

Opposing intraspecific vs. interspecific diversity effects on herbivory and growth in subtropical experimental tree assemblages

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Abstract

Aims

Positive plant diversity–ecosystem function relations are ultimately driven by variation in functional traits among individuals that form a community. To date, research has largely focused on the role of species diversity for ecosystem functioning. However, substantial intraspecific trait variation is common and a significant part of this variation caused by genetic differences among individuals. Here, we studied the relative importance of species diversity and seed family (SF) diversity within species for growth and herbivory in experimental subtropical tree assemblages.

Methods

In 2010, we set up a field experiment in subtropical China, using four species from the local species pool. Trees were raised from seeds, with seeds from the same mother tree forming an SF. We established 23 plots containing one or four species (species diversity treatment) and one or four SFs per species (SF diversity treatment). Tree growth (stem diameter, plant height and crown expansion) and herbivory (percentage leaf loss due to leaf chewers) were monitored annually from 2011 to 2013.

Important findings

Tree species richness promoted growth but had no effect on herbivory. In contrast, SF diversity reduced growth and increased herbivory but only so in species mixtures. Most of the observed effects were time dependent, with the largest effect found in 2013. Our results suggest that biodiversity can affect plant performance directly via tree species–species interactions, or context dependent, via potential effects on inter-trophic interactions. Two important conclusions should be drawn from our findings. Firstly, in future studies regarding biodiversity and ecosystem functioning (BEF) relationships, intraspecific genetic diversity should be given similar weight as species diversity as it has often been neglected and its effects are not well understood. Secondly, we demonstrate opposite effects of biodiversity among and within species, stressing the importance to consider the effects of multiple levels of biodiversity simultaneously.

Keywords: BEF-China, species diversity, genetic diversity, growth, herbivory

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INTRODUCTION

Exploring potential links between biodiversity and ecosystem functioning (BEF) is a major challenge in contemporary ecology. As a consequence of anthropogenic ecosystem degradation, local species diversity is changing, a process that has the potential to alter ecosystem functions such as nutrient cycling (Cardinale *et al.* 2002) or biomass production (Tilman *et al.* 1996). The biodiversity component of BEF experiments is strongly focused on the effects of species diversity (Balvanera *et al.* 2006). Such effects of species diversity on ecosystem functions are caused by functional trait diversity among species (Hooper *et al.* 2005) and are of central interest in biodiversity research. However, considerable proportions of trait variation are found within species (Siefert *et al.* 2015). Consequently, both interspecific and intraspecific trait variation may evoke biodiversity effects on ecosystem functioning.

Effects of species diversity on ecosystem functions are proposedly caused via complementarity and sampling effects (Hooper *et al.* 2005). Firstly, complementarity effects can comprise biotic or abiotic stress relief (e.g. by nurse plants), resource enhancement (Bruno *et al.* 2003; Fowler 1986) and niche differentiation among species (Tilman *et al.* 1997a). For example, an increase in total water and nitrogen uptake was observed in communities of species with differing rooting depths or between N-fixing and non-fixing species, respectively (Hooper 1998; van Ruijven and Berendse 2005). Similarly, an increase in resource use efficiency was demonstrated by Sun *et al.* (2017) who reported a higher fine root production in mixtures than in monocultures. Secondly, the sampling effect states that some species affect ecosystems more strongly than others, due to inherently high productivity or competitive ability (Tilman *et al.* 1997b). Thus, increasing species richness also increases the probability of encountering such a species which affects ecosystem functions directly rather than by interactive effects of multiple species (Hector *et al.* 1999; Peng *et al.* 2017). Because the above processes are ultimately due to trait variation, both interspecific and intraspecific trait variation may similarly cause such effects. In fact, genotypes have been shown to cause intraspecific facilitation (Ellers *et al.* 2011) or intraspecific complementarity (Reusch *et al.* 2005), and genotype identity can induce sampling effects, e.g. on herbivory (Castagneyrol *et al.* 2012). Thus, processes that drive genotype diversity–ecosystem functioning relationships are equivalent to those outlined for species diversity.

Intraspecific diversity can have strong effects on ecosystem functioning (Cook-Patton *et al.* 2011; Crutsinger *et al.* 2006; Whitham *et al.* 2003). Intraspecific genetic diversity rather than phenotypic plasticity is relevant here because many functional plant traits are highly heritable (Johnson *et al.* 2009; Zeng *et al.* 2017a). The identity of plant genotypes in plant mixtures have been shown to affect nutrient cycling (Li *et al.* 2017), e.g. nitrogen mineralization or nutrient immobilization (Schweitzer *et al.* 2004, 2005). Higher genetic diversity may lead to increased community-level plant biomass

(Drummond and Vellend 2012), elevated levels of chemical defences (Moreira *et al.* 2014) or increased plant survival (Parker *et al.* 2010). However, despite its importance for ecosystem functioning, intraspecific genetic diversity has received comparably little attention in BEF research, particularly in forest BEF experiments. Other causes of positive biodiversity–productivity relationships might be mediated through biotic interactions, e.g. between plants and herbivores. Genotypic diversity may be more (Crawford and Rudgers 2013), equally (Cook-Patton *et al.* 2011) or not important (Abdala-Roberts *et al.* 2015) relative to species diversity in structuring arthropod communities. With respect to herbivory, both reduced (Parker *et al.* 2010) and increased herbivory (Castagneyrol *et al.* 2012) have been found with increasing genetic diversity.

Biodiversity–ecosystem functioning research has often focused on primary production. Nevertheless, species diversity can also affect trophic interactions. Regarding herbivory, two general processes have been observed. Firstly, herbivore damage may depend on neighbour identity such that herbivory is reduced when focal plants grow in proximity of highly defended or unpalatable neighbours or, conversely, that herbivory is increased if focal plants have highly palatable neighbours. Such neighbourhood-dependant effects are known as associational resistance and associational susceptibility (Agrawal *et al.* 2006) and play important roles in tree communities (Erickson *et al.* 2012; Plath *et al.* 2012; Stastny and Agrawal 2014). Secondly, herbivory depends on the density of host plants, affecting the likelihood of an oligophagous herbivore to find a suitable host. This can then either lead to increased (resource concentration, Root 1973) or decreased herbivory (resource dilution, Otway *et al.* 2005). In contrast, herbivory by polyphagous herbivores may increase due to a broad dietary mix provided by high plant diversity (e.g. Brezzi *et al.* 2017; Schuldt *et al.* 2010).

The present study focuses on effects of both species and intraspecific genetic diversity on tree growth and herbivory in young experimental tree stands. We established a factorial species diversity–genetic diversity experiment in a subtropical biodiversity hotspot in Southeast China and conducted serial measurements of individual tree growth and herbivory over the course of 3 years to address the following questions: (i) Do tree growth and herbivory depend on species diversity? (ii) Are growth and herbivory driven by genetic diversity? (iii) Do effects of species and genetic diversity interact, and (iv) are these effects time dependent?

MATERIALS AND METHODS

Experimental setup

In 2009, a forest BEF experiment was established by the Biodiversity and Ecosystem Functioning China project (BEF-China) at Xingangshan Township, Dexing, Jiangxi Province, China (see Bruelheide *et al.* 2014, for details). Randomly scattered within site B, we used 23 plots, 25.8×25.8 m in size (1 mu, traditional Chinese unit), each harbouring 400 evenly

spaced trees arranged in a 20×20 rectangular grid. From the local species pool, we selected two deciduous species, *Alniphyllum fortunei* (HEMSLEY) MAKINO (Styracaceae) and *Idesia polycarpa* MAXIMOWICZ (Salicaceae) and two evergreen species, *Cinnamomum camphora* (L.) PRESL. (Lauraceae) and *Daphniphyllum oldhamii* (HEMSLEY) ROSENTHAL (Daphniphyllaceae). All of our target species are trees (*D. oldhamii* classified as tree/shrub) growing up to 30 m in height. Economically, *C. camphora* and *D. oldhamii* are used for timber production, the former species also being used for the extraction of camphor (Flora of China). Plants originated from seeds that were collected in the nearby Gutianshan National Nature Reserve. Seeds were collected from different mother trees, with seeds from the same mother tree forming a seed family (SF), which genetically is considered to consist of half-sibs. The use of SFs allowed us to manipulate the level of genetic diversity as members of a single SF are on average genetically more closely related and, thus, genetically less diverse than members of different SFs. This is supported by preliminary analyses based on microsatellite data in two of the species showing larger kinship coefficients within SFs than among SFs (S. G. Michalski and W. Durka, unpublished data). We manipulated species diversity (SD) and genetic diversity (in terms of SF richness) in a crossed design. Species diversity was either one species (species monocultures) or four species (species mixtures) and genetic diversity was either one SF (SF monoculture) or four SFs (SF mixture). All seedlings were raised in two local nurseries and transplanted into the field in autumn 2010 at the approximate age of 16 months. We aimed at using eight SFs per species, however, owing to the different availability of seeds, the number of SFs per species varied between eight in *I. polycarpa* and 15 in *D. oldhamii* (supplementary Table S1). However, the additional SFs made up only 3.7% of the final data set. All analyses were performed on the full and a reduced data set containing only SFs that were present in all diversity levels. Qualitatively, results of the full and reduced data set did not differ, hence we present the findings based on the latter. In total, we planted 40 different species monocultures (8 different SF monocultures and 2 different SF mixtures in each of 4 species) and 13 species mixtures (7 SF monocultures and 6 SF mixtures, Table 1). Due to the large number of monocultures of species and SFs, we used ¼ plots of 10×10 individuals for species monocultures, but full plots for species mixtures. In each treatment, species and SFs were planted randomly and in equal quantities. Of the 9200 individuals planted in 2010, 58% established in 2011 and survived until 2013. Mean survival among species ranged between 37% in *I. polycarpa* and 84% in *C. camphora* (supplementary Table S1).

Plant growth and herbivory

Annually between 2011 and 2013, we measured growth and herbivory between September and October. Measurements included stem diameter at ground height (dgh), plant height, crown diameter and herbivory. Stem diameter was measured

Table 1: Number of replicates per level of species and genetic diversity

Species	SD	GD	No of different SF compositions	Plot size (mu)
<i>Alniphyllum fortunei</i>	1	1	8	0.25
	1	4	2	0.25
<i>Cinnamomum camphora</i>	1	1	8	0.25
	1	4	2	0.25
<i>Daphniphyllum oldhamii</i>	1	1	8	0.25
	1	4	2	0.25
<i>Idesia polycarpa</i>	1	1	8	0.25
	1	4	2	0.25
All four species	4	1	7	1
	4	4	6	1

Abbreviations: SF = seed family; SD = species diversity; GD = genetic diversity. Plot size is given in mu, a traditional Chinese unit of area (25.8×25.8 m), with 1 mu being the size of a full plot with 400 individuals.

as the diameter of the root collar both in north–south and east–west direction and averaged for data analyses. Similarly, crown diameter was measured as the maximal crown expansion in both north–south and east–west direction and also averaged. We further measured tree height as the vertical distance from the soil surface to the highest green leaf. Herbivory was estimated visually as percentage missing leaf area due to insect feeding on seven randomly chosen leaves per tree and later averaged and square root transformed per individual. Lepidoptera are the most, while some beetle families the second most common herbivores according to field observation in the natural forest from the same region (Schuldt *et al.* 2010)

Statistical analyses

All data were analysed by analysis of variance (Schmid *et al.* 2017; aov function of R 3.2, R Core Team 2015), with group-wise means weighted by underlying sample size and factors fitted sequentially corresponding to the hierarchy of our experimental design (Table 2). In biodiversity studies, species diversity effects are generally tested using different species mixtures as replicates (Schmid *et al.* 2002). In our study, there was only a single four-species mixture so that community composition effectively was equal to the variation among species in monoculture. We further tested species richness effects using plot as replicate, i.e. whether particular monocultures and four-species mixtures were different. With the same rationale, effects of genetic diversity were first tested against plot, later against Species × Plot as replicate. Species effects were separated into two components. First, we tested for species identity effects in monocultures (using plots as replicates); second, we tested species identity effects in multispecies mixtures (using Species × Plot as replicate). To test whether the effects of biodiversity depended on time, we repeated the above tests as interactions with time after testing time against Time × Plot variances. As

Table 2: Model structure and results of the linear model analyses

Term	df	Error	F and significance			
			Stem diam.	Height	Crown diam.	Herbivory
Species diversity	1	Sp.mono	0.7	0.22	0.13	0.06
Species diversity	1	Plot	7.94*	0.041*	2.77	1.33
Species in Sp.mono	3	Plot	11.31***	21.67***	21.42***	23.81***
Genetic diversity	1	Plot	0.53	0.13	1.21	0.1
Species diversity × Genetic diversity	1	Plot	0.23	<0.01	<0.01	0.64
Plot	18					
Seed family composition	34	Subplot	4.21***	3.78***	6.23***	1.2
Species in Sp.mix	3	Subplot × Species	192.71***	307.02***	297.78***	84.72***
Sp.mix × Genetic diversity	3	Subplot × Species	6.14***	4.54**	5.32**	3.07*
Subplot	33					
Subplot × Species	141					
Time	2	Time × Plot	534.79***	690.03***	434.48***	44.74***
Time × Species div.	2	Time × Sp.mono	0.9	0.2	0.13	0.22
Time × Species div.	2	Time × Plot	2.9	1.95	0.77	1.37
Time × Species in Sp.mono	6	Time × Plot	3.21*	9.76***	5.91***	6.13***
Time × Genetic diversity	2	Time × Plot	0.06	0.13	0.38	1.9
Time × Species diversity × Genetic diversity	2	Time × Plot	0.71	1.37	0.78	1.04
Time × Plot	36					
Time × Seed family composition	68	Time × Subplot	3.18***	2.53***	5.33***	1.22
Time × Species in species mixtures	6	Time × Subplot × Species	44.97***	45.1***	21.44***	46.37***
Time × Sp.mix × Genetic diversity	6	Time × Subplot × Species	2.34*	1.49	1.46	0.95
Time × Subplot	66					
Time × Subplot × Species	279					

Abbreviations: Sp.mono = species monocultures, Sp.mix = species mixture, Species div. = species diversity. Numerator (Term) and denominator (Error) are given with their respective degrees of freedom (df). For growth and herbivory, *F* values and significances are given to the right.

we assumed potential effects and interactions to be strongest when species and individuals physically interact, we separately examined data from the last year of measurements. To test whether our measurements were affected by tree mortality, we correlated growth and herbivory of monoculture plots with within-plot tree density for each year and species separately. However, of the 48 performed correlations, only 4 were significant ($P < 0.05$), one in each species, and in different years (data not shown). Thus, we considered these as spurious effects and did not further take into account mortality or tree density in our analyses.

RESULTS

All measures of growth and herbivory depended on species identity, both in species monocultures and species mixtures (Fig. 1; Table 2). *Alniphyllum fortunei* was overall the tallest species, whereas *I. polycarpa* exhibited the highest levels of herbivory. Species effects interacted with time (Table 2) and revealed strong temporal variation, most noticeably seen in *I. polycarpa* which suffered more than twice as much herbivory in 2013 when compared with other species in the same year (Fig. 1B, D, F and H).

Species diversity had a significant positive effect on stem diameter ($F_{1,18} = 7.94$, $P = 0.012$, Fig. 2A) and height ($F_{1,18} = 4.85$, $P = 0.041$, Fig. 2C). Mean stem diameter and height were 9.2% and 4.9% larger in species polycultures, respectively. Species diversity effects on stem diameter also varied over time, indicated by a marginally significant Species diversity × Time interaction ($F_{2,36} = 2.9$, $P = 0.069$, Fig. 2B). Analysing data from 2013 also yielded significant positive species diversity effects on both stem diameter and height ($F_{1,18} = 8.02$, $P = 0.012$ and $F_{1,18} = 5.02$, $P = 0.038$, respectively) which was not the case in 2012.

We did not find a statistically significant overall effect of SF richness on growth and herbivory, nor did we find a significant interaction of species and SF diversity. However, statistically significant SF richness × Species identity interactions were found for polycultures (Table 2), indicating that species were affected differently by genetic diversity, but only when grown in species mixtures. Higher genetic diversity resulted in a reduction of growth when compared with genetic monocultures (Fig. 3A, left panel). In contrast, herbivory increased with higher genetic diversity (Fig. 3D, left panel). The effects of genetic diversity on growth were independent of time, with the exception of stem diameter ($F_{6,279} = 2.34$, $P = 0.033$, Table 2).

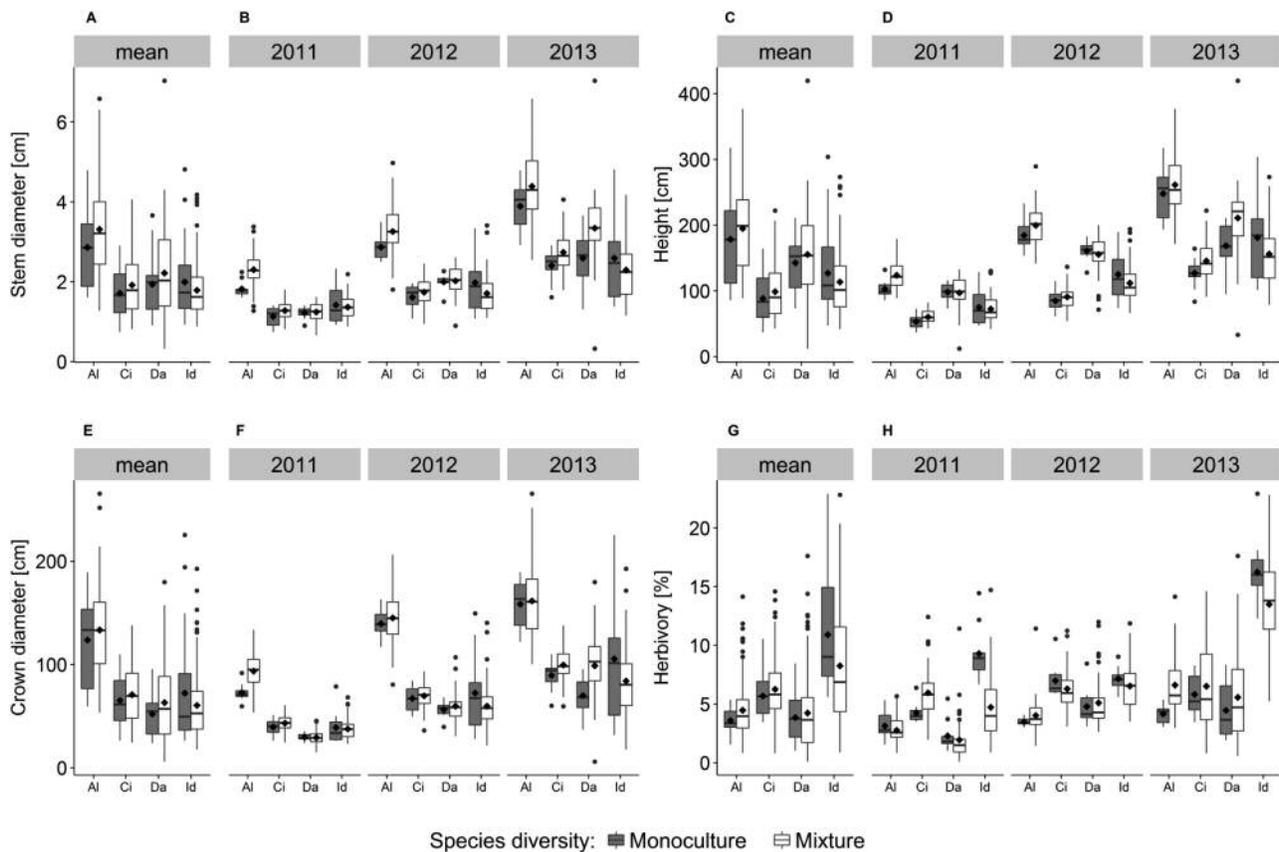


Figure 1: species-specific growth (A, B: stem diameter; C, D: height; E, F: crown diameter) and herbivory (G, H). Effect is shown as overall (A, C, E, G) and annual mean (B, D, F, H) in both, species monocultures and species mixtures. Means are shown as rectangles within boxes. Al = *Alniphyllum fortunei*, Ci = *Cinnamomum camphora*, Da = *Daphniphyllum oldhamii*, Id = *Idesia polycarpa*.

Lastly, SF composition consistently explained a statistically significant fraction of variance in growth measures (Table 2). Effects were also found as significant interactions with time for all growth variables (Table 2). Surprisingly, herbivory was not affected by SF composition, neither overall nor over time.

DISCUSSION

We found that species and genetic diversity had contrasting effects on growth. Generally, growth increased with species diversity, while in species mixtures, growth decreased with genetic diversity. In contrast, herbivory was not affected by species diversity but rather increased with genetic diversity in species mixtures. These effects were significant after accounting for prevalent species identity effects. Our findings not only stress the importance of functional differences between species for ecosystem functioning but also demonstrate that intraspecific genetic diversity can exert strong effects on community performance at the same time, even contrasting the effects of species diversity. This study is one of the few that directly assessed the influence of both the genetic and the species levels of biodiversity simultaneously in experimental forest communities (but see Zeng *et al.* 2017b).

Genetic diversity effects

Genetic diversity affected growth and herbivory but only in species mixtures. Growth was reduced, whereas herbivory increased in plots with four SFs. In other words, in species polycultures, genetically rich communities grew slower while suffering higher levels of herbivory than genetic monocultures. Increasing herbivory with increasing SF diversity might be due to dietary mixing (e.g. Bernays *et al.* 1994) or associational susceptibility (reviewed in Barbosa *et al.* 2009) and was also observed when increasing plant genetic diversity (Castagneyrol *et al.* 2012; Kotowska *et al.* 2010). However, the negative effect of genetic diversity on tree growth to be negative was surprising as other studies reported opposite patterns (e.g. Schweitzer *et al.* 2005) and considering the overall positive effect of species diversity on growth. How would growth increase with species diversity while it decreases with genetic diversity in species-rich communities? Although growth and herbivory have been found to be positively correlated (Cook-Patton *et al.* 2011; Crutsinger *et al.* 2006), the opposite is also possible as Zvereva *et al.* (2012) showed that low-to-moderate amounts of simulated herbivory severely reduced growth in *Betula pubescens* subsp. *czerepanovii* saplings. Thus, we hypothesize that high genetic diversity in polycultures

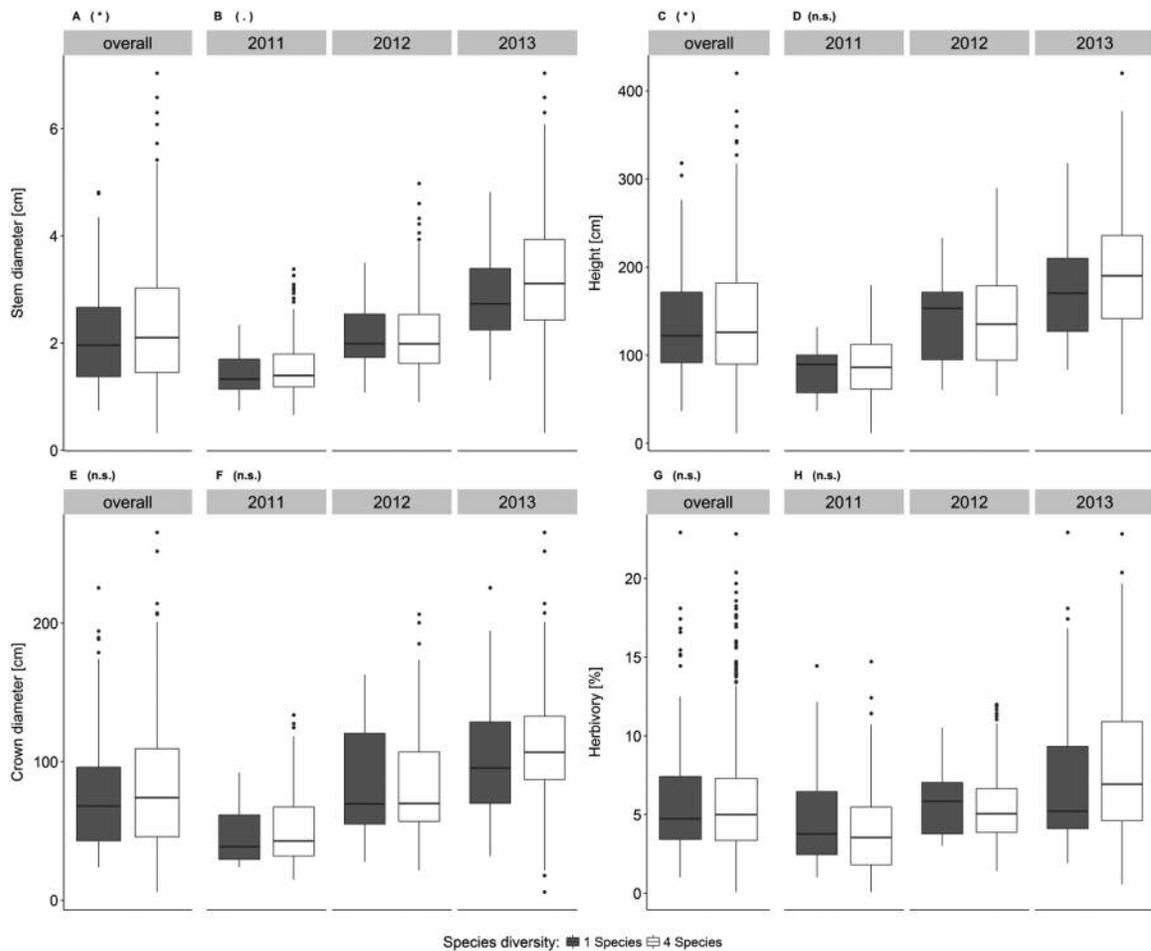


Figure 2: effect of species diversity on growth (A, B: stem diameter; C, D: height; E, F: crown diameter) and herbivory (G, H). Effect is shown as overall (A, C, E, G) and annual mean (B, D, F, H). (n.s.) = not significant, (.) = marginally significant, * $P < 0.05$.

favours herbivory, possibly via dietary mixing (Bernays *et al.* 1994) or increased generalist herbivore load (associational susceptibility, Barbosa *et al.* 2009; Plath *et al.* 2012). As herbivory increases, it negatively affects growth by altering assimilate distribution or reducing photosynthetic leaf area. This interpretation is further supported by a recent study conducted on the experimental sites of the BEF-China project, reporting a negative correlation between herbivory and growth (Schuldt *et al.* 2015). The authors found herbivory to increase with species richness and most of the herbivore damage was caused by grasshoppers and lepidopteran caterpillars, both of which are assumed to be generalists (Bernays and Chapman 2000; Schuldt *et al.* 2014). Similarly, in the BEF-China experiment, the most abundant herbivore taxa were Lepidoptera, Curculionidae and Auchenorrhyncha, which showed a high degree of generalism in host use (J. Y. Zhang *et al.*, resubmitted for publication). Such generalism in feeding behaviour may lead to associational susceptibility of target plants, if more palatable species in a plot attract more herbivores who then also attack a less palatable target species. An alternative hypothesis arises from the findings of

Crawford and Rudgers (2013), who observed the effects of genetic diversity in a dominant species on arthropod community composition and on community biomass production (Crawford and Rudgers 2012). They argued that herbivores may be sensitive to emergent community properties, which can be strongly affected by dominant species. Accordingly, in our study, growth and herbivory in species polycultures could be affected by genetic diversity in a single rather than all species. For example, genetic diversity in *I. polycarpa*, which exhibited the highest level of herbivory, could be linked to traits that affect herbivory (Eichenberg *et al.* 2015). Among the four species studied, *I. polycarpa* ranked lowest in leaf concentration of total phenolics (D. Eichenberg and H. Bruelheide, unpublished) and thus, invested the least in structural defence. In contrast, genetic diversity in *A. fortunei*, the tallest species, may mainly have affected growth. This would not necessitate a causal relationship between growth and herbivory. Whether or not causally related in our case, we demonstrated that plant–herbivore interactions as well as plant growth in interacting tree species are differently affected by intraspecific diversity in different species

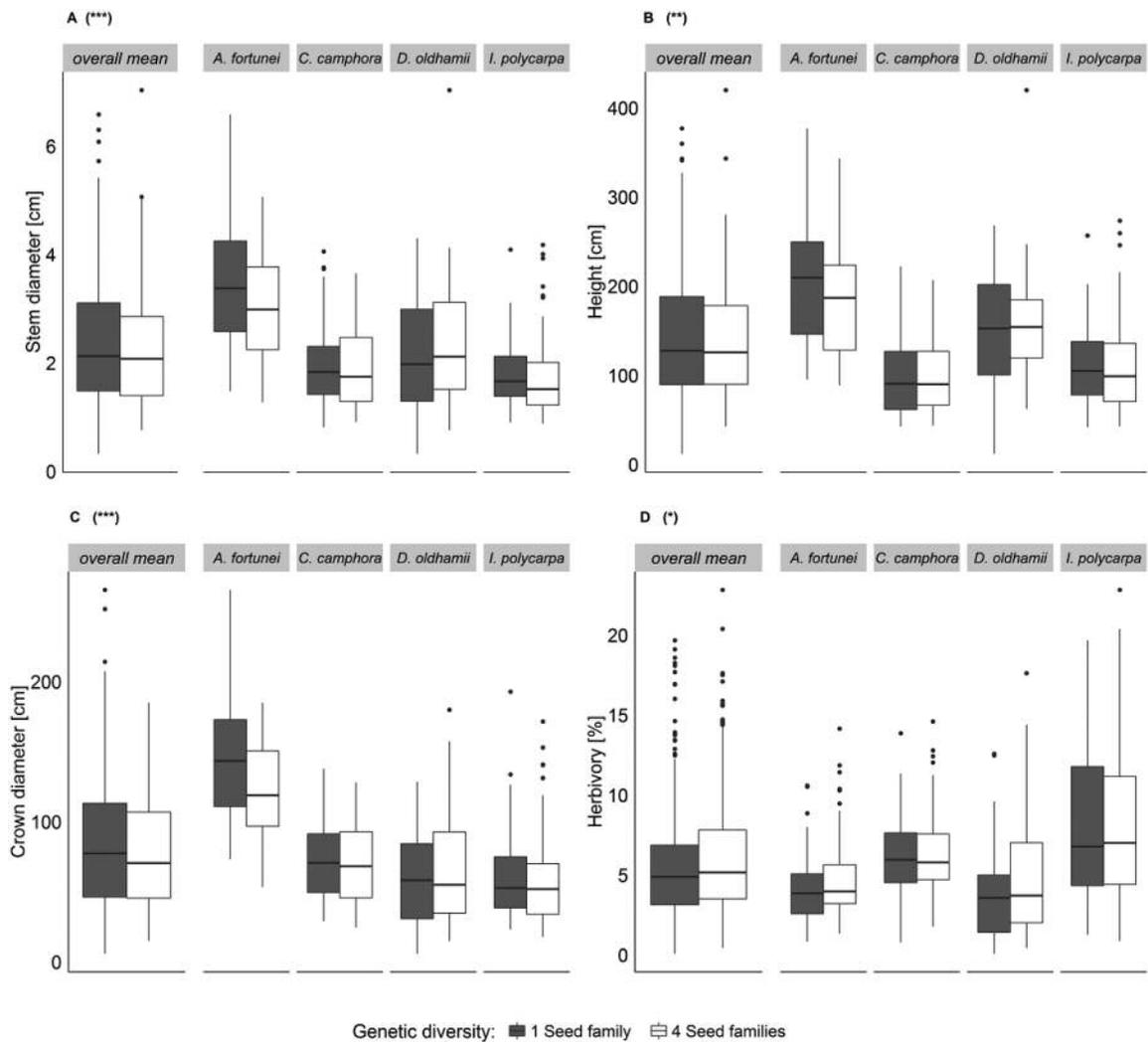


Figure 3: effect of genetic diversity on growth (**A**: stem diameter; **B**: height; **C**: crown diameter) and herbivory (**D**) in species mixtures. Overall and species-specific means are shown. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species diversity effects

We found a positive effect of species richness on growth among subtropical tree species. Similar results were found previously (e.g. [Vila et al. 2013](#), for temperate forests) and could be due to complementary resource use of different species in mixtures, allowing a more complete utilization of available resources, the alleviation of abiotic and/or biotic stress via interspecific facilitation or sampling effects of especially impactful species. Specifically, resources such as light or nutrients might be acquired and/or used more efficiently in heterogeneous plant assemblies due to complementary crown or root architectures, respectively. Following [Ishii and Asano \(2010\)](#), species' spatio-temporal differentiation in light acquisition could allow complementarity among species. As the species in the present study differ substantially in height (e.g. *A. fortunei* is about twice as tall as *C. camphora*), we cannot rule out a sampling effect of *A. fortunei* potentially driving the overall pattern, but it is also plausible that these differences

lead to a multilayered weave of canopies increasing the light-capture efficiency of the community as a whole. Similarly, belowground niche partitioning, e.g. due to differing rooting depth in species mixtures, was shown to affect biomass productivity ([Berendse 1982](#); [Hooper 1998](#)) and could affect mixed communities in a similar manner as their aboveground counterpart by allowing for a more complete use of belowground resources such as water or nutrients. Essentially, heterogeneity is expected to allow species to fill available 'space' more completely, both physically and ecologically. This heterogeneity could not only lead to complementarity effects (as e.g. in [Wacker et al. 2008](#)) but also lead to the alleviation of stress. Similarly, complementary crown and/or root architectures in mixed species communities could reduce the effects of drought or heat. Shade cast by larger species might reduce heat stress in smaller species or lower the rate of soil water evaporation. Drought and heat stress could be important drivers and negatively affect tree growth considering that our

experimental site was clear-cut prior to planting and soil surface temperatures exceeded 70°C in exposed locations (C. Z. Hahn, personal observation).

Our species pool was comprised of two evergreen and two deciduous species and thus species mixtures always contained both functional groups. The importance of functional group diversity for ecosystem functioning has been pointed out previously (e.g. [Loreau et al. 2001](#); [Reich et al. 2004](#); [Tilman et al. 1997a](#)). The combination of evergreen and deciduous species might not only lead to spatio-temporal niche differentiation as described above but also affect resource dynamics via, e.g. litter quality and decomposition rates. Leaf chemical properties and timing of senescence can affect resource availability and retention times (see [Richards et al. 2010](#) and references therein) and might be more favourable in mixtures of evergreen and deciduous species than in their respective monocultures. Irrespective of the underlying mechanisms, our findings provide evidence that growth in forest communities is positively correlated with species richness ([Baruffol et al. 2013](#); [Piotto 2008](#)).

Our results suggest that the effects of species and genetic diversity might be context dependant. Growth was positively affected by the number of species present (i.e. complementarity, facilitation or sampling effects), whereas growth was negatively affected by the number of genotypes in polycultures (i.e. associational susceptibility or dietary mixing resulting in reduced growth). Thus, the influence as well as the mode of operation of genetic diversity might need further empirical evaluation as species and genetic diversity are rarely manipulated simultaneously and only manipulating one level of biodiversity might give an incomplete picture.

Temporal dynamics

We observed that within only 3 years after establishment, growth and herbivory were affected either by species richness or, in a special case, by genetic diversity within species, showing that community responses to biodiversity establish quickly in subtropical forests, a conclusion also made by [Schuldt et al. \(2015\)](#). Evidence gathered from 20 years of BEF research also suggests that effects of biodiversity on ecosystem functioning are likely to strengthen over time ([Cardinale et al. 2012](#)). We found multiple interactions of time with growth and herbivory. Effects of diversity treatments were most pronounced in the last year (supplementary Figs S1–3) and would have remained undetected in earlier years. This also suggests a time lag in the community response to diversity treatments. At the beginning of our measurements, tree canopies were not closed and only started to do so in the last year, indicating that competition may increase in the future. Thus, although we could not confirm an overall effect of intraspecific genetic diversity, it will be interesting to follow the development in the future. If genetic diversity is expressed in traits that require physical contact among individuals to produce a community response, effects of genetic variation are expected to become stronger in the future.

CONCLUSIONS

Subtropical forests harbour substantial amounts of diversity, but studies regarding biodiversity–ecosystem functioning processes in this ecosystem remain scarce. We showed that species diversity affects tree growth at early developmental stages and that there is considerable within species genetic variation among SFs. Furthermore, genetic diversity might indirectly affect growth through interactions at higher trophic levels. This underlines the importance of tree species and genetic diversity as drivers of ecosystem functioning. In the context of ongoing habitat fragmentation and species loss, our study also suggests that changes in both species and genetic diversity can affect ecosystem functioning and services, even in opposing ways, findings with far-reaching consequences for forest management and conservation.

SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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