qs	<i>Quercus serrata</i> Thunberg	d b
ss	<i>Schima superba</i> Gardn. & Champion	e b
Pool 2		
cg	<i>Cyclobalanopsis glauca</i> (Thunberg) Oersted	e b
cl	<i>Cunninghamia lanceolata</i> (Lamb.) Hook.	e c
dh	<i>Dalbergia hupeana</i> Hance	d b
pm	<i>Pinus massoniana</i> Lamb.	e c
Pool 3		
cm	<i>Cyclobalanopsis myrsinaefolia</i> Oersted	e b
cs	<i>Castanopsis sclerophylla</i> Schottky	e b
lg	<i>Lithocarpus glaber</i> (Thunberg) Nakai	e b
sm	<i>Sapindus mukorossi</i> Gaertner	d b

Notes: Species names are listed with authors and abbreviations. Leaf habit refers to seasonality (d, deciduous; e, evergreen) and habit (b, broad leaved; c, coniferous). Species were combined within each of the three independent pools, creating all possible monocultures, two-species mixtures, and the four-species mixture.

Jiangxi province, China (29°06'29" N, 117°55'28" E, 100 m above sea level). The experiment was composed of 12 tree species, which were organized in three pools of four species each (Table 2); for each pool, all monocultures, all two species combinations, and the four species mixture were planted in 1 × 1 m² plots composed of 16 tree saplings arranged on a 4 × 4 grid with 25 cm distance between individuals. The central four trees in each plot reflected the species distribution of the whole plot, i.e., four individuals of one species in monocultures, two individuals per species in two-species mixtures and one individual per species in four-species mixtures. The shade treatment was implemented by covering plots with a cloth that was attached to top and sides of a wooden frame. The experiment was replicated in four blocks and encompassed 264 plots (3 pools × 11 mixtures × 2 light levels × 4 blocks). Plots were surrounded by narrow drainage ditches and walkways, resulting in a 75 cm distance between plot edges. The climate at the site is subtropical monsoon with a mean annual precipitation and temperature of 2000 mm and 15°C, respectively.

Vertical leaf and wood distribution

After 1.5 growing seasons, the four central trees were harvested aboveground (blocks 1–3, September 2010; block 4, June 2010). The biomass of these 1,056

individuals was divided into 50 cm height intervals, separately for leaves and wood. All samples were dried and weighed.

Traits

We estimated functional differences between pairs of species based on traits recorded in monoculture, using Euclidean distances (traits standardized to unit variance). Traits were leaf habit (broadleaf vs. conifer) and seasonality (evergreen vs. deciduous), leaf mass fraction, wood density, specific leaf area, leaf dry matter content, the maximum height of each species, and mean leaf height (trait distance d_1). We repeated the trait-related analyses excluding the latter two traits (trait distance d_2) because these may be more directly size-related than the other traits. However, all of these traits are correlated to some extent because they are related to fundamental trade-offs that underlie plant growth strategies.

Data analysis

All data were analyzed by analysis of variance using asreml (VSN International, Hemel Hempstead, UK) or aov (R 3.3, R Core Team 2016). For plot-level data, species richness (log-transformed), light, and block were fitted as fixed effects. Species composition and its interaction with the light treatment were included as random effects that defined the error strata for tests of species richness and species richness × light. Biomass data were asymmetrically distributed. Nevertheless, to implement the null hypotheses of purely additive effects in the absence of a true diversity effect, these data were not transformed. Any transformation that compresses large values more than smaller ones, e.g., log or square root, would have introduced spurious diversity effects even if the null hypothesis was true. Instead, the larger variance in the more productive light treatment was accounted for by fitting separate residual variances for the light treatments (idh option in asreml). As last fixed effect, we further fitted presence–absence contrasts for the most productive species in each pool (*Dalbergia hupeana*, *Elaeocarpus decipiens*, *Sapindus mukorossi*). These contrasts accounted for the systematic effect of these species and remedied the asymmetric residual distribution (Schmid et al. 2017). We report significances together with F values and degrees of freedom. Note that denominator degrees of freedom are approximate in these mixed models and can be fractional.

We calculated the relative yield (RY) of the species in two-species mixtures as the ratio of aboveground biomass (wood plus leaves) in mixtures and monoculture. We accounted for the different number of trees of a species in monoculture and mixture by expressing biomass per number of planted trees of that species. A RY of 1, therefore, indicates identical intra- and interspecific competition. We tested for the significance of RY changes from monoculture to mixture by fitting a linear model

with the terms block, light treatment, and species richness. The dependent variable analyzed was the biomass of the species divided by the number of trees of that species originally planted in the respective plots. The data set used in this analysis consisted of a subset with only the biomass of the respective species in monoculture and in the two-species mixture under consideration. A significant effect of species richness in this model indicates a significant change in the relative yield of planted individual trees.

Metrics that use monoculture data as reference (net biodiversity effects, complementarity, and selection effects, niche overlap changes) were calculated by averaging across blocks yielding data aggregated at the level of community composition–light-treatment combinations ($n = 18 \times 2$). These data were more stable than metrics that were calculated for each block separately and averaged later. For all species present in a mixture, the average height \bar{h} of leaf and wood distributions was determined as the height of gravity of their distribution ρ_h

$$\bar{h} = \frac{\int_0^{h_{\max}} h \rho_h dh}{\int_0^{h_{\max}} \rho_h dh}$$

The vertical breadth of these distributions was quantified as their standard deviation

$$\sigma_h = \sqrt{\int_0^{h_{\max}} \rho_h (h - \bar{h})^2 dh}$$

assuming a uniform distribution within each 50-cm harvest interval (a “histogram shape”). We favored this metric over Levins’ B (Levins 1968) because the latter implies no particular ordering of categories along a niche axis, i.e., the distance among height intervals is not measured on an interval scale. The overlap of leaf and wood distributions of species coexisting in a two-species mixture was calculated as proportional similarity (Colwell and Futuyma 1971)

$$PS_{A,B} = 1 - \frac{1}{2} \sum_i |x_{A,i} - x_{B,i}|$$

where $x_{A,i}$ and $x_{B,i}$ denote the fraction of biomass species A and B allocate to vertical interval i .

We then calculated the shift in overlap of distributions from when species were growing separately in monocultures to when species were competing in the same mixtures (the index $X|Y$ denotes species X in mixture Y):

$$\Delta PS = PS_{A|AB,B|AB} - PS_{A|A,B|B}$$

All these data were analyzed using linear models with species composition as a random term.

Finally, the different results were synthesized using structural equation models. Structural equation modeling uses the covariance structure between variables in the data set to estimate coefficients or putative cause–effect relationships in a priori path models. This analysis is exploratory in nature and complements (but does not replace) significance testing with models that reflect

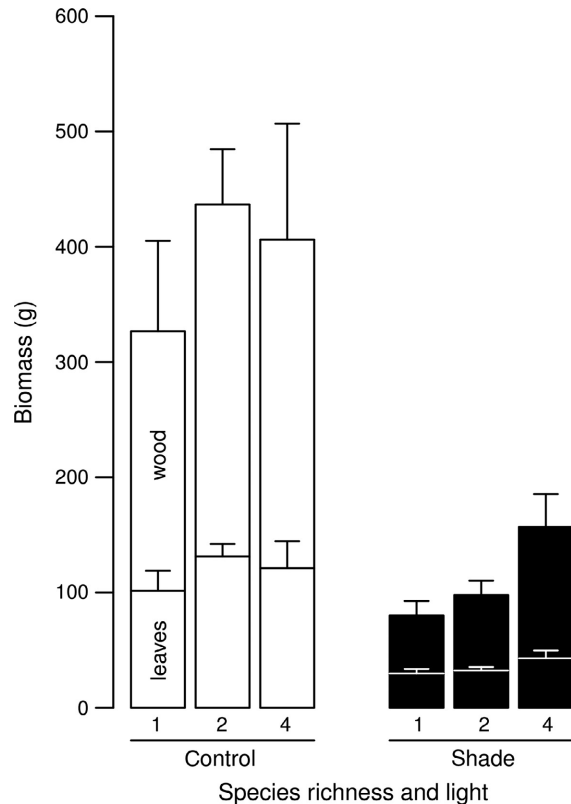


FIG. 1. Aboveground biomass of the four central individuals (0.25 m^2 ground area) for the different tree species richness levels (1, 2, and 4 species) and the light availability levels (control, shade). The lower part of the bars indicates the mass and standard error of the leaf fraction, whereas the upper part indicates woody biomass. The top error bar indicates the standard error of the sum of the two.

experimental designs. Models were fitted by maximum likelihood using the lavaan software (*available online*).⁵ Complementarity and selection effects in two-species mixtures (Loreau and Hector 2001) were modeled as functions of light treatment, the proportional similarity of monoculture vertical leaf distributions, the shift in proportional similarity from monoculture to mixture, and the functional distance between species. We allowed for direct links as well as indirect links via shifts in proportional similarity of leaf niches. Nonsignificant links were removed, except for the links between the shift in distributions and complementarity and selection effects, since these address a main hypothesis of our work.

RESULTS

Tree growth and biomass

Plot-level aboveground biomass increased with species richness (Fig. 1; $F_{1,20.3} = 30$, $P < 0.001$) and with light availability ($F_{1,30.5} = 31$, $P < 0.001$), and these effects

⁵<http://lavaan.ugent.be>

were independent (species richness \times light: ns). When the leaf and wood fractions were analyzed separately, the effect of light remained. However, the effect of species richness was only significant for wood ($F_{1,20,3} = 33$, $P < 0.001$) and there possibly was a similar trend for leaves ($F_{1,60,6} = 2.8$, $P = 0.1$).

Vertical leaf and wood distributions

Communities and species within communities differed significantly in the vertical distributions of leaf biomass (Fig. 2) and wood biomass. The vertical location of leaf and wood, estimated as height of gravity of the respective distributions, did not depend on species richness (Fig. 2). The breadth of leaf and wood distributions, estimated as standard deviation of the vertical distribution of leaves and wood, also was independent of species richness (Fig. 2).

Pairwise competition effects

Interspecific competition in mixture always favored at least one of the plant partners relative to the monoculture situation, i.e., the observed yield of this species in mixture was higher than the expected yield based on its performance in monoculture (relative yield >1 ; Fig. 3). In 13 cases, the relative yield increase (i.e., competition reduction) concerned both partners, and this effect was statistically significant in 10 cases ($P < 0.05$) and marginally significant in two cases ($P < 0.1$). In five cases (of which 3 were statistically significant at $P < 0.05$), the competition change was asymmetric, i.e., positive effects on one species occurred at the expense of the other species. When the antagonistic pattern was found, the relative yield increase for one species was always larger than the relative yield decrease for the other species (symbols right of diagonal in Fig. 3).

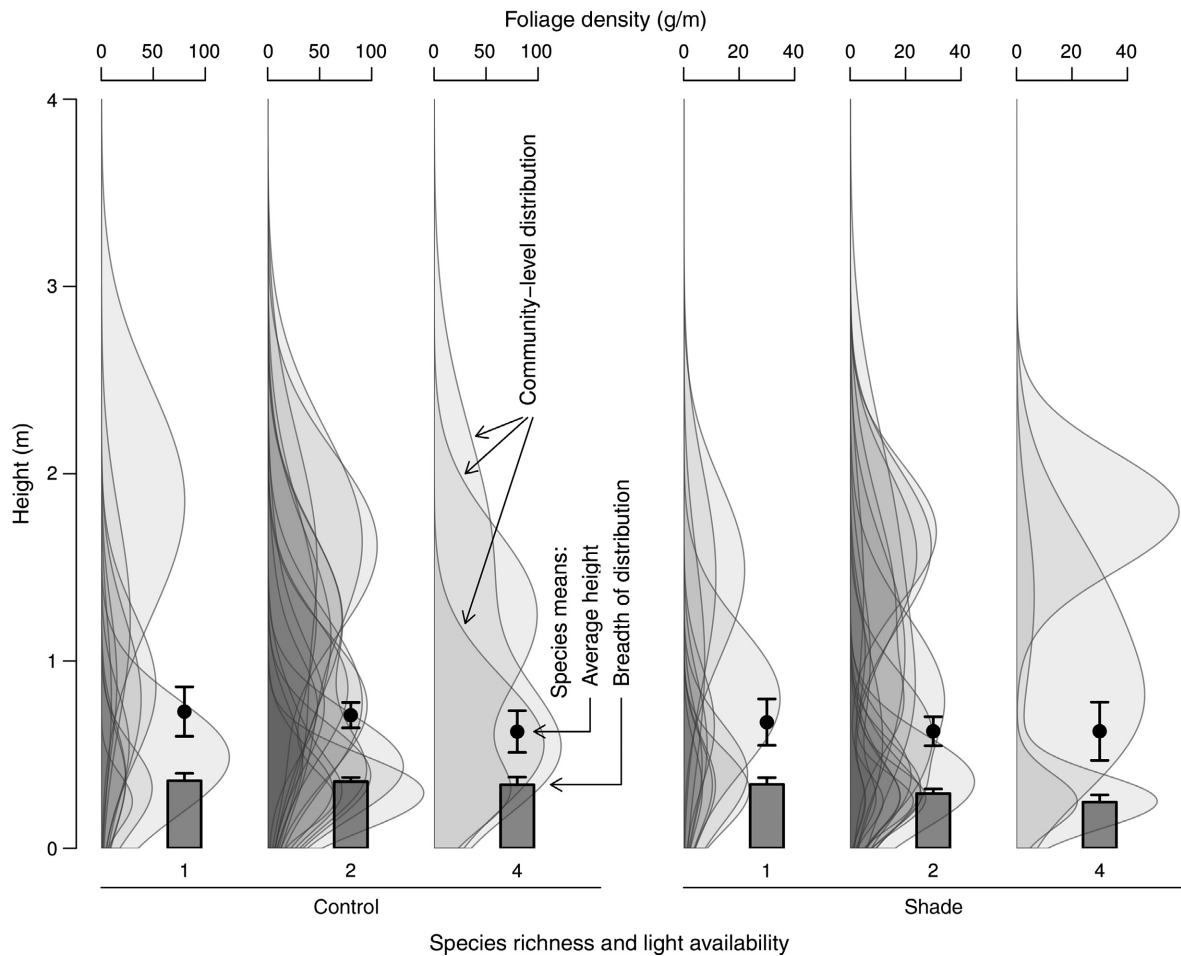


FIG. 2. Species and community-level vertical leaf distribution. Data are shown for the different tree species richness and light availability treatments. Gray areas show community-level vertical leaf density profiles for each species mixture. These profiles were calculated as the sum of the profiles of the component species. Each species' profile was assumed to follow a normal distribution, with mean and variance determined from the harvest data. Mean species-level leaf height and the vertical breadth (standard deviation) of the leaf distributions are shown as dots and bars, respectively. Error bars of mean height and distribution breadth show standard errors, using species composition as replicate (data were averaged across the species in each mixture, resulting in $n = 12$ for monocultures, $n = 18$ for two-species mixtures, and $n = 3$ for four-species mixtures).

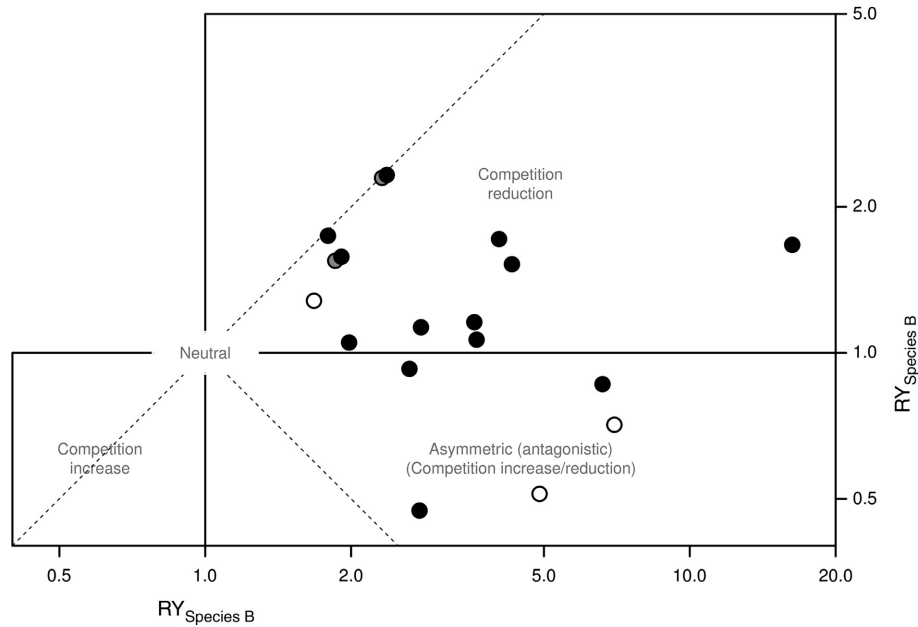


FIG. 3. Interspecific interactions in two-species mixtures, plotted as relative yield (RY) changes of individual trees of the species involved. The species with the larger relative change is on the abscissa. Quadrants indicate a competition reduction for both partners (top right), an asymmetric (antagonistic) effect (one partner benefits at the expense of the other partner; bottom right), or an increase in competition for both species (bottom left). The color of the symbols indicates the significance of effects (black, $P < 0.05$; gray, $P < 0.1$; white, $P \geq 0.1$). Gray lines indicate responses for indistinguishable intra- and interspecific interactions.

Complementarity and selection effects

In the 18 different two-species mixtures, complementarity effects sensu Loreau and Hector (2001) were significantly positive for total aboveground biomass, leaf biomass, and wood biomass ($F_{1,17} > 23$, $P < 0.001$ for all three variables). Complementarity effects also were larger in light than in shade ($F_{1,17} > 17$, $P < 0.001$ for all three variables). The corresponding selection effects for all fractions did not significantly deviate from zero ($F_{1,17} < 1.5$, $P > 0.2$ for all three variables). Net biodiversity effects were significantly positively ($F_{1,20,4} = 12.5$,

$P = 0.002$) related to differences in leaf distribution in the corresponding monocultures (i.e., negatively to the proportional similarity of leaf distributions in monocultures, Fig. 4).

Shifts in vertical canopy space use

There was a significant reduction in overlap of vertical leaf distributions when pairwise species mixtures were compared to the situation in monoculture ($F_{1,17} = 4.7$, $P < 0.05$), and this shift was marginally significantly larger in shade than in full light ($F_{1,17} = 3.4$,

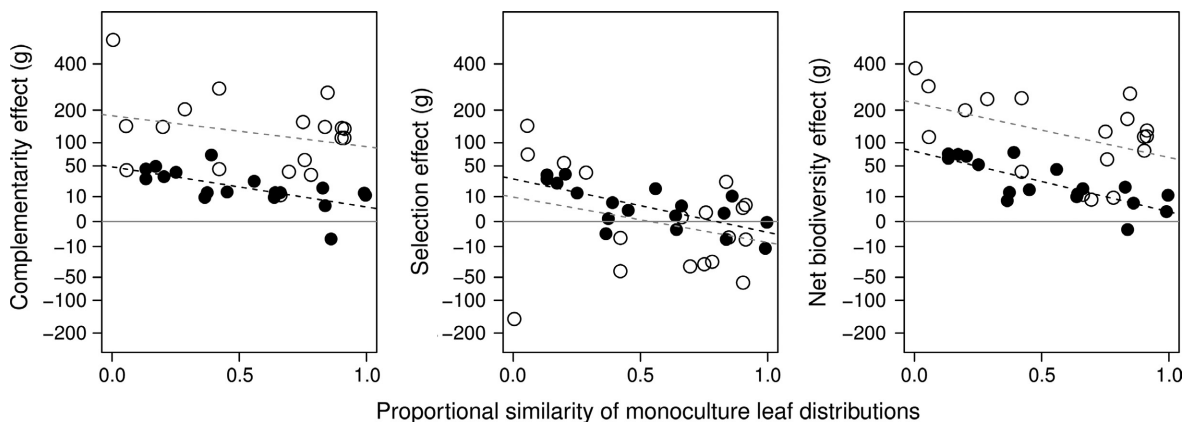


FIG. 4. Complementarity, selection, and net biodiversity effects in two-species mixtures in light (open symbols) and shade (closed symbols) as a function of the proportional similarity of vertical leaf distributions (assessed in monocultures). Dashed lines indicate model predictions.

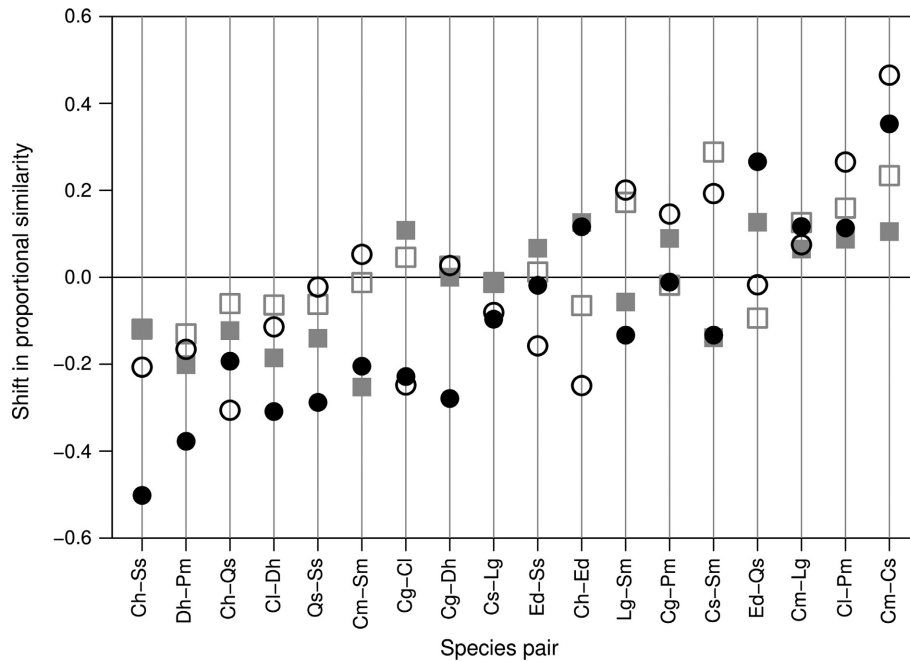


FIG. 5. Shifts in vertical leaf (circles) and wood (squares) distribution overlap, expressed as change in proportional similarity from monocultures to mixtures. Data are shown for each species pair in light (open symbols) and shade (closed symbols). See Table 1 for species codes.

$P = 0.08$). Trends identical in direction were found for wood distribution overlap but these were not statistically significant. Shifts in proportional similarity of leaf distributions under interspecific competition also differed among the particular species pairs ($F_{17,17} = 3.2$, $P = 0.01$; Fig. 5). Again, similar trends were observed for wood distributions but these were not statistically significant.

In shade but not in control plots, the changes in proportional similarity of leaf distributions in mixed stands relative to reference monocultures depended on functional trait distances between species (leaves, $F_{1,16} = 5.5$, $P < 0.05$ and $F_{1,16} = 6.6$, $P < 0.05$ for trait distances d_1 and d_2 , respectively; wood, $F_{1,16} = 6.6$, $P < 0.05$ and $F_{1,16} = 3.5$, $P = 0.08$ for d_1 and d_2 , respectively). Species more distant in trait space shifted their distributions

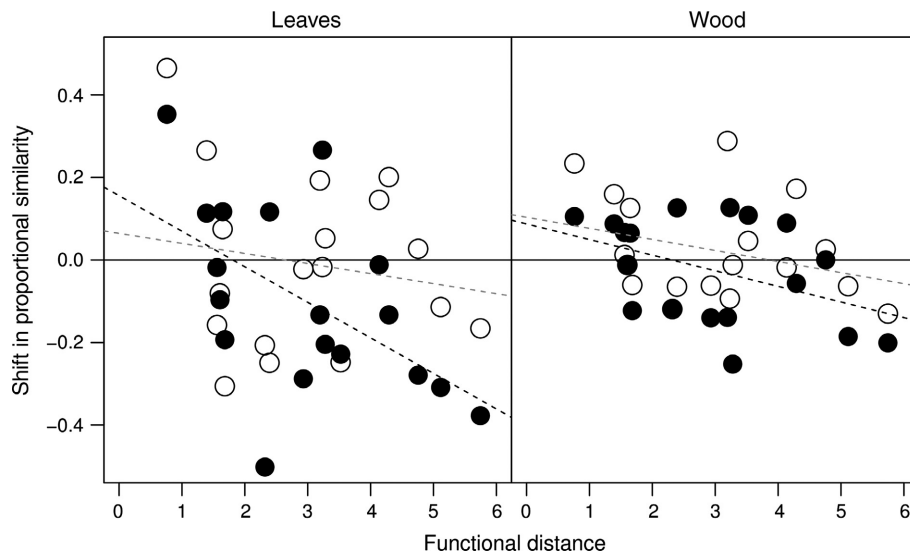


FIG. 6. Shifts in similarity of vertical distributions when moving from monocultures to mixtures, for leaves and wood, as a function of functional trait distance d_2 (see Materials and Methods). In light (open symbols) but not in shade (solid symbols), these shifts are statistically significant for leaves ($F_{1,16} = 6.6$, $P < 0.05$) and marginally significant for wood ($F_{1,16} = 3.5$, $P = 0.08$).

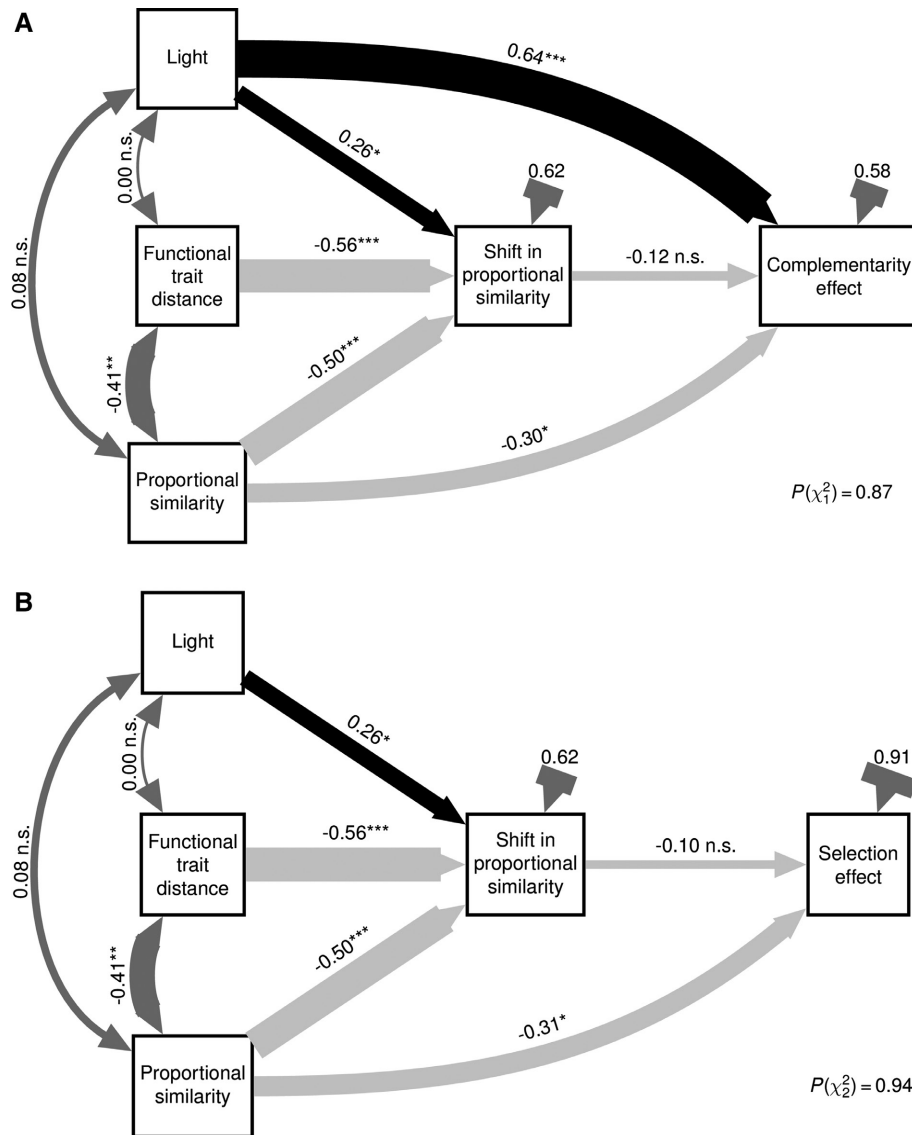


FIG. 7. Path diagrams showing the relations, for two-species mixtures, of (A) complementarity effects and (B) selection effects with light levels, functional trait distances, proportional similarity of monoculture leaf distributions, and the shift of these distributions when moving from intraspecific (monocultures) to interspecific competition (mixtures). Even though not statistically significant, the link between the shift in proportional similarity and complementarity and selection effects was kept because it reflects a key hypothesis tested. The link from light to selection effects was small and non-significant and therefore dropped from the lower path diagram. Arrows indicate standardized path coefficients (black, positive; gray, negative). Gray double arrows indicate correlations between exogenous variables. Nonsignificant χ^2 tests indicate a good agreement of observed and model-implied covariance structure. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; n.s., not significant.

further apart under interspecific competition, reducing overlap. Conversely, shifts in the opposite direction were found for species with very similar traits (Fig. 6).

Interrelation of effects

We modelled complementarity and selection effects in dependence of the light availability treatment, the functional trait distance of species pairs, their proportional similarity of monoculture leaf distributions, and the shift of these distributions under interspecific relative to

intraspecific competition (Fig. 7). Light significantly increased complementarity effects but not selection effects. Complementarity and selection effects were significantly smaller when monoculture leaf distributions were more similar. The path coefficient for the links from the shift in monoculture leaf distribution similarity to complementarity effects and selection effects was negative, as hypothesized, but small and not statistically significant.

Trait distances and proportional similarity of leaf distributions were negatively correlated. Shifts in leaf distributions were negatively correlated to both these drivers

when analyzed separately ($r = -0.35$ for trait distances and $r = -0.16$ for the proportional similarity of monoculture leaf distributions; Pearson's product moment correlation). These correlations became stronger when correcting for the effect of the other driver in a structural equation model (standardized path coefficients of -0.56 and -0.50 ; $P < 0.001$; Fig. 7).

DISCUSSION

Our analysis suggests that the increased productivity of developing subtropical tree stands was driven by interspecific niche complementarity. Tree species that were more different with respect to vertical biomass allocation and growth-related functional traits generated larger net biodiversity effects when combined in mixed stands, and this effect was larger in light than in shade.

A feature of our experimental design was that it contained a large number of realized bipartite species combinations that were statistically replicated, enabling an analysis of responses of specific community compositions in relation to differences in vertical biomass allocation of their component species. Interestingly, in approximately two-thirds of the combinations both species benefitted relative to their monoculture situation. In the remaining one-third of combinations the relative biomass gain of the "winner" always was larger than the relative loss of the "loser," i.e., relative yield totals (RYT) exceeded 1. Net biodiversity effects were always positive, often significantly so, except for a single community in shade where the net effect averaged slightly below zero, but not significantly so. These findings together with positive complementarity effects strongly suggest that niche complementarity among species was driving the community-level biomass increase we observed with increasing species richness.

It is difficult to distinguish between specific forms of interspecific interactions in the substitutive experimental designs typically adopted in biodiversity experiments because trees are planted at constant density and still compete with conspecifics when in monoculture. Our data suggest that interspecific competition was lower than intraspecific competition in most cases (competition reduction), often for both partners, but there also might have been cases with an additional element of facilitation. Complementarity through facilitation has been observed in grassland biodiversity experiments with legumes (Spehn et al. 2002, Hooper and Dukes 2004), where these effects could be related to increased N acquisition, increased N-use efficiency, and reduced N losses (Niklaus et al. 2001, 2016, Scherer-Lorenzen et al. 2003, Fargione et al. 2007). Complementarity effects, however, also are at play in the absence of obvious facilitation mechanisms (van Ruijven and Berendse 2003). Several grassland biodiversity experiments have indicated that complementarity effects *sensu* Loreau and Hector (2001) develop progressively with time, replacing initial selection effects (Cardinale et al. 2007, Fargione et al. 2007). Less is

known about tree communities. In a field experiment with temperate tree species, using high-density stands of young trees as in our study, Tobner et al. (2016) found weak evidence for positive biodiversity-productivity relationships and no transgressive overyielding; statistically significant positive net biodiversity effects were found in a few mixtures, and these effects were largely driven by selection effects, with complementarity effects playing a subordinate role only. In contrast, our study shows that complementarity effects can already dominate community responses to species richness in experimental tree stands in early stages of stand development, in particular when these effects are promoted by high tree densities.

Plant growth can be limited by many resources, including nutrients, water, CO₂ and light, and trophic interactions may also be important. Liebig's law of the minimum suggests, based on stoichiometric considerations, that there is one resource (or at least very few) that limit growth. However, from an economic perspective, one would expect that plants allocate their resources in a way that leads to simultaneous co-limitation by multiple resources, thus avoiding over-investment in the acquisition of one resource when others are limiting (Bloom et al. 1985). Such a balanced strategy can be achieved through architectural plasticity by fine-tuning the proportions of organ growth, e.g., of root length (nutrient uptake) and leaf area (photosynthetic capacity). Indeed, co-limitations are frequently found in natural ecosystems (Gruner et al. 2008, Harpole et al. 2011). From a photosynthesis-centered viewpoint, however, one might also argue that light takes a special role because competition is likely to be extraordinarily asymmetric, with taller individuals being able to efficiently pre-empt light through shading, i.e., they benefit from light partitioning without reciprocal effect for smaller individuals. Indeed, plants deploy higher than optimal leaf area in the upper canopy to benefit from the suppression of smaller-sized neighbors (Anten and Hirose 2001). Also, extra carbon gains from increased light interception might allow an individual to escape other limitations through carbon investment into the acquisition of these resources.

Our study included a factorial light vs. shade treatment. Depending on the competition mechanisms at play, contrasting consequences for biodiversity effects might be expected. If light exacerbates size differences among species by disproportionately favoring growth of the taller species at the expense of the smaller competitor, dominance increase and biomass gains could be driven by selection effects. Alternatively, higher light levels might increase the total available light gradient ("biotope space"; Dimitrakopoulos and Schmid 2004), allowing coexistence of multiple, distinct, strategies with respect to light climate. In our study, complementarity and net biodiversity effects increased with light intensity, which supports the latter possibility. Similar effects were found in herbaceous communities (Fridley 2003) and attributed to light-use complementarity. However, there are also

alternative explanations. First, the size-related benefits ultimately may be smaller than one might expect from the asymmetric nature of light competition because maintaining size incurs a cost for supportive tissue, i.e., a higher leaf mass ratio (Werger et al. 2002). Ultimately, competition for light may thus not be so different in nature than competition for other resources. Second, faster (exponential) growth of the taller species in high light will shift crowns apart in vertical space, allowing for a larger architectural complementarity and better spatial biomass packing, a mechanism that is not directly mediated by rates of photosynthesis. Data from mixed tree plantations in which light interception increased but not biomass (le Maire et al. 2013) support the idea that light interception and growth are not necessarily coupled. Similarly, higher biomass in more diverse mature subtropical forest stands was achieved at similar leaf area in a nature reserve near our study, but associated with a higher diversity in tree height (Castro-Izaguirre et al. 2016). Third, while community-level productivity was related to light, complementarity effects and thus biodiversity–productivity relationships might have been driven by complementarity for resources other than light and aboveground space per se. It is conceivable, for example, that size differences also have implications for spatial patterns of belowground resource extraction, including water, and for pathogen transmission rates, which might depend on vertical canopy structure as found in field trials with rice varieties (Zhu et al. 2000).

Species shifted their leaf and wood distributions when grown in mixture relative to the monoculture situation. Disentangling the effects of trait distances and the similarity of monoculture leaf distributions was not straightforward, since these drivers were (negatively) correlated, i.e., species pairs further apart in functional trait space also had vertical leaf distributions that overlapped less (their similarity was lower). The functional traits we considered in our calculations were growth-related, i.e., they characterized allocation strategies. One of the distance metrics contained size-related information (d_1) whereas the other (d_2) did not, but results were very similar for both distance measures. We found that leaf distributions often shifted apart when they overlapped, likely as result of competition-driven phenotypic plasticity. At the same time, the size and overlap-independent effect of functional distance between species suggests that species had a greater capacity to plastically adjust their biomass allocation when they differed in functional traits, i.e., growth strategy. We did not find a statistically significant effect of increases in complementarity through this mechanism, although the sign of the path coefficient matched our hypothesis. This effect, if real, may have been too small to be detected given the statistical power of our design.

In conclusion, our data indicate that complementarity effects are important in driving biodiversity–productivity relationships in communities of young trees, and that these effects are positively related to often plastically

increased differences in vertical leaf niches and differences in growth strategies between species. Whether net biodiversity effects are related to light interception and subsequent effects on photosynthesis remains unclear and is difficult to test without direct manipulation of light profiles (Hautier et al. 2009). Foraging for light clearly is important and involves many morphological and physiological adaptations (Evans and Poorter 2001, Falster and Westoby 2003, Ishii and Asano 2010). However, there also is evidence that photosynthetic rates reflect limitations for other resources, including water (Muller et al. 2011, Pantin et al. 2011). Increased carbon assimilation rates could thus rather be the consequences of overyielding than the cause. Several studies hint in this direction. For example, Sapjanskas et al. (2014) modeled light partitioning in tropical forest assemblages and concluded that light partitioning occurred but that these effects were too small to explain growth enhancements observed in species-rich mixtures. In temperate forest, Jucker et al. (2015) found positive effects of species richness on crown packing and light interception, but no effect on growth. It may thus be premature to attribute enhanced growth in species mixtures to complementarity in light use. One possibility is that complementarity is for canopy space per se, or that size differences promote complementarity for other resources, including soils, or for trophic interactions.

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M. Baruffol collected field data. P. A. Niklaus analyzed the data and wrote the first draft of the manuscript. B. Schmid, J. S. He, and K. Ma contributed to the design of the experiment. All authors contributed to the final revisions of the manuscript.

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