

# Genetic richness affects trait variation but not community productivity in a tree diversity experiment

Franca J. Bongers<sup>1</sup> , Bernhard Schmid<sup>2</sup> , Walter Durka<sup>3,4</sup> , Shan Li<sup>1</sup>, Helge Bruelheide<sup>4,5</sup> , Christoph Z. Hahn<sup>3,6</sup> , Haoru Yan<sup>1,7</sup>, Keping Ma<sup>1</sup>  and Xiaojuan Liu<sup>1</sup> 

<sup>1</sup>State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, 100093 Beijing, China; <sup>2</sup>Department of Geography, University of Zurich, 8057 Zurich, Switzerland; <sup>3</sup>Department of Community Ecology, UFZ – Helmholtz Centre for Environmental Research, Theodor-Lieser-Str. 4, 06120 Halle, Germany; <sup>4</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany; <sup>5</sup>Institute of Biology, Martin Luther University Halle-Wittenberg, D-06108, Halle, Germany; <sup>6</sup>Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7ZB, UK; <sup>7</sup>College of Life Sciences, University of Chinese Academy of Sciences, 100049 Beijing, China

## Summary

Authors for correspondence:

Keping Ma

Tel: +86 10 62836223

Email: kpma@ibcas.ac.cn

Xiaojuan Liu

Tel: +86 10 62836051

Email: liuxiaojuan06@ibcas.ac.cn

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- Biodiversity–ecosystem functioning experiments found that productivity generally increases with species richness, but less is known about effects of within-species genetic richness and potential interactions between the two. While functional differences between species can explain species richness effects, empirical evidence regarding functional differences between genotypes within species and potential consequences for productivity is largely lacking.
- We therefore measured within- and among-species variation in functional traits and growth and determined stand-level tree biomass in a large forest experiment factorially manipulating species and genetic richness in subtropical China.
- Within-species variation across genetic seed families, in addition to variation across species, explained a substantial amount of trait variation. Furthermore, trait responses to species and genetic richness varied significantly within and between species. Multivariate trait variation was larger among individuals from species mixtures than those from species monocultures, but similar among individuals from genetically diverse vs genetically uniform monocultures. Correspondingly, species but not genetic richness had a positive effect on stand-level tree biomass.
- We argue that identifying functional diversity within and among species in forest communities is necessary to separate effects of species and genetic diversity on tree growth and community productivity.

## Introduction

Biodiversity–ecosystem functioning (BEF) research has repeatedly demonstrated that increases in plant species richness can lead to increases in plant productivity (Tilman *et al.*, 1996; Hector *et al.*, 1999; Liang *et al.*, 2016; Huang *et al.*, 2018) and other ecosystem functions (Balvanera *et al.*, 2006; Isbell *et al.*, 2011). Plant species can be different in their use of resources, their resistance to natural enemies or their responses to abiotic conditions. Differences in these ecological functions can lead to differences in productivity and fitness over a range of environmental conditions. Based on niche theory, increasing species richness is hypothesized to increase plant productivity as a result of the increased diversity of ecological functions within communities (McGill *et al.*, 2006; Turnbull *et al.*, 2016).

Identifying the ecologically relevant functions of species is challenging, but the use of physiological and morphological traits to measure, describe and predict functions of individuals, species

and ecosystems has become common practice in ecology (Wright *et al.*, 2004; Bruelheide *et al.*, 2018; Kattge *et al.*, 2020). In addition, it is commonly assumed that differences in ecological functions would be related to and identified by differences in trait values among species (McGill *et al.*, 2006). However, general relationships between traits and their functions are still elusive as a result of, among other things, the dependency on abiotic and biotic environmental conditions and the use of species mean values instead of individual values (Shipley *et al.*, 2016; Yang *et al.*, 2018). The assumption that higher functional trait diversity at the community level has a positive effect on community productivity has been tested and sometimes confirmed by relationships between community-level trait diversity and community productivity (Kröber *et al.*, 2015; Tobner *et al.*, 2016; Wagg *et al.*, 2017; Roscher *et al.*, 2018b).

Assuming that community trait diversity only depends on species mean trait values ignores trait variation within and trait overlap between species and therefore overestimates species

differences in niche and ecological functionality (Violle *et al.*, 2012). The degree of intraspecific trait variation is determined by genetic differences and plastic responses to local environmental conditions. Although intraspecific trait variation is often smaller than interspecific trait variation (Albert *et al.*, 2010; Hulshof & Swenson, 2010; Poorter *et al.*, 2018), intraspecific trait variation can still affect community functioning (Hughes *et al.*, 2008; Bolnick *et al.*, 2011; Siefert *et al.*, 2015; Des Roches *et al.*, 2018). In addition species that coexist in mixtures are also expected to further minimize overlap to avoid strong interspecific competition (Kraft *et al.*, 2008; Zupping-Dingley *et al.*, 2014; Turnbull *et al.*, 2016). This so-called niche differentiation by species in diverse communities could result from plastic or genetic shifts in species functional trait values (Zupping-Dingley *et al.*, 2014; Lipowsky *et al.*, 2015; Roscher *et al.*, 2015) by which total variation among individuals from mixtures increases compared with individuals from monocultures.

While most designed BEF experiments focus on effects of species diversity (reviewed in Tilman *et al.*, 2014; Verheyen *et al.*, 2016; Weisser *et al.*, 2017), it is conceivable that within-species genetic or even epigenetic diversity also affects plant productivity and other ecosystem functions (Schmid, 1994; Crutsinger *et al.*, 2006; Kotowska *et al.*, 2010; Latzel *et al.*, 2013; Prieto *et al.*, 2015; Hahn *et al.*, 2017; Zeng *et al.*, 2017). While positive effects of within-species diversity on plant productivity have been observed (Booth & Grime, 2003; Hughes & Stachowicz, 2004; Crutsinger *et al.*, 2006; Kotowska *et al.*, 2010; Cook-Patton *et al.*, 2011; Drummond & Vellend, 2012), to date explicit empirical tests of whether this is a result of functional differences between genotypes have, to our knowledge, only been done for the model species *Arabidopsis thaliana* (Wuest & Niklaus, 2018) and rice (Montazeaud *et al.*, 2018). Especially in tree communities, the degree of trait variation created by within-species genetic diversity has not yet been determined. In addition, there is a principal lack of information about the effects of genetic diversity on tree productivity (Fischer *et al.*, 2017; Hahn *et al.*, 2017; Zeng *et al.*, 2017). Most studies of tree communities looked at effects of genetic diversity on the interaction between plants and arthropod communities (e.g. diversity and abundance of insects) (Barton *et al.*, 2015; Campos-Navarrete *et al.*, 2015; Cao *et al.*, 2018; Barantal *et al.*, 2019). Overall, identifying functional trait variation among groups of tree individuals of known genetic relationship (here seed families; individuals from the same seed family share the same mother) within and between species in forest communities would be the first step towards identifying ecologically relevant biological processes that underlie effects of species and genetic diversity on tree growth and community productivity.

In this study, we evaluated functional trait variation among species and among different seed families within species across two degrees of species richness (one vs four species) factorially crossed with two degrees of genetic richness (one vs four seed families per species) in experimental tree communities 8 yr after establishment. First, we studied how much of the observed trait variation was explained by species and seed-family identity, species and genetic richness and the interactions between them. Second, we determined to what extent species and seed families

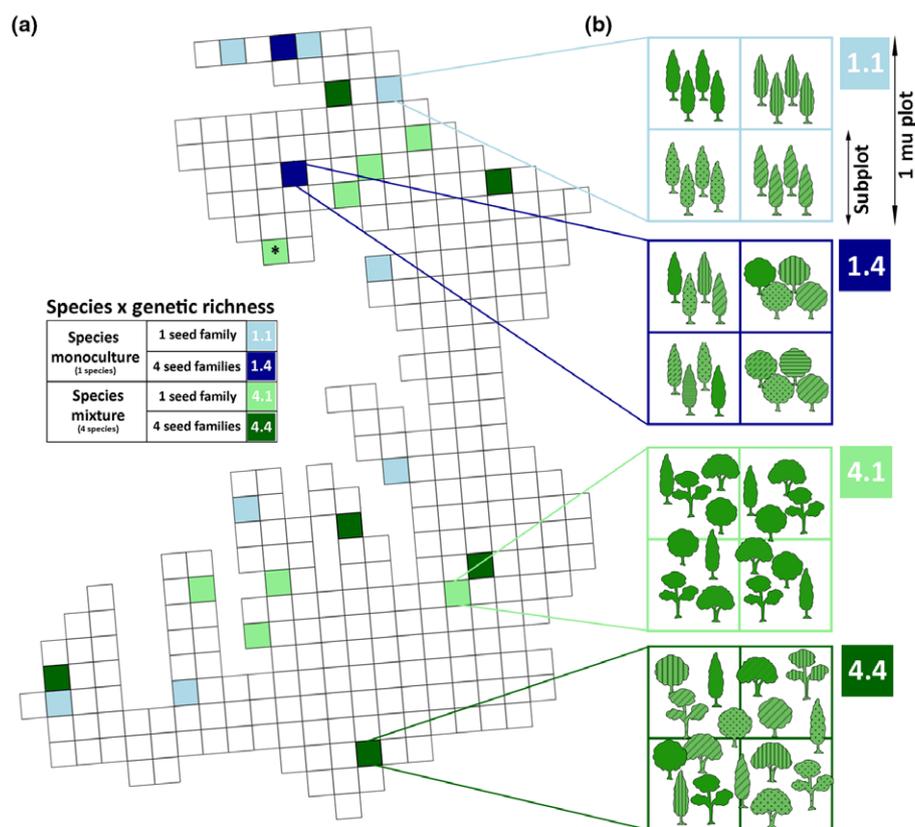
were distinct in their trait values. Third, we determined if species or genetic richness affected the multivariate trait variation among the measured individuals. Finally, we determined if species and genetic richness affected individual tree growth and stand-level biomass. We hypothesized that in addition to species identity, within-species seed-family identity would explain a part of the overall trait variation. We expected that increasing species and genetic richness would both have a positive effect on tree growth and stand biomass, although a smaller effect was expected for genetic than for species richness, owing to smaller ecological differences expected between genotypes within species.

## Materials and Methods

### Experimental site

A species  $\times$  genetic tree diversity experiment was set up as part of the so-called BEF-China experiment (Bruehlheide *et al.*, 2014) located near Xingangshan, Dexing City, Jiangxi Province, China. The region is typical of the Chinese subtropics with a mean annual temperature of 16.7°C and a mean annual precipitation of 1821 mm. In 2010, 24 plots of the BEF-China experiment were used for the genetic diversity experiment (Fig. 1; Hahn *et al.*, 2017). In short, each square plot with an area of 0.067 ha (1 mu) was planted with 400 individuals belonging to one or all of the four tree species *Alniphyllum fortunei*, *Cinnamomum camphora*, *Daphniphyllum oldhamii* and *Idesia polycarpa*. These species were chosen based on the fact that two are deciduous (*A. fortunei* and *I. polycarpa*) and two are evergreen (*C. camphora* and *D. oldhamii*). In addition, the taxonomic differences among species, the quantity of seedlings from different seed families (see later for more information about seed families) and the species' expected survival contributed to the selection of these four species. The species richness was one or four per plot. Within each plot the planted individuals belonged to one or four different seed families per species, resulting in a full factorial design of species  $\times$  genetic richness (Fig. 1). Here, 'genetic richness' refers to within-species number of seed families and was created by collecting seeds and producing seedlings from different mother trees. Seed families therefore represented something between full- and half-sib families, depending on how many father trees pollinated the seeds of a single mother tree. Assuming that there are genetic differences between mother trees and thus seed families, we therefore use the term 'genetic richness' as shorthand for 'seed-family richness'. The seed families were collected in the Gutianshan National Nature Reserve, Zhejiang Province, China, which is close to the BEF-China experiment (40 km away).

Because of the availability of only 24 plots (1 mu each) for this experiment, subplots of 0.25 mu were used as our main experimental unit. All treatments with a single species, that is species monocultures, were established per subplot, and every seed family occurred once as seed-family monoculture in a subplot and one or two times in species monoculture with four seed families per subplot (Supporting Information Table S1; Fig. 1). Species mixtures were planted on whole 1 mu plots, providing four subplots of identical species  $\times$  seed family composition (Table S1).



**Fig. 1** Overview of the designed genetic tree experiment within BEF-China. (a) In total there were 24 plots. Each square plot with an area of 1 mu (0.067 ha) was planted with 400 individuals belonging to one or all of the four tree species *Alniphyllum fortunei*, *Cinnamomum camphora*, *Daphniphyllum oldhamii* and *Idesia polycarpa*. The species richness per plot was one or four and genetic richness per species was also one or four, resulting in a full factorial design of species  $\times$  genetic richness (represented by 1.1, 1.4, 4.1 and 4.4 levels; see legend). (b) Each 1 mu plot was subdivided into four subplots, which were used to create different seed-family monocultures in the 1.1 richness and different seed-family compositions of four seed families in the 1.4 richness level. In total there were two 1 mu plots per species and a half 1 mu plot per species for the 1.1 and 1.4 richness levels respectively (see Supporting Information Table S1 for species-seed family compositions). Within four-species mixtures the four subplots per 1 mu plot had identical seed families per species compositions. In total there were eight and six 1 mu plots for the 4.1 and 4.4 richness levels, respectively (Table S1). Different species are represented by tree shapes, while different seed families are represented by tree coloring. The asterisk (\*) indicates the plot that was not established as a result of logistic constraints.

Using subplots for species monocultures allowed us to reduce the total number of plots and seedlings to be planted, and using 1 mu plots for species mixtures allowed us to have enough replicates of species and seed families within each plot. Seed-family compositions were not replicated in multiple plots in order to have a larger number of different seed-family compositions. Different compositions at each richness level were considered the relevant degree of replication. Individual trees came from nine seed families in *A. fortunei* and *C. camphora*, eight seed families in *I. polycarpa* and 15 seed families in *D. oldhamii* (Table S1).

### Functional traits

Eight functional traits were measured in 2017 and 2018 for 547 individuals across all seed families and species in the four different species  $\times$  genetic richness combinations (see Table S2 for number of individuals per seed family per species per richness level). For each individual we measured wood density (WD), leaf area (LA), specific leaf area (SLA), Chl content (CHL), leaf nitrogen content (LN), leaf carbon content (LC), stomatal density

(SD) and stomatal aperture (SA). These traits were chosen because of their association with growth strategies and functions within the community (Wright *et al.*, 2004; Diaz *et al.*, 2016; Bruehlheide *et al.*, 2018). In this study we did not measure ecological functions directly, but rather associated variation in trait values with variation in ecological functions.

Wood density ( $\text{g cm}^{-3}$ ) was estimated on one branch segment per tree by dividing the oven-dried weight (80°C, 48 h) through the water-displaced fresh volume. We used branch-WD to represent stem-WD because the two are generally highly correlated (Swenson & Enquist, 2008). Four to five leaves were sampled per tree, scanned for area (LA, in  $\text{cm}^2$ ) and dried for 48 h at 70°C for DW, after which SLA ( $\text{cm}^2 \text{g}^{-1}$ ) was calculated. Chl content per area was estimated based on three measurements per leaf with a SPAD meter (SPAD-502; Minolta Camera, Tokyo, Japan). LN and LC (%) were determined using the CHNOS Elemental Analyzer Vario EL III (Elementar Analysensysteme GmbH, Hanau, Germany). For each individual tree three stomatal imprints were made and analyzed under a microscope (Nikon 80i) to calculate SD ( $\text{count mm}^{-2}$ ) and for a total of five stomata the inner stomatal

length and width were measured to calculate SA ( $\mu\text{m}^2$ ) based on an elliptical shape. All leaves used for trait measurements were fresh and healthy without any dirt, physical damage or fungal infections.

### Multivariate hypervolumes

To estimate the total multivariate trait variation among individuals per richness level, multivariate trait hypervolumes were calculated using multidimensional kernel density estimation within the 'hypervolume\_gaussian' function of the `HYPERVOLUME` package in R (Blonder *et al.*, 2014, 2018), assuming default settings (among others, Silverman bandwidth estimation and 95% probability threshold). The size of a hypervolume depends on the number of observations and dimensions, which in our case are the individuals and traits, respectively. In addition, an accurate approximation of the hypervolume size is sensitive to correlations among dimensions and to the ratio between observations and dimensions (Blonder *et al.*, 2018 recommended to use no more different dimensions than the number of  $\log(\text{observations})$ ). Therefore we used only three trait dimensions and constructed various hypervolumes with an equal number of observations to properly compare hypervolumes across species and richness levels. To avoid biases based on the selection of traits, we used the first three uncorrelated axes of a principal component analysis created by the eight traits (together explaining 71% of variation; Fig. S1). The values of these three axes were assumed to provide a more holistic representation of ecological function than any set of three particular traits. Nevertheless, we also performed additional hypervolume simulations to explore the effect of species and genetic richness on multivariate trait variation using particular traits (Figs S2, S3).

To assess potential effects of variability for comparing sizes of hypervolumes across richness levels, we simulated 500 hypervolumes per richness level using bootstrapping (similar to that done by Bittebiere *et al.*, 2019). We randomly sampled individuals, with replacement per species and richness level depending on the particular comparison. First, to test if the hypervolume of all species together or species-specific hypervolumes were affected by species richness, we sampled 29 observations per species from species monocultures versus species mixtures (ignoring the genetic richness levels). The 29 observations per species were pooled together per species monoculture versus species mixtures and these 116 observations were used to calculate the hypervolume size of the four species together. For the species separately, each hypervolume was based on the 29 sampled observations. We used 29 observations because that was the lowest number of observations in species monocultures (see Table S2). Second, to test if the hypervolume was affected by genetic richness (i.e. number of seed families per species), nine observations per species from each species  $\times$  genetic richness level were sampled. To test the effect of genetic richness in species monocultures, hypervolumes for each species separately were calculated using these nine observations. To test the effect of genetic richness on top of species richness, the nine samples per species were pooled to calculate hypervolumes for all species together. Nine values were sampled because that was the lowest number of observations (for *I. polycarpa* monoculture with one seed family; see Table S2).

### Individual tree growth and stand-level tree biomass

Individual tree biomass (kg) was calculated for all trees within the experiment, excluding the outer two rows of trees per 1 mu plot to avoid border effects. Individual tree biomass was calculated as  $H \times \text{BA} \times \text{CV}$ , where  $H$  is the height (in m), BA is the basal area at the ground (in  $\text{m}^2$ ) and CV is a correction factor for stem shape and WD, estimated by Huang *et al.* (2018). We tested if this method would be considerably different from using individual measured WD in the estimation of tree biomass. For the 547 individuals for which we measured WD directly, we calculated biomass by multiplying the volume estimate with WD. Because the correlation between the two methods was high ( $R^2 = 0.97$ ), we decided to use the Huang *et al.* (2018) method throughout for consistency. Individual tree growth was calculated as the relative biomass growth rate between 2013 and 2018, that is, the difference between the log-transformed biomasses from the two dates. Stand-level tree biomass ( $\text{Mg ha}^{-1}$ ) was calculated per subplot (quarter of the 1 mu plot) as the sum of all alive trees.

### Statistical analysis

To determine how trait and growth variation among individual trees was affected by explanatory factors, ANOVAs were fitted with sequential order of the terms species identity, seed-family identity, species  $\times$  genetic richness combination (or its contrasts, i.e. the factorial species richness + genetic richness + interaction), interactions of these and, finally, the 1 mu plot. Similar ANOVAs with sequentially fitted factors were performed for each species separately to estimate the relative contribution of each explanatory factor on trait variation for each species. Species effects were tested against seed families and richness effects against 1 mu plot variation, while all other effects were tested against the residual variation. All ANOVAs were performed with the 'aov' function in R. Note that this procedure corresponds to mixed-model analysis of variance but allows greater flexibility in assessing contributions of random effects than other implementations of mixed-model analyses, such as those based on residual maximum likelihood methods (for a detailed explanation of this model choice, see Schmid *et al.*, 2017).

To determine which pairs of species or seed families within species had significantly different trait values, *post hoc* analyses after one-way ANOVAs were performed, taking all individuals together or per species independently ('TukeyHSD' function in R). All trait values, except for Chl values, were log-transformed before analysis to increase data normality. In addition, we checked the normality and homoscedasticity of the residuals of the performed ANOVAs.

The effect of species and genetic richness, their interaction and species identity on individual tree growth was calculated with an ANOVA with sequential order of species richness, genetic richness, the interaction of species  $\times$  genetic richness, species identity and the interaction of species identity with species  $\times$  genetic richness. Stand-level biomass was tested with an ANOVA with sequential order of the terms species richness, genetic richness, the interaction of species  $\times$  genetic richness, monoculture species

and the interaction between monoculture species and genetic richness. For both analyses, the 1 mu plot functioned as error term.

## Results

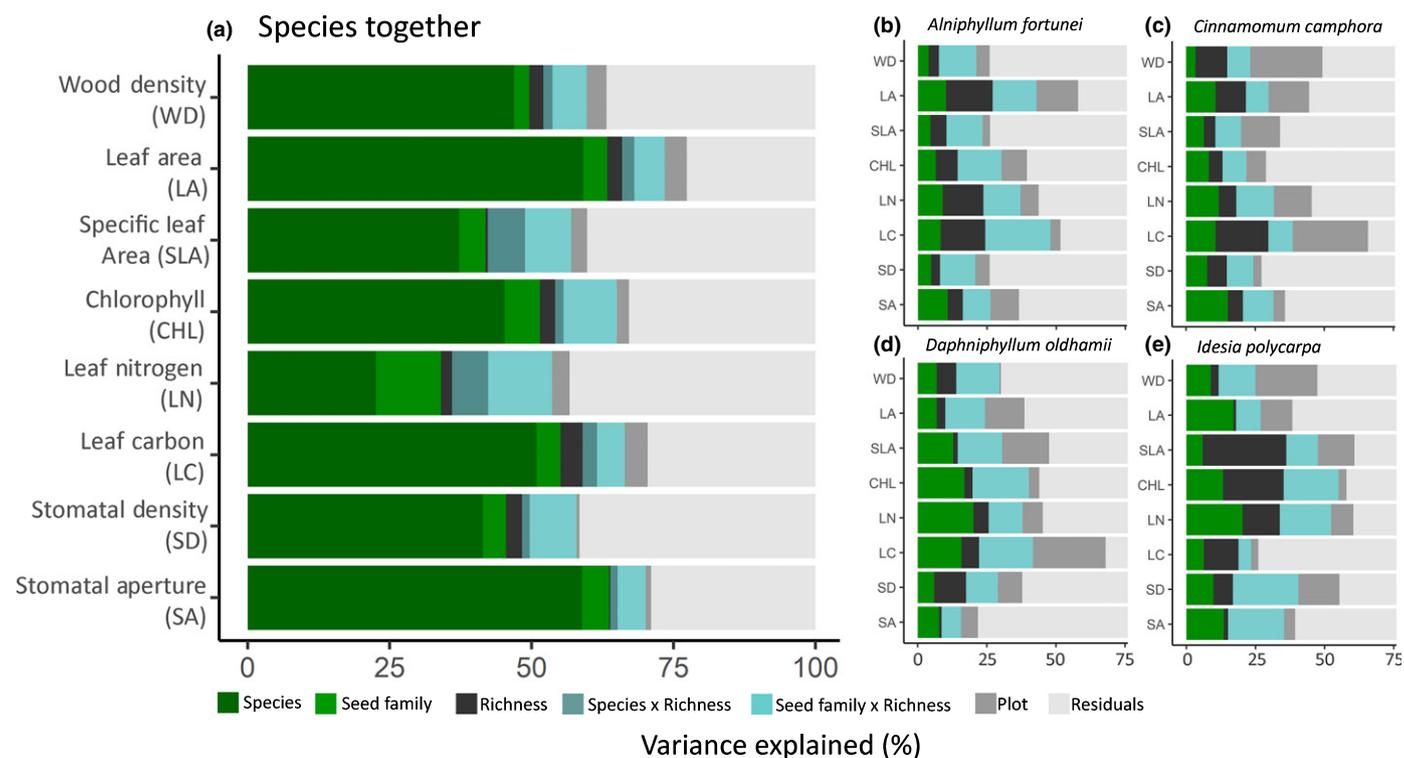
### Partitioning functional trait variation

Analyzing the total variation in the eight functional traits measured on 547 individuals we observed that a large part was a result of variation among the four tree species (22.61–59.09%; Fig. 2; Table S2) and a further substantial part (2.69–11.45%) was a result of variation among seed families within tree species, supporting our assumption that seed families differed genetically. The amount of trait variation explained by species and seed families varied from trait to trait. For example, compared with the other traits, LN varied relatively less among species but more among seed families within species (Fig. 2).

The effects of species and genetic richness combined explained only a small part of total observed trait variation (0.16–3.85%), with species richness generally explaining more variation than genetic richness (Table S2). These small main effects were related to different responses of species and seed families to the richness treatment. The corresponding interaction terms

species  $\times$  richness and seed family  $\times$  richness explained 1.33–6.58% and 4.87%–11.23% of variation, respectively (Fig. 2; Table S3). In the separate analysis for each of the four species, the relative contribution of seed families to the total within-species variation in the measured traits was quite large, but richness effects and interactions among the two, that is variation in the responses of individual seed families to richness, were of similar importance (Fig. 2b–e). On average, differences among seed families explained 7.2%, 9.3%, 11.7% and 11.9% of trait variation in *A. fortunei*, *C. camphora*, *D. oldhamii* and *I. polycarpa*, respectively. Among the structural traits (WD, LA and SLA), seed families explained most variation in LA for three species (the exception was *D. oldhamii* where seed families explained most variation in SLA). Among the chemical traits (CHL, LN and LC), seed families explained most variation in LN, namely 20% in *I. polycarpa* and *D. oldhamii*. In addition, for all four species, seed families explained more variation in SA than in SD.

The relative percentage of variation explained by richness was highly variable and ranged from 30% of the variation in SLA for *I. polycarpa* to 0.9% of variation in SA for *D. oldhamii* (Fig. 2b–e). In addition, the different responses of seed families to richness explained 4.6–23.7% of trait variation in the different species. This is illustrated in the reaction-norm plots shown in Fig. S4. Although no seed family showed a consistent up or down change



**Fig. 2** Contributions of the different explanatory terms to the total variation in eight measured traits. (a–e) Shown are the percentages of explained variation (increments of total sum-of-squares as terms are sequentially fitted to the ANOVA model from left to right) per trait for all species together (a) and for the four species analyzed separately (b–e). Note that for the latter the terms ‘species’ (dark green) and ‘species  $\times$  richness’ (dark turquoise) do not exist. See legend for color key of terms ‘species’ (species identity), ‘Seed family’ (seed family identity), ‘richness’ (species  $\times$  genetic richness combination, four levels), ‘species  $\times$  richness’ (species specific responses to richness), ‘seed families  $\times$  richness’ (seed-family specific responses to richness), ‘plot’ (identity of 1 mu plot) and ‘residuals’ (remaining variation). Exact values for percentage explained variance for all species together (a), and related statistics, are shown in Supporting Information Table S3.

in trait value with richness, their reaction norms illustrate that seed families differed in their trait-specific plastic responses to richness.

### Trait differences between species and seed families within species

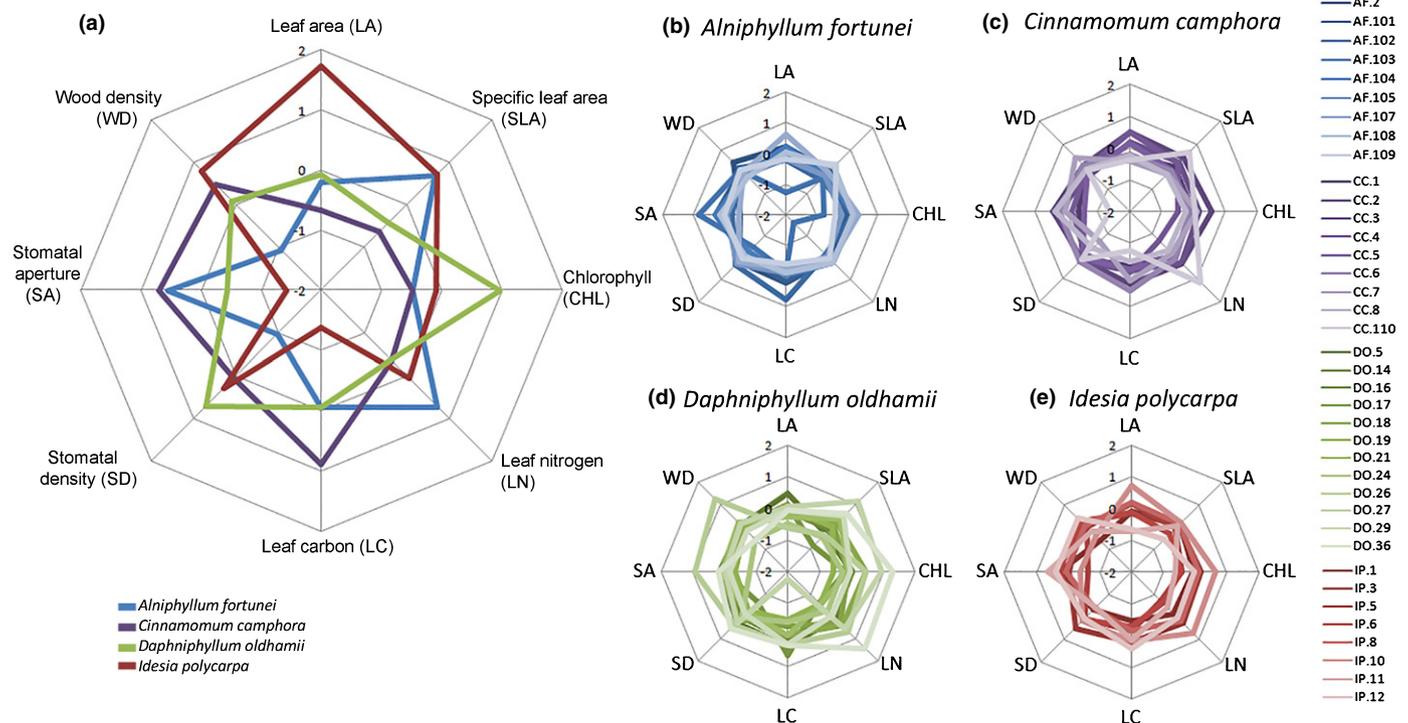
The extent to which species differed in their traits varied among traits; for example, *I. polycarpa* had larger LA and *D. oldhamii* had higher CHL compared with the other species (Fig. 3a; Table S4). For other traits, some of the species had similar values, such as *I. polycarpa* and *A. fortunei* for SLA and *C. camphora* and *D. oldhamii* for LN. Considering all eight traits together demonstrated that the four species differed in multivariate trait space (Fig. 3a). This could also be seen in the ordinations obtained with the first three axes of the principal component analysis (together explaining 71%; Fig. S1).

Comparing the eight traits among seed families within species resulted in various significant pairwise seed-family comparisons (Table S4). Using the same polygon plots as for the comparison among species (Fig. 3a), it can be seen that some seed families are distinct from other seed families (Fig. 3b–e). Compared with other seed families, seed family AF.103 (see Table S2 for a list of all seed families) had distinct values for LA, LN and SA in *A. fortunei* and CC.110 had distinct values for LN and SA in *C. camphora*. In *I. polycarpa* IP.10 had distinct values for LA and

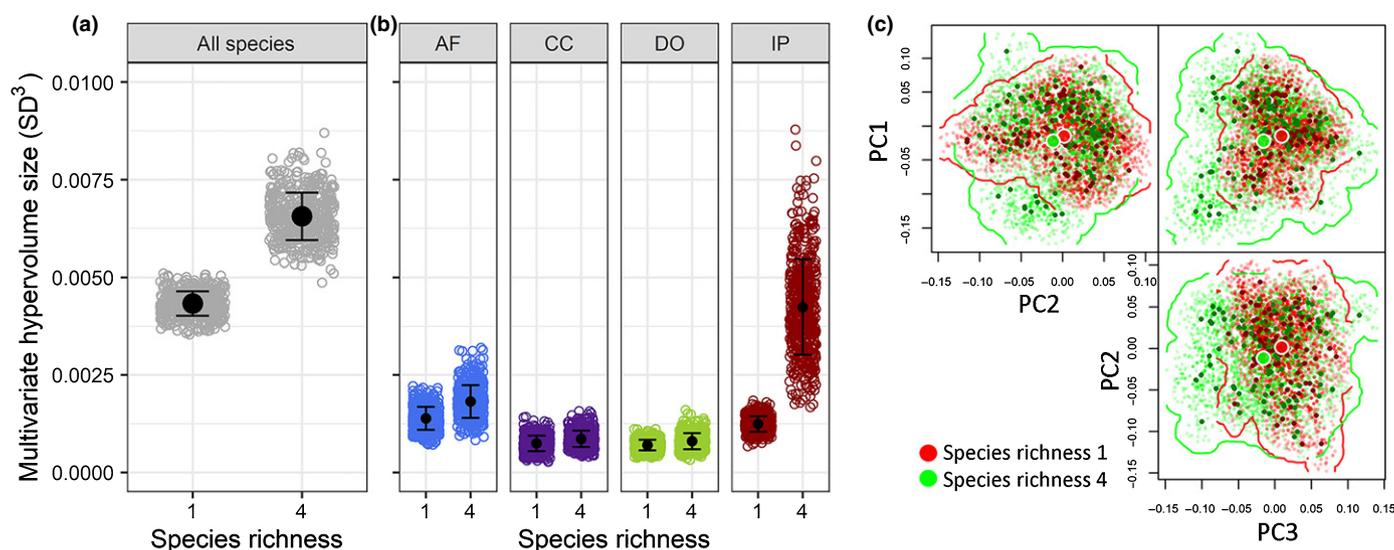
LN. The differences between seed families were most pronounced for chemical traits in *D. oldhamii*, with distinct values in CHL for DO.19, in LN for DO.36 and in LC for DO.27 and other seed families.

### Multivariate trait hypervolumes created by individuals from different richness levels

Despite the relatively small main effect of richness on trait variation across the four species, richness did affect trait values differently between species and seed families, indicated by the interaction effects of species or seed families with richness (Table S3). The multivariate hypervolume created by individuals from species mixtures was larger than that created by individuals from monocultures when the four species were combined (0.0065 vs 0.0043 SD<sup>3</sup>;  $P < 0.001$ ; Fig. 4a). Hypervolume sizes were also higher for the separate species, especially for *A. fortunei* and *I. polycarpa* ( $P < 0.001$  for all species; Fig. 4b; see Fig. S5 for an example of hypervolumes per species in species monocultures versus species mixtures). This analysis disregarded the difference in genetic richness. The increased hypervolume size represents higher differences among the measured individuals when individuals interact with heterospecific individuals in species mixtures compared with conspecific individuals in species monocultures. The volume centroids of the species shifted slightly between the species-richness levels one and four, which suggests that on



**Fig. 3** Illustration of relative mean trait values of species and seed families within species. Species are identified with different colors and seed families by various shades of colors and identification numbers (see legends and Supporting Information Table S2 for the full list of seed families). (a–e) The polygons connect scaled values (mean = 0 and SD = 1 after log-transformation if required) for each trait for the four species (a) and for the seed families within the species *Alniphyllum fortunei* (b), *Cinnamomum camphora* (c), *Daphniphyllum oldhamii* (d) and *Idesia polycarpa* (e). For trait means of seed families (b–e), trait values were scaled for each species separately. See Table S4 for significant differences between species and seed-family pairs per trait.



**Fig. 4** Multivariate trait hypervolume sizes of all species combined and each species separately, calculated using individuals from low or high (one vs four) species richness. (a) Hypervolume sizes of individuals from all four species from species monocultures vs species mixtures; (b) hypervolume sizes of individuals per species separate from species monocultures vs mixtures; (c) visualization of hypervolumes created by individuals from all species together from species monocultures vs mixtures (the two hypervolumes have a size of 0.0037 and 0.0071  $\text{SD}^3$  for species monoculture and mixture, respectively). For each value on the x-axis 500 bootstrapped volumes were obtained, calculated with 29 randomly sampled individuals, with replacement, per species per species richness (b) or the summed 116 sampled individuals per species richness (a). See Supporting Information Table S2 for the number of individuals available per sampling (per species per species richness). AF, *Alniphyllum fortunei*; CC, *Cinnamomum camphora*; DO, *Daphniphyllum oldhamii*; IP, *Idesia polycarpa*. Individual open dots represent individual hypervolume sizes; black solid items are mean values  $\pm 1$  SD. See the Materials and Methods section for detailed explanation of calculations regarding the multivariate hypervolumes.

average the species became more distinct in the species mixtures compared with monocultures (Fig. S6).

Increasing the genetic richness had a different effect on the multivariate hypervolume size (Fig. 5). In species monocultures, the hypervolumes created by individuals from plots with a genetic richness of four seed families were smaller or larger than the hypervolumes created by individuals from plots with a genetic richness of one seed family. Volumes of *A. fortunei* and *I. polycarpa* were smaller; for genetic richness four vs one the hypervolume sizes were 0.0010 vs 0.0015 and 0.0007 vs 0.0014  $\text{SD}^3$  for *A. fortunei* and *I. polycarpa*, respectively, while volumes of *C. camphora* and *D. oldhamii* were slightly larger (0.00051 vs 0.00045 and 0.00068 vs 0.00061  $\text{SD}^3$  for *C. camphora* and *D. oldhamii*, respectively) ( $P < 0.001$  for all species; Fig. 5a). In species mixtures, the total hypervolume size created by individuals from all four species with a genetic richness of four seed families was similar to the hypervolume size created by individuals from species mixtures with a genetic richness of one seed family (both 0.0074  $\text{SD}^3$ ;  $P = 0.54$ ; Fig. 5b). Moreover, the results from the multiple specific trait combinations showed that the effect of richness on the hypervolume size was similar across all trait combinations, while the effect of genetic richness in species mixtures was slightly different (Figs S2, S3).

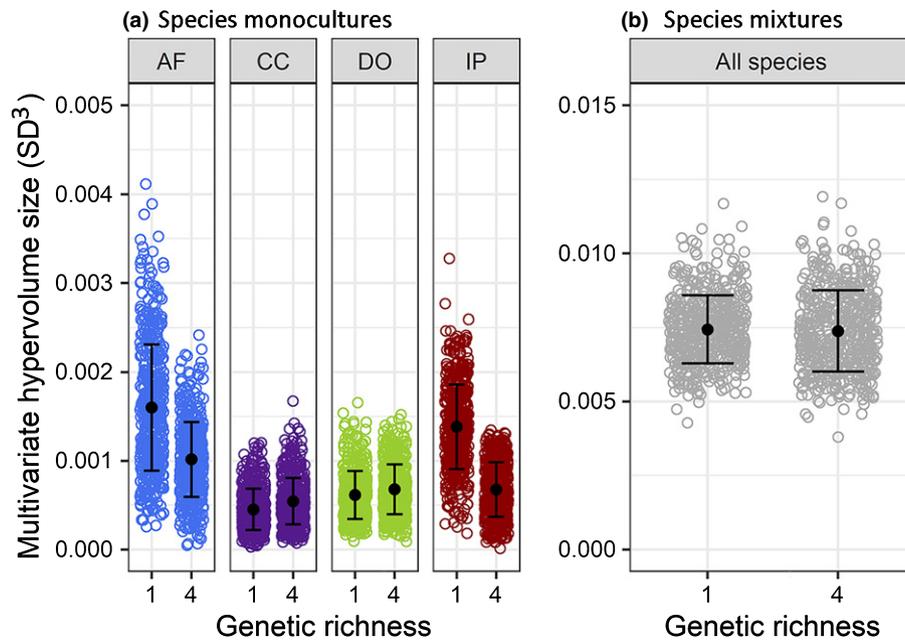
#### Individual tree growth and stand-level biomass

Individual growth of the 547 individuals was, just as the traits, primarily determined by species, followed by seed families and their interaction with richness (Table S3), demonstrating that

growth was also highly variable among species and seed families and that both showed variation in their responses to species  $\times$  genetic richness combinations (Fig. S4). However, tree growth was not significantly affected in the same direction by richness as shown by the small effects of the species and genetic richness combination (Table S3). In addition, across all individuals within the experiment (total 2073 individuals) individual growth was not significantly affected by species or genetic richness (Fig. 6a,b; Table S5). Nevertheless, growth was different among species and both the species and genetic richness effects were species-specific, as indicated by the interaction terms (Fig. 6a,b; Table S5). At the community level, standing tree biomass after 8 yr of growth was significantly higher in the four-species mixture than in the average monoculture, while stand-level tree biomass was not affected by genetic richness (Fig. 6c; Table S5). Additionally, there were significant differences in stand volumes between the four species in monoculture, but no species-specific genetic richness effect (Fig. 6d).

#### Discussion

We analyzed trait variation among species and within species among seed families in a full-factorial species  $\times$  genetic richness tree biodiversity experiment and assessed if trait variation played a role in the effect of species and genetic richness on individual tree growth and stand-level tree biomass after 8 yr of community development. We observed that seed families explained a substantial amount of trait variation, on top of the amount explained by differences between species. In addition, trait values changed plastically in response to richness, with variation in these



**Fig. 5** Multivariate trait hypervolume sizes of each species separately or all species combined in species monocultures or mixtures, calculated using individuals from low or high genetic richness. (a) Hypervolume size per species separately in low and high genetic richness (one vs four seed families per species) in species monocultures. (b) Hypervolume size of all species together in low and high genetic richness (one vs four seed families per species) in species mixtures. For each value on the x-axis, 500 bootstrapped volumes were obtained, calculated with nine randomly sampled individuals, with replacement, per species per genetic richness in species monoculture (a) or 36 sampled individuals per genetic richness in species mixtures (b). The 36 individuals consisted of nine individuals per species. See Supporting Information Table S2 for the number of individuals available per sampling (per species per species  $\times$  genetic richness). AF, *Alniphyllum fortunei*; CC, *Cinnamomum camphora*; DO, *Daphniphyllum oldhamii*; IP, *Ilex polycarpa*. Individual open dots represent individual hypervolume sizes; black solid items are mean values  $\pm$  1 SD.

responses both among species and among seed families within species. Multivariate trait variation among individuals was increased in the four-species mixture compared with the monocultures, while it was slightly decreased or stayed constant with increasing within-species genetic richness. Overall, species richness had a positive effect on stand-level tree biomass, while an effect of genetic richness was absent.

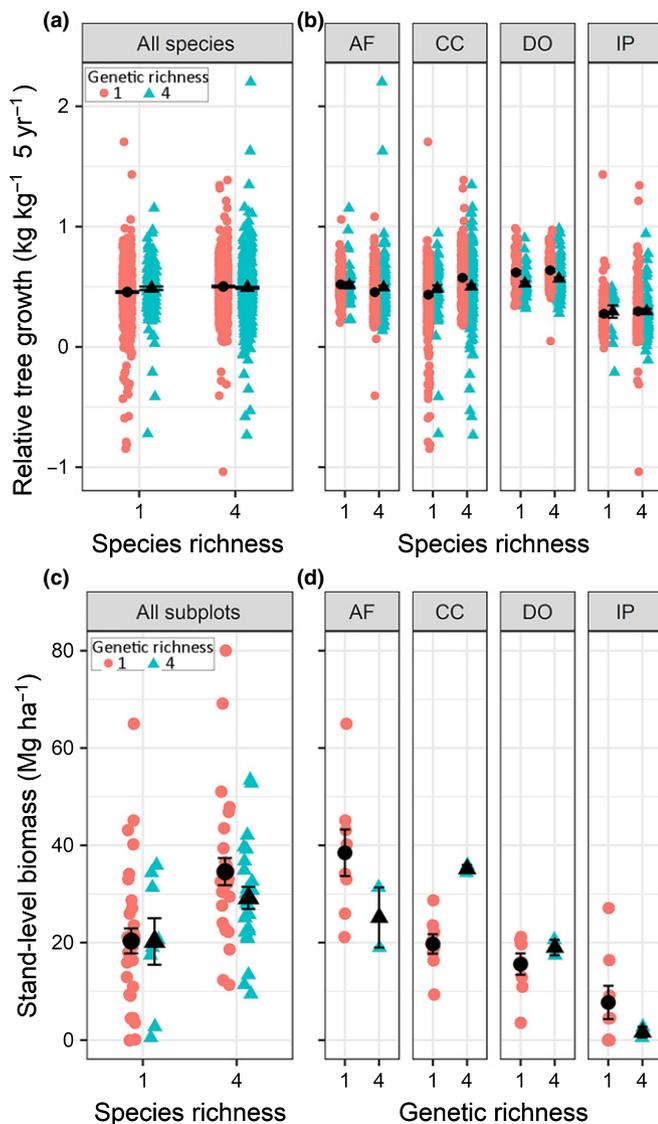
#### Trait variation among species and seed families

Trait variation was mainly determined by differences between species, but differences between seed families within species also explained a substantial amount of variation, which fits with previous studies showing the relative contribution of intraspecific trait variation to total trait variation (Albert *et al.*, 2010; Hulshof & Swenson, 2010; Poorter *et al.*, 2018). Intraspecific trait variation was created by both within-genetic components (seed family) and plastic responses to environmental conditions. Previous work assigned intraspecific trait variation to overall plasticity (Lipowsky *et al.*, 2015; Roscher *et al.*, 2018a; Benavides *et al.*, 2019) without separation of genetic vs environmental components. Here, we attempted such a separation by explicitly including a within-species genetic component (seed family identity) of trait variation and also analyzing effects of species and genetic richness on trait variation. These findings add to an increasing body of literature demonstrating that while species' mean trait values can be useful to assess large-scale variation (Wright *et al.*, 2004; Diaz *et al.*, 2016; Bruelheide *et al.*, 2018), within-species

trait variation must be included if effects of functional diversity on plant growth and ecosystem functioning are analyzed (Hughes *et al.*, 2008; Bolnick *et al.*, 2011; Violle *et al.*, 2012; Siefert *et al.*, 2015; Des Roches *et al.*, 2018).

Leaf area, LC and SA were the three traits most distinct between species. Leaf area variation was mainly a result of the much bigger leaves of *I. polycarpa* compared with the other species, while LC and SA were mainly determined by the difference between *I. polycarpa* and *C. camphora*. LN was mostly explained by variation among seed families, especially seed families from *D. oldhamii*. This fits with observations of Albert *et al.* (2010), who showed that, compared with other traits, intraspecific variation was highest for LN. Trait variation among seed families may be maintained by the heterogeneous neighborhoods encountered by individual trees in these species-rich subtropical forests (Ang *et al.*, 2016) and by sibling competition and Janzen–Connell effects within species (Eck *et al.*, 2019). Indeed, in a recent study it was found that species-rich experimental forests maintained a higher genetic diversity in two dipterocarp species than did monocultures (Ang *et al.*, 2016).

A limitation of our study was that the expectation of differences among seed families was based on the assumption of higher genetic relatedness among individuals within than between seed families; individuals from the same seed family came from the same mother tree and were therefore considered to be at least half-sibs. Future research should analyze the genetic relatedness among our individuals in more detail to better assess the genetic contribution to phenotypic variation.



**Fig. 6** Individual tree growth and stand-level biomass per species  $\times$  genetic richness combination. (a, b) Relative individual tree biomass growth for each species  $\times$  genetic richness level, for all individuals together (a,  $n = 2073$ ) or per species separately (b). (c, d) Stand-level biomass for each species  $\times$  genetic richness level, for all plots (c,  $n = 92$ ) and for the species monocultures separately (d). Species  $\times$  genetic richness level contains values of one vs four species and one vs four seed families. Pink dots and blue triangles represent individual trees (a, b) or subplots (c, d) with one or four seed families per species, respectively. Large black items are mean values  $\pm$  1 SE per species  $\times$  genetic richness combination. AF, *Alniphyllum fortunei*; CC, *Cinnamomum camphora*; DO, *Daphniphyllum oldhamii*; IP, *Idesia polycarpa*. See Supporting Information Table S5 for the related statistics.

### Univariate and multivariate trait variation as a result of species and genetic richness

In addition to the trait variation among species and seed families, we also found significant trait variation within species and seed families that was a result of plasticity in response to species  $\times$  genetic richness treatments. Trait variation as a result of responses to species richness has been observed in other BEF-related studies

(Roscher *et al.*, 2011, 2018a; Lipowsky *et al.*, 2015; Benavides *et al.*, 2019; Bongers *et al.*, 2020) and has been shown to result in positive effects on productivity (Zuppinge-Dingley *et al.*, 2014; Zhu *et al.*, 2015). However, in these previous studies it was not tested if these phenotypic responses were a result of genetic differences or plasticity within genetic groups to environmental conditions (plasticity in the strict sense of its definition; see Bradshaw, 1965), because the genetic relationship between plants was not known.

The observed trait plasticity in response to richness led to higher multivariate trait diversity among individuals from species mixtures than from species monocultures, which was represented by increased multivariate hypervolume sizes. This effect was mainly a result of *A. fortunei* and *I. polycarpa*, because these species increased their hypervolume sizes and also slightly shifted their volume centroids. By contrast, increasing the genetic richness from one to four seed families affected the multivariate trait variation, depending on the species identity in species monocultures, while it had no effect on multivariate trait variation in the four-species mixture. However, increasing multivariate trait variation with increasing genetic richness was observed in the species mixture when using different sets of traits (Fig. S3). This could be related to the role of specific traits and illustrates that a true holistic interpretation of the ecological functions of individuals within a community remains challenging. Within this study, we believe that the use of principal component axes instead of sets of traits is a more appropriate method to estimate variation in ecological functions among individuals. Nevertheless, the fact that *A. fortunei* and *I. polycarpa* are both deciduous species and *C. camphora* and *D. oldhamii* are evergreen species suggests that this single trait could explain the difference in trait plasticity that determined multivariate trait variation change in response to both species and genetic richness (Valladares *et al.*, 2000; Böhnke & Bruehlheide, 2013).

Changes in multivariate trait variation as a result of species or genetic richness may be related to various processes. Higher species richness can increase the local environmental heterogeneity among all individuals and thus leads to increased differences among individuals. While higher genetic richness has less effect on local environmental heterogeneity it could reduce sibling competition and therefore increase asymmetries and differences among individuals (Willson *et al.*, 1987; Weiner, 1990). By contrast, increased genetic richness can also reduce asymmetric competition and thus reduce individual variation. The different changes of the multivariate trait variation among individuals with increasing genetic richness illustrates that different processes can be at play within and among species. Further experiments would be needed to determine the relative roles of different drivers, for example competitive asymmetry or niche overlap, influencing differences between individuals. Linking this kind of knowledge to trait and growth variation will be an additional step towards understanding the ecological and functional mechanisms underlying BEF relationships.

The increased multivariate trait variation among individuals with increasing species richness as a result of species-specific trait shifts would be consistent with the hypothesis that individuals

and species try to minimize niche overlap to avoid competition (see e.g. Zuppinger-Dingley *et al.*, 2014). The observation that species-specific multivariate trait variation increased with increasing species richness has also recently been shown for trees (Benavides *et al.*, 2019) but is opposite to some previous findings regarding grasses (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2018). The increased multivariate trait variation within species in species mixtures could be a result of larger heterogeneity of local environmental conditions and neighbor interactions compared with species monocultures. Decreased multivariate trait variation within species can be related to minimizing niche overlap among species, which could be functional in decreasing resource competition, as expected based on niche theory in diverse systems (Turnbull *et al.*, 2016). Nevertheless, to determine if species or individuals shift their functional niche in diverse systems, more detailed studies are required that measure time- or space-specific traits (Niklaus *et al.*, 2017; Williams *et al.*, 2017) or actual resource uptake (von Felten *et al.*, 2009; Ashton *et al.*, 2010).

### Species richness, but not genetic richness within species, increased stand-level productivity

Over an 8 yr growth period, species richness positively affected stand-level tree biomass, but against our expectations no significant effect of genetic richness within species was observed. As expected, total trait variation among individuals in species mixtures was larger than the sum of the variation of the individuals from monocultures. This suggests niche differentiation among species and could be a mechanism contributing to the increased stand-level productivity in four species mixtures compared with the average monocultures (Zuppinger-Dingley *et al.*, 2014).

Although seed families did significantly contribute to trait variation within species, increased multivariate trait variation among individuals from more genetically rich communities was not observed within species mixtures and was only observed for two out of the four species in separate monocultures. This lack of effect could therefore explain the absence of strong genetic effects on individual growth and community-level productivity. Our results extend those of Fischer *et al.* (2017), who also found significant trait and growth differences between genotypes but no relationship between genetic richness and stand productivity within the single species *Populus fremontii*. The absence of an overall increased stand-level biomass in genetically rich communities across all four species could also be the result of opposite growth responses of the four species to the species  $\times$  genetic richness treatment combinations.

In this context it should be noted that *A. fortunei* and *I. polycarpa* had decreased stand-level biomass and decreased multivariate trait variation under higher genetic richness, whereas *C. camphora* and *D. oldhamii* showed the opposite responses. These observations do match our hypothesis that the size of multivariate trait variation links to community productivity. Two recent studies that also test for such a relation between genetically based functional trait variation within species and species-level functioning in one case found positive effects and trait variation

for *A. thaliana* (Wuest & Niklaus, 2018) and, in another case, no effect despite trait variation for rice (Montazeaud *et al.*, 2018). Thus, although there are several studies that report positive effects of genetic richness on (mostly single-species) ecosystem functioning (Schmid, 1994; Crutsinger *et al.*, 2006; Kotowska *et al.*, 2010; Prieto *et al.*, 2015; Cao *et al.*, 2018), it remains unknown to what extent these effects can be related to genetically caused functional trait variation within species. In addition, it remains to be studied if such effects could be extrapolated from single-species to multispecies communities.

There could also be a difference between trees and other organisms with regard to effects of genetic richness on ecosystem functioning and a difference between the type of ecosystem function considered. No or weak effects of within-species genetic richness on tree or plant growth and productivity have been reported in several other studies (Crawford & Rudgers, 2012; Prieto *et al.*, 2015; Schöb *et al.*, 2015; Hahn *et al.*, 2017; Zeng *et al.*, 2017). By contrast, strong within-plant-species genetic richness effects on fungal pathogens or herbivore abundance or diversity have been reported several times (Schmid, 1994; Crutsinger *et al.*, 2006; Johnson *et al.*, 2006; Barton *et al.*, 2015; Campos-Navarrete *et al.*, 2015; Cao *et al.*, 2018; Barantal *et al.*, 2019). For the same plots as in our study, Cao *et al.* (2018) also found a positive trend of increasing within-plant genetic richness on top of species richness for higher-level trophic community interactions, which is an important ecosystem process in forests.

### Conclusion

While previous studies found that increasing functional diversity with increasing species richness can explain parts of positive BEF relationships, the extent to which genetically caused functional trait diversity has similar effects has so far remained unknown. Here we explicitly separated the variation in functional traits between and within species into genetic components and species  $\times$  genetic richness-induced plasticities. While species richness effects on trait variation could be related to increased stand-level functional diversity and tree biomass, genetic richness had a limited effect on increasing trait variation in species monocultures or species mixtures and consequently we did not find significant effects of genetic richness on stand-level productivity. Our research presents, to our knowledge, one of the few cases where the effects of genetic diversity within species and richness-driven plasticity on functional trait variation and stand-level forest characteristics have been analyzed.

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## Author contributions

KM, BS, HB, WD and XL designed the experiment and FJB, SL, WD, CZH and HY collected data. FJB, BS and XL performed data analyses. FJB, BS and XL wrote the paper. All authors contributed to the final preparation of the manuscript.

## ORCID

Franca J. Bongers  <https://orcid.org/0000-0001-9517-4932>  
 Helge Bruelheide  <https://orcid.org/0000-0003-3135-0356>  
 Walter Durka  <https://orcid.org/0000-0002-6611-2246>  
 Christoph Z. Hahn  <https://orcid.org/0000-0002-8399-4682>  
 Xiaojuan Liu  <https://orcid.org/0000-0002-9292-4432>  
 Keping Ma  <https://orcid.org/0000-0001-9112-5340>  
 Bernhard Schmid  <https://orcid.org/0000-0002-8430-3214>

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Visualization of the loading of the eight traits on the first three axes of the principal component ordinations performed using 547 individuals.

**Fig. S2** Additional analyses showing multivariate trait hypervolume sizes of all species combined and for each species separately, calculated using individuals from low or high (one vs four) species richness.

**Fig. S3** Additional analyses showing multivariate trait hypervolume sizes of each species separately in species monoculture or all species combined in species mixtures, calculated using individuals from low or high genetic richness.

**Fig. S4** Trait values and growth rate reaction-norms of seed families within species for species  $\times$  genetic richness.

**Fig. S5** Visualization of one of the 500 simulated hypervolumes per species separately in species monoculture versus species mixtures.

**Fig. S6** Dimension-specific hypervolume centroids per species within species monocultures and species mixtures.

**Table S1** Overview of the species and seed-family composition per plot for each species  $\times$  genetic richness combination.

**Table S2** Number of individuals per species per seed family that were measured for functional traits and growth for each species  $\times$  genetic richness combination.

**Table S3** Summary of linear model analyses of species, seed-family and richness effects on eight traits and relative tree growth, considering factors in hierarchical structure.

**Table S4** List of species pairs that were nonsignificant and seed-family pairs within species that were significantly different for a specific trait ( $P < 0.05$ ).

**Table S5** Summary results of ANOVAs testing the effect of species and genetic richness on individual tree growth (2013–2018) and stand-level tree biomass (2018).

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