

# Species-specific effects of genetic diversity and species diversity of experimental communities on early tree performance

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## Abstract

### Aims

Changing biodiversity can affect ecosystem functioning. However, the role of genetic diversity within species, relative to the one of species diversity, has hardly been addressed.

### Methods

To address the effects of both genetic diversity and species diversity during the important stage of early tree life, we used eight seed families (SF) taken from each of 12 evergreen and deciduous tree species of subtropical forest to perform a factorial experiment. We established 264 communities of 16 trees each. Each community had a species diversity of either one or four species and a genetic diversity of either one, two or four SF per species. We measured plant survival, growth rate, final biomass and herbivory 20 months after sowing.

### Important Findings

Species differed from each other in biomass, growth rate, herbivory and survival ( $P < 0.001$ ). Deciduous species tended to have

much higher biomass ( $P < 0.1$ ) and experienced higher herbivory ( $P < 0.05$ ) than evergreen species. Species diversity affected the performance of different species differently (species diversity by species interaction,  $P < 0.001$  for all variables but survival). Biomass differed between SF and increasing genetic diversity from one to two, and from two to four, SF per species increased biomass for some species and decreased it for others ( $P < 0.001$ ). Our study showed pronounced species-specific responses of early tree performance to species diversity and less pronounced responses to genetic diversity. These species-specific responses suggest feedbacks of species diversity and genetic diversity on future species composition.

**Keywords:** biodiversity-ecosystem functioning, tree, biomass, herbivory, survival, subtropical China, allometry

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## INTRODUCTION

The central biodiversity-ecosystem functioning (BEF) hypothesis postulates that, everything else being equal, an increase in diversity can improve plant performance and ecosystem functioning (Tilman 1999). This effect may arise through niche differentiation, i.e. complementary use of limiting resources, through facilitation, i.e. beneficial effects of one species on an intermediary resource fostering other species, or through a sampling effect, i.e. the greater chance of a larger community to include one or several better performing species (Fridley 2001; Tilman 1999). The BEF hypothesis

has been experimentally tested in grasslands, marine ecosystems and microcosms (Duffy 2006; Hector *et al.* 1999; Latta *et al.* 2011; Tilman *et al.* 1996). Only recently, BEF research has proceeded to establish experiments with trees (Nadrowski *et al.* 2010; Scherer-Lorenzen *et al.* 2005). Especially in the subtropics, which are rich in deciduous and evergreen tree and shrub species, BEF experiments are scarce.

Usually biodiversity effects on ecosystem functioning are addressed as effects of species diversity (Hector *et al.* 1999; Loreau *et al.* 2001; Tilman 1999), because species differ from each other in functional characteristics and in their responses to biotic interactions. In contrast, genetic diversity has largely

been neglected in BEF research and only few more recent studies have demonstrated potential links between genetic diversity in plant communities and ecosystem functioning (Booth and Grime 2003; Fridley and Grime 2010; Hughes et al. 2008; Li et al. 2017a; Roger et al. 2012; Schöb et al. 2015; Silvertown et al. 2009; Vellend 2006).

A direct comparison of the consequences of plant genotypic and species diversity showed that increasing either genotypic diversity, within one herb species of old fields in North America, or species diversity within old-field communities resulted in equivalent increases in aboveground primary production (Cook-Patton et al. 2011).

In an experimental subtropical forest system, a positive relationship between herbivory of tree saplings and species diversity was found (Schuldt et al. 2010). However, while genetic diversity of plants may affect herbivores (Crutsinger et al. 2006; Evans et al. 2012), the relative effect of genetic diversity and species diversity on tree herbivory has not been addressed (except for Hahn et al. 2017b).

To distinguish potential effects of species diversity and genetic diversity on ecosystem functioning, a factorial experiment is needed. Furthermore, such an experiment needs to be performed with many species and genotypes of maternal seed families (SF) to assess whether general conclusions can be drawn on how species diversity and genetic diversity affect plant performance. Recently, several studies addressed simultaneous effects of species diversity and genetic diversity on the functioning of herbaceous vegetation (Booth and Grime 2003; Crawford and Rudgers 2012; Fridley and Grime 2010; Nestmann et al. 2011; Prieto et al. 2015; Schöb et al. 2015). However, experimental evidence from woody species is still lacking almost completely (but see Hahn et al. 2017b).

Here, we investigate the effects of genetic diversity and of species diversity on the early performance of experimental communities of subtropical tree species. We focused on the early performance of young tree stands as an important phase of

stand development. Moreover, because this would be likely to affect later stand composition, we were especially interested in whether species differed in their responses to different community diversities. Because subtropical forests harbor both deciduous and evergreen species, which differ considerably in their morphological and physiological traits (Kröber and Bruelheide 2014, Li et al. 2017b), their susceptibility to herbivory and their responses to environmental variation (Powers and Tiffin 2010), we used five deciduous and seven evergreen species of subtropical broad-leaved forest in China for our experiment. Communities of 16 individuals were established with either one or four tree species and with one, two or four SF per species in a factorial design. We assessed survival, growth and herbivory for 20 months, tested effects of species diversity and genetic diversity on early tree performance and herbivory and tested whether these effects differed between deciduous and evergreen species and between species within these functional groups.

## MATERIALS AND METHODS

### Species and seed sampling

We chose 12 tree species, five deciduous and seven evergreen, of Chinese subtropical broad-leaved forest (Table 1). We collected seeds near Gutianshan National Nature Reserve, in Zhejiang Province (29°10'19"N, 118°03'50"E). These locations are representative of species-rich Chinese mixed broad-leaved forests, where evergreen species dominate in abundance, but not in numbers (Bruelheide et al. 2011; Yu et al. 2001). For each species, seeds were collected as separate SF from 8 maternal trees in autumn 2008, except *Liquidambar formosana* which just had 7 maternal trees available. To preserve the vitality of the seeds, we mixed the seeds with plant ash, and kept them moist but well aerated.

### Experimental design

In March 2009, we established an experiment on a former agricultural field near Xingangshan in Jiangxi Province

**Table 1:** the 12 tree species, attributed to three pools, used for our diversity experiment

Pool	Code	Species	Family	D/E	<i>a</i>	<i>b</i>	<i>R</i> <sup>2</sup>
1	Ca	<i>Choerospondias axillaris</i>	Anacardiaceae	D	0.875	-2.154	0.97
1	Lf	<i>Liquidambar formosana</i>	Hamamelidaceae	D	0.819	-1.788	0.82
1	Cs	<i>Castanopsis sclerophylla</i>	Fagaceae	E	0.647	-1.066	0.96
1	Lg	<i>Lithocarpus glaber</i>	Fagaceae	E	0.617	-0.956	0.89
2	Af	<i>Alniphyllum fortunei</i>	Styracaceae	D	0.948	-2.348	0.97
2	Rc	<i>Rhus chinensis</i>	Anacardiaceae	D	0.727	-1.108	0.80
2	Ce	<i>Castanopsis eyrei</i>	Fagaceae	E	0.528	-0.932	0.91
2	Ss	<i>Schima superba</i>	Theaceae	E	0.693	-1.178	0.97
3	Dm	<i>Distylium myricoides</i>	Hamamelidaceae	E	0.683	-1.255	0.90
3	Ip	<i>Idesia polycarpa</i>	Salicaceae	D	0.496	-0.930	0.66
3	Cg	<i>Cyclobalanopsis glauca</i>	Fagaceae	E	0.574	-0.900	0.71
3	Do	<i>Daphniphyllum oldhamii</i>	Daphniphyllaceae	E	0.677	-1.286	0.96

D/E denotes deciduous and evergreen species, respectively. The last three columns give parameters and *R*<sup>2</sup> for species-specific allometries of 2-year-old saplings:  $\log(\text{biomass[g]}) = a \times \log(D^2 \times H) + b$ , where *D* is the basal diameter and *H* is stem height.

(29°6′18″N, 117°55′15″E). The climate there is subtropical with mean annual precipitation of ~2000 mm and a mean temperature of 15.1°C (Geißler *et al.* 2012).

We established 264 experimental plots of 1 × 1 m<sup>2</sup> size arranged in four adjacent blocks of 66 plots each. Each plot had four times four, i.e. 16, sowing positions at 25 cm distance. Drainage ditches were installed between plot rows and all plots were shaded in the first year with black shading net, which attenuated light by ~50%. As saplings grew 1–3 m tall during the course of the experiment, with intermingling crowns, this set-up enabled us to study communities of interacting trees. The 12 species were randomly assigned to three species pools of four species each, with the restriction that pools contained both evergreen and deciduous species (two each in two pools, one deciduous and three evergreen species in the third pool, Table 1).

For each species pool, the full factorial design for the experiment included two species diversity levels (one and four) and three genetic diversity levels (one, two and four SF). The 88 plots per species pool comprised 32 one-species—one-seed-family plots, 16 one-species—two-seed-family plots, 16 one-species—four-seed-family plots, eight four-species—one-seed-family plots, eight four-species—two-seed-family plots and eight four-species—four-seed-family plots. In the two- and four-seed-family plots, SF were randomly assigned to plots with the restriction that all SF were equally represented. In total, across the three species pools there were 264 plots and 4224 sowing positions. The 264 combinations of treatments, species and seed family compositions were randomly assigned to the 264 plots. For each plot the foreseen 16 seed portions were randomly assigned to the 16 sowing positions.

At each sowing position, about one litre of sandy-loamy soil was added and 3 to 10 seeds were sown in March 2009. Additional seeds of all SF were sown close to the experimental blocks as back-up for replanting. Since more than one seedling germinated in most cases, we kept one seedling per sowing position and removed all others in March 2010. For the few positions without seedling, we planted one seedling of the corresponding seed family from the back-up stock in March 2010.

### Performance measurements

At the individual level, we measured stem height and basal diameter of the saplings every two months (August 2009; October 2009; December 2009; March 2010; May 2010; July 2010; September 2010; November 2010). Aboveground woody biomass was determined using species-specific allometries that had been determined from the back-up plants sown at the same time as the experimental plants and adjacent to the experiment using the formula  $\log(\text{biomass}[\text{g}]) = a \times \log(D^2 \times H) + b$ , where  $D$  and  $H$  are basal diameter [mm] and height [cm], respectively. The parameters and relevant coefficients of the formula are given in Table 1. We calculated the growth rate (relative growth rate, RGR [ $\text{g g}^{-1} \text{month}^{-1}$ ]) as the slope of the natural-log-transformed biomass regressed

on time. In fall 2010, we checked the survival for all individuals and counted the numbers of branches per plant. At the same time, we assessed herbivory as the percentage of leaf area consumed per plant by randomly choosing 20 leaves of each individual and visually assigning them to one of eight classes (0, 0–1%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–100%). For each plant, we averaged the 20 estimates of leaf loss. To test the method, we compared our estimates with precise measures of leaf loss determined from scans of 160 randomly collected leaves, which showed a good match between observed values (0, 0.48%, 3.45%, 8.46%, 15.76%, 28.4%, 52.29%, 80.71%) and estimated class. At the plot level, we removed all weeds (i.e. species other than the sown ones) five times between September 2009 to September 2010.

### Data analysis

To analyse both diversity and species identity effects, for each response variable we calculated the mean values of each of the six combinations of genetic diversity and species diversity for each of the 12 species. Then we used analysis of variance to analyse effects of genetic diversity, species diversity, evergreen and deciduous species, and their interactions, similar to the principles described by Schmid *et al.* (2017). Species diversity, genetic diversity and the difference between deciduous and evergreen species were treated as fixed effects, and species as random effects. In a second analysis, we also included SF within species as a random factor and its two-way interactions with the other factors. We performed all the analyses with R v. 2.13.1 (R Development Core Team 2011).

## RESULTS

Species differed significantly from each other in all five performance measures ( $P < 0.001$ , Table 2). Deciduous species tended to have much higher biomass ( $P < 0.06$ ) and also higher herbivory ( $P < 0.05$ ) than evergreen species.

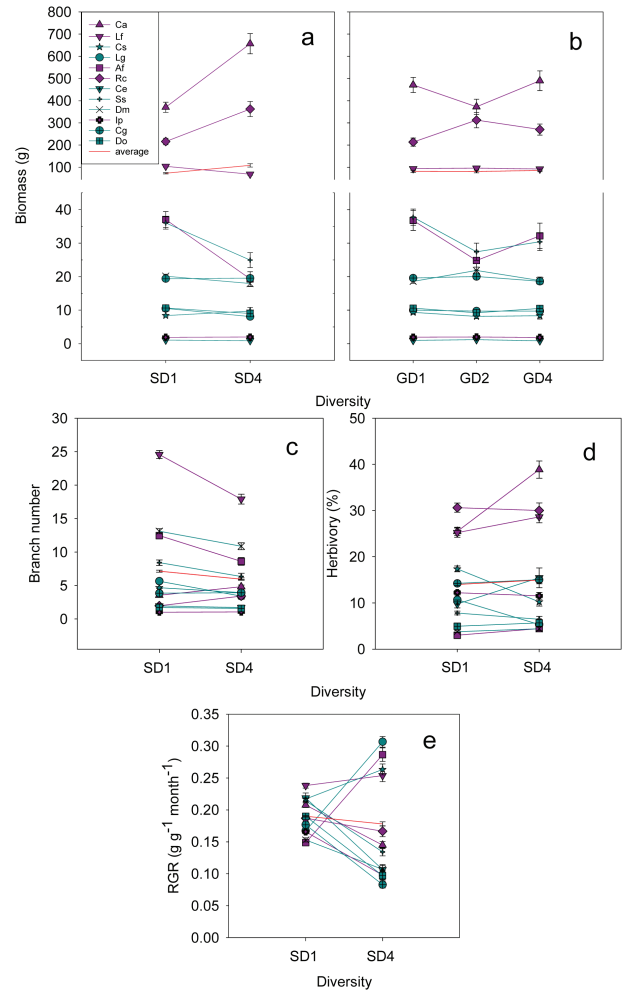
Species diversity affected different species differently ( $P < 0.001$  for all measures except for survival; Table 2). The two largest species, which were deciduous, responded with higher biomass to increasing species diversity (Fig. 1a). However, one other of the five deciduous species in the experiment and one evergreen had lower biomass at higher species diversity, and the overall species diversity effect was not significant (Table 2).

The five species with the highest number of branches had fewer branches at higher species diversity, while two other species had more branches at higher species diversity (Fig. 1c). While two deciduous species tended to increase their branch number in mixture, overall both deciduous and evergreen species decreased it (deciduous–evergreen by species diversity interaction not significant,  $P > 0.76$ , Table 2, Fig. 1c). Two deciduous and one evergreen species showed increased herbivory rates at higher species diversity and two evergreen species showed lower herbivory rates (Fig. 1d).

**Table 2:** ANOVA model to test the effects of species diversity (SD) and genetic diversity (GD) on 12 deciduous (D) and evergreen (E) tree species (SP)

Source	Biomass (g)			RGR (g g <sup>-1</sup> month <sup>-1</sup> )			Branch number			Herbivory (%)			Survival rate			
	df	MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
SD	1	16 691	1.392	0.265	6.79E-03	0.571	0.467	26.84	3.161	0.106	13.91	0.354	0.565	6.90E-05	0.007	0.935
D/E	1	504 449	4.560	0.058	4.85E-03	0.376	0.553	139.1	0.661	0.435	2394.66	5.404	<b>0.042</b>	0.07	0.226	0.645
SP	10	110 624	6.95.748	<b>&lt;0.001</b>	1.29E-02	74.566	<b>&lt;0.001</b>	210.36	478.091	<b>&lt;0.001</b>	443.12	58.691	<b>&lt;0.001</b>	0.31	31.000	<b>&lt;0.001</b>
SD:D/E	1	26 674	2.225	0.167	4.89E-03	0.411	0.536	0.79	0.093	0.767	75.81	1.929	0.195	4.40E-05	0.004	0.948
SD:SP	10	11 988	75.396	<b>&lt;0.001</b>	1.19E-02	68.786	<b>&lt;0.001</b>	8.49	19.295	<b>&lt;0.001</b>	39.29	5.204	<b>0.001</b>	0.01	1.000	0.473
GD	2	419	0.273	0.764	4.88E-04	2.638	0.096	0.29	0.426	0.659	3.1	0.595	0.561	4.62E-03	1.121	0.345
SD:GD	2	130	0.818	0.454	3.97E-04	2.295	0.124	0.21	0.477	0.627	0.12	0.016	0.984	0.01	1.000	0.384
D/E:GD	2	497	0.323	0.727	7.71E-05	0.417	0.665	0.25	0.368	0.697	2.67	0.512	0.607	0.01	2.427	0.114
SP:GD	20	1537	9.667	<b>&lt;0.001</b>	1.85E-04	1.069	0.437	0.68	1.545	0.161	5.21	0.690	0.796	4.12E-03	0.412	0.975
Residuals	22	159			1.73E-04			0.44			7.55			0.01		

Significant effects in boldface. Abbreviations: ANOVA = analysis of variance, df = degree of freedom, MS = mean squares.



**Figure 1:** Tree responses to the experimental diversity levels. SD1 and SD4 denote species diversity levels of one and four species, respectively. GD1, GD2 and GD4 denote genetic diversity levels of one, two and four seed families, respectively. Biomass (a, b), branch number (c), percentage of consumed leaf mass (herbivory (%)) (d) were measured 20 months after the start of the experiment. Relative growth rate RGR (e) refers to a period of 17 months before harvest (see Methods). Dark red indicates deciduous species, green evergreen species and light red indicates mean performance. Species codes are as in Table 1. Biomass and relative growth rate are given for dry biomass. Symbols indicate means ± SE. Abbreviation: SE = standard error. See color figure in Online.

Relative growth rate was higher at higher species diversity for two evergreen and two deciduous species. In contrast, it was lower at higher species diversity for the other eight species (Fig. 1e).

Relative growth rate was marginally significantly affected by genetic diversity ( $P < 0.1$ ). Higher genetic diversity led to increased biomass for some species and decreased it for others ( $P < 0.001$ ; Fig. 1b). In particular, genetic diversity affected four of the five largest species, three of which had lower biomass in communities of two seed family per species than in communities of single SF per species. However, in communities with four SF per species these biomass changes were largely reversed.

While different SF differed in their biomass ( $F = 1.69$ , degree of freedom = 83, 485,  $P < 0.001$ ), responses of plants to species diversity and to genetic diversity did not differ between SF.

## DISCUSSION

### Effects of species diversity on plant performance

The functional groups of evergreens and deciduous species showed strong performance differences in early tree life. Deciduous species usually are pioneer species preferring full sunlight, and thus profit from the early growth conditions (Eamus 1999). Deciduous and evergreen species are expected to show different responses to environmental variation (Powers and Tiffin 2010). In our experiment, deciduous species generally grew faster and had higher biomass and branch number after 20 months. Moreover, two deciduous species increased their branch number in mixture, although overall both deciduous and evergreen species decreased it. It would be interesting to perform a diversity experiment with small trees in the understory of a subtropical forest to test, whether this would reverse the responses of evergreen and deciduous species, e.g. due to higher crown efficiency of the evergreen species (Kröber and Bruelheide 2014).

The different responses of different species-to-species diversity imply that species diversity can feed back on future community composition (Schmidtke *et al.* 2010). Such feedback includes that species able to benefit from the early successional stage become dominant, which improves the growth conditions for late-successional species, as reported for natural subtropical forests (Bruelheide *et al.* 2011).

Herbivory can be strongly affected by species identity, species traits and species diversity (Barone 1998; Bischoff and Trémulot 2011; Haddad *et al.* 2001). In our study, deciduous species suffered higher herbivory than evergreens (Table 2), as expected from their more palatable leaves (Stock *et al.* 1993). Moreover, there was pronounced variation among deciduous and among evergreen species in herbivory, possibly due to different herbivore specialization (Root 1973) or different plant defence (Kempel *et al.* 2013). According to resource-concentration theory, a reduction in damage by specialized herbivores might be expected as host plant concentration decreases with increasing plant diversity (Barone 1998, 2000; Dyer *et al.* 2007). However, Schuldt *et al.* (2010) did not find such a pattern when analyzing herbivory levels of ten evergreen species. Instead, they detected a positive herbivory-plant diversity relationship in the forest ecosystem where the species in our experiment originate from. Their study suggested a higher impact of generalist herbivores than usually assumed, and the herbivore species were supposed to profit from a broad dietary mix provided by high plant diversity (Schuldt *et al.* 2010). We found species-specific herbivory responses to species diversity. While two deciduous and one evergreen species experienced increased herbivory at higher species diversity, two evergreen species had lower herbivory (Fig. 1d).

This might reflect that resource concentration, generalist herbivore impact and possibly species-specific defence all play a role in shaping the herbivory response to changed species diversity. Interestingly, herbivory of two of the deciduous trees suffering most herbivory already in monoculture, increased in mixture, suggesting that herbivores might have moved from evergreen to deciduous species. This suggests that species richness effects on herbivory in natural subtropical forest, such as the ones found by Schuldt *et al.* (2010), depend on the proportion of deciduous species in the ecosystem.

### Effects of genetic diversity on plant performance

Genetic diversity is a component of biodiversity that has often been neglected in BEF research, but which may affect productivity, growth and stability of populations, inter-specific interactions within communities and ecosystem-level processes (Hughes *et al.* 2008). For the tree species used in this experiment, Zeng *et al.* (2017) showed significant heritability both of growth and of plasticity in growth, suggesting that the identity of genotypes and the amount of genetic variation within a community will affect growth both; in the short term, e.g. by plastic responses to current community context, and in the long term, by evolutionary responses to changing environmental conditions. Bell (1991) and Smithson and Lenne (1996) suggested that increasing genetic diversity contributed to increasing primary productivity in their studies. In our study, mean biomass did not change with genetic diversity. This came about by positive effects of changes in genetic diversity in some cases and negative ones in others (Fig. 1b). Importantly, this implies that genetic diversity can have a feedback on future species composition.

Individual genotypes vary in their resistance and susceptibility to herbivory (Fritz and Price 1988; Maddox and Root 1987). Moreover, it was suggested that increasing genotypic diversity increases aboveground herbivore diversity (Crutsinger *et al.* 2006). In our study, however, genetic diversity did not affect community herbivory, similar to the results of Johnson *et al.* (2006).

Overall, the effects of genetic diversity were smaller and less frequent than those of species diversity (Table 2, Fig. 1). Whether stronger effects of genetic diversity on community performance occur in later life stages, when competition is more pronounced, as suggested by Hughes *et al.* (2008) and Vellend and Geber (2005), remains an open question. In this context, it is interesting to note that the biomass of four of the five largest species responded to genetic diversity, while the one of the other eight species did not, which may indicate longer term effects if genetic diversity. This idea might be further supported by the finding that in natural stands of subtropical trees molecular marker diversity tended to decline in later successional stages (Hahn *et al.* 2017a), as expected due to reduced population sizes of several species due to competitive exclusion.

We did not detect interacting effects of genetic diversity and species diversity (Table 2). Thus, both levels of diversity affected performance additively. It will be interesting to see in

experiments with adult trees, whether genetic diversity will later rather affect the performance of communities of low or of high species diversity.

## CONCLUSION

In conclusion, our study of early tree performance showed pronounced species-specific responses to species diversity, and less pronounced species-specific responses to genetic diversity. This exemplifies how species identity may contribute to the explanation of experimental outcomes finding (Peng *et al.* 2017) or not finding (Hahn *et al.* 2017b) species diversity effects on ecosystem functions. The observed species-specific responses during early tree life suggest feedbacks of species diversity and genetic diversity on future species composition, where species performing especially well due to diversity effects in early life may dominate later species composition in such stands due to competitive suppression or even exclusion of other species.

As the use of multiple species allowed us to show that diversity effects differ between target species, our results highlight the benefits of using many species in experiments (van Kleunen *et al.* 2014). Moreover, they are encouraging for future BEF experiments with larger trees.

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