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Research

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Summary

- Afforestation projects using species mixtures are expected to better support ecosystem services than monoculture plantations. While grassland studies have shown natural selection favoring high-performance genotypes in species-rich communities, this has not been explored in forests.
- We used seed-family identity (known maternity) to represent genetic identity and investigated how this affected the biomass accumulation (i.e. growth) of individual trees ($n = 13\,435$) along a species richness gradient (1–16 species) and over stand age (9 yr) in a forest biodiversity experiment.
- We found that among the eight species tested, different seed families responded differently to species richness, some of them growing relatively better in low-diversity plots and others in high-diversity plots. Furthermore, within-species growth variation increased with species richness and stand age, while between-species variation decreased with stand age.
- These results indicate that seed families within species and their reaction norms along the species richness gradient vary considerably and thus can explain a substantial proportion of the overall variation in tree growth. Our findings suggest that the growth and associated ecosystem services of species-rich mixtures in afforestation projects can be optimized by artificially selecting seed families with high mixture performance in biodiversity experiments.

Introduction

Forest loss resulting from human activities threatens biodiversity and the essential ecosystem functions and services provided by forests (Newbold *et al.*, 2015; van der Plas *et al.*, 2016). Afforestation is a crucial strategy to prevent forest loss and maintain forest ecosystem functioning (Bastin *et al.*, 2019; Chazdon & Brancalion, 2019). To achieve the desired gains, it has been suggested to consider the number of tree species (Huang *et al.*, 2018; Feng *et al.*, 2022; Messier *et al.*, 2022), species identity, community composition (Ma *et al.*, 2021; Zhang *et al.*, 2025), and species functional traits (Bongers *et al.*, 2021). However, the performance of individuals within a species is not uniform because of genetic variation. Thus, investigating whether and how we should take into account the genetic identity of trees, in addition to species identity and diversity, may improve our capacity to sustain ecosystem functions in afforestation projects.

Individuals with the same genetic identity may differ in their growth across environments (Stearns & Koella, 1986; Schmid, 1992; Sultan, 2000). Furthermore, genetically distinct individuals may react differentially to the same environmental variation, such as stress gradients (Paschke *et al.*, 2003). Species richness, as an important aspect of the biotic environment, can affect the growth of individual trees through plant–plant interactions (Fichtner *et al.*, 2018), plant–animal interactions (Li *et al.*, 2023), and by affecting abiotic microenvironments (Wright *et al.*, 2017). In particular, grassland experiments have shown that community species richness can act as an evolutionary selective force interacting with standing genetic variation to favor, over multiple generations, genotypes that are best suited to grow in

diverse species mixtures (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2019).

In fact, studying standing genetic variation for biodiversity-specific performance may be more straightforward in forest, than in grassland, biodiversity experiments. This is because trees with a known genetic background can be individually monitored as the stands age, allowing their performance to be measured across a species richness gradient within a single generation. If trees with different genetic identities respond differentially to species richness, we may anticipate long-term evolutionary shifts. This foresight allows us to artificially select seed families with high mixture performance when designing species-rich mixture plantations for afforestation projects with the aim to optimize ecosystem functions related to tree growth. This was not possible in the mentioned grassland experiments, where evolutionarily distinct monoculture and mixture genotypes within species could only be identified after natural selection had taken its course (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2019). In a tropical forest biodiversity experiment, it was found that species richness significantly affected the genetic diversity of test species, presumably through selection from standing variation (Ang *et al.*, 2016), suggesting that standing variation in reaction norms to species richness within species not only occurs in grassland but also in forest ecosystems.

Genotype-by-environment interactions not only reflect that plants with different genetic identities have different growth responses to an environmental gradient, but they also imply that the contribution of genetic identity to variation in growth, known as heritability (Hoffmann & Parsons, 1991; Hoffmann & Hercus, 2000), varies across the environmental gradient. Heritability represents the proportion of total phenotypic variation attributable to additive genetic effects and is influenced by both genetic (apparent genetic variation) and environmental factors (Falconer, 1989; Hoffmann & Parsons, 1991; Kearsey & Pooni, 1996). It is important to note that 'apparent genetic variation' refers not to genomic variation, but rather to phenotypic variation between genotypes, which is observable and measurable in a given environment. Understanding how heritability changes across different environments is crucial for predicting the adaptive responses of plants to environmental shifts.

In well-mixed multispecies plant communities (the case of our experiment), the frequency of interspecific relative to intraspecific neighbor relations increases with species richness. If the species have similar competitive ability but different niches (the case of our experiment, see Huang *et al.*, 2018), this can result in a less stressful competition environment (Levine & HilleRisLambers, 2009; Kunstler *et al.*, 2016; Fichtner *et al.*, 2018). Studies of both animals and plants have found that the contribution of genetic identity to phenotypic variation among individuals, that is an individual's 'genetic potential', is generally larger in favorable environments (Hoffmann & Merilä, 1999; Merilä & Sheldon, 2001; Shama *et al.*, 2011), because less stressful environmental conditions allow an individual to achieve its inherited maximum trait expression, such as maximum growth, reproduction, or stress resistance (Hermisson & Wagner, 2004; Charmantier & Garant, 2005). Aside from providing a less stressful competition environment, species richness can also promote community functional diversity (Díaz & Cabido, 2001; Tang *et al.*, 2022) and structural complexity (Coverdale & Davies, 2023), thus increasing environmental heterogeneity. Species richness may influence the absolute contributions of genetic and environmental variation to phenotypic variation, although the relative genetic contribution, that is the quotient of genetic to total variation (heritability), may remain relatively constant. However, no empirical study has tested how genetic and environmental variation contribute to phenotype variation and heritability within tree species along a species richness gradient.

The contribution of genetic variation to plant growth can change over stand age due to both changes in the internal (ontogeny) or external environment (e.g. plant–plant interactions); where these changes in genetic variation with the changing environment during ontogeny are equivalent to genetic identity by stand age interactions in a combined analysis across years (Axtell & Bowman, 2008; Ma *et al.*, 2020; Barton, 2024). For example, plants can change their biomass allocation from a fast- (high investment into leaves) to a slow-growth strategy (high investment into stems and roots) over stand age (Müller *et al.*, 2000). This shift is attributed to the need for successful establishment during the fragile early stage, followed by increased access to resources in later stages, allowing for resource allocation to other functions like reproduction (Dayrell *et al.*, 2018; Barton, 2024). Additionally, plants respond to local environments (le Roux *et al.*, 2013; Spasojevic *et al.*, 2014) and the interactions with neighbor plants (Yang & Rudolf, 2010; Lasky *et al.*, 2015) can vary through plant development. These ontogenetic effects, resulting from both genetic variation among genotypes and their interactions with species richness, accumulate over the course of plant development and contribute to within-species variation (Henn & Damschen, 2021). As the absolute variation within species increases with stand age, it may lead to a decrease in the relative contribution of among-species variation to total variation in tree growth, equalizing species-specific growth. This equalization of growth can balance competitive abilities and thereby promote coexistence among species (Chesson, 2000; Kunstler *et al.*, 2016). Also, strong variation in tree performance can emerge as plants grow and age (Lusk & Warton, 2007; Dayrell *et al.*, 2018) and, as noted previously, high species diversity may increase plants' capacity to express inherited maximum trait expression by creating a less competitive environment.

To test how genetic identity affects tree growth across tree species richness and over stand age, we used growth data from eight tree species with maternal information grown from 2012 to 2021 in a large forest biodiversity experiment in subtropical China (Bruelheide *et al.*, 2014; Huang *et al.*, 2018; Liu *et al.*, 2022) (BEF-China) (Fig. 1a,b). These trees were planted across 137 plots of 20×20 planting positions in monocultures and 2-, 4-, 8-, and 16-species mixtures (Supporting Information Fig. S1). The individual labeling of genotypes in large forest experiments poses significant challenges and is impractical for direct application in afforestation. Therefore, seed-family identity, where trees share a common mother, was employed in this study to represent genetic identity (Fig. 1a). We additionally used

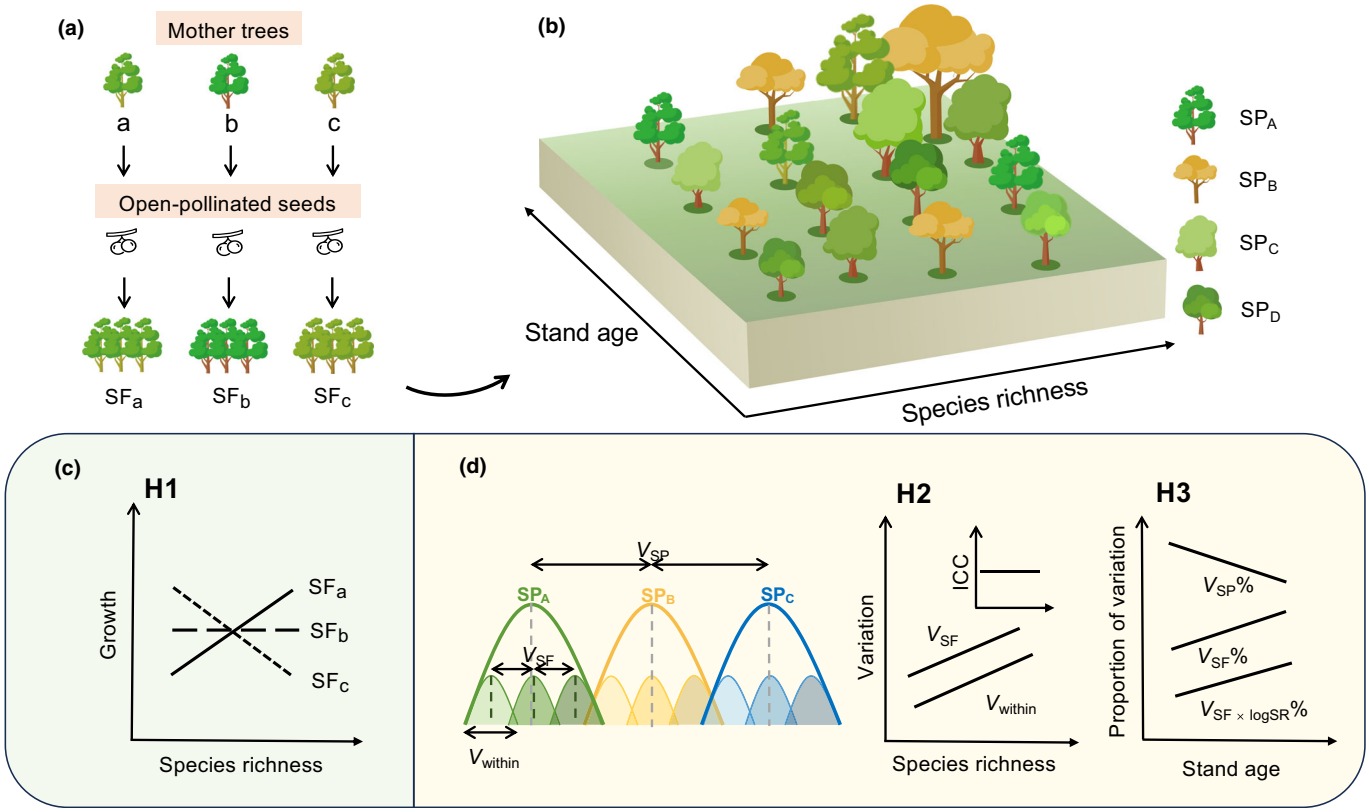

Fig. 1 Overview of the research hypotheses. (a) Conceptual figure showing the seed-family design. (b) Illustration of the experimental design. Seeds from known mother trees (Mother a, Mother b, etc.) of eight species (SP_A, SP_B, etc.) were collected from neighboring natural forests and the resulting saplings were planted in our experiment across different species-richness levels and grown for 9 yr. Their seed-family identity (SF_a, SF_b, etc.) was labeled to indicate genetic identity. (c) Illustration of the interaction pattern between genetic identity and species richness (H1): trees with different genetic identities (SF_a, SF_b, SF_c) may respond differentially to species richness, SF_a representing a seed family with good mixture performance, SF_c representing one with relatively good monoculture performance, and SF_b does not respond to species richness. (d) Illustration of the variation of tree growth among species (V_{SP}), within species among seed families (V_{SF}), and within seed families among individuals (V_{within}), that is residual variation due to remaining genetic and environmental variation within seed families and plots; and the second and third hypotheses of this study. H2: both variation explained by seed-family identity (V_{SF}) and within-seed family variation (V_{within}) are expected to increase with species richness due to less competition and more environmental heterogeneity in more diverse communities, respectively, and thereby the contribution of seed-family identity (quantified as intraclass correlation coefficient; $ICC = V_{SF}/(V_{SF} + V_{within})$) is expected to remain more or less constant with species richness. H3: the proportions of variation explained by seed-family identity and its interaction with species richness are expected to increase with stand age due to their cumulative effects throughout ontogeny. Conversely, the proportion of variation explained by species identity is anticipated to decrease with stand age, as equalizing growth among species can balance their competitive abilities and enhance coexistence.

genotyping-by-sequencing (GBS) on a subset of 673 trees to check whether trees within seed families were indeed more closely related than trees between seed families. We used aboveground cumulative biomass to indicate tree growth. First, we tested how seed-family identity affected tree growth across the tree species richness gradient (H1, Fig. 1c). Specifically, we predict that trees from different seed families respond differently to species richness, that is, some grow relatively better in monoculture and others in highly diverse communities. Such crossing reaction norms are typical when there are trade-offs that prevent genotypes from performing well across all environments. Second, we hypothesize that the variation in cumulative biomass among seed families (V_{SF} in H2, Fig. 1d) and within seed families (V_{within} in H2, Fig. 1d) increases with species richness. More diverse communities are expected to create less stressful competitive environments, which allow trees to better express their inherited maximum growth potential. Furthermore, it is conceivable that more diverse communities increase the growth variation within seed families by enhancing environmental heterogeneity. In combination, these two hypotheses could result in a constant expression of growth heritability across species richness (ICC in H2, Fig. 1d). Third, we assess how the contributions to variation in tree growth of species identity, seed-family identity, and its interactions with species richness change with stand age. We hypothesize that the effects of seed-family identity and its interaction with species richness increase with stand age due to accumulated genetic differences in trait expression, while the contribution of species identity decreases with stand age because of light competition leading to similar tree heights among the different species (H3, Fig. 1d).

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Table 1 The eight study species and the numbers of seed families (# sf), tree individuals (# indiv) in 2012, and the results of genetic distance tests.

Species	# sf	# indiv	*R* value (# sf/# Indiv)	*P* value
Alniphyllum fortunei	22	3069	0.194 (15/176)	**0.001**
Castanopsis eyrei	14	1432	0.024 (2/23)	0.262
Castanopsis fargesii	27	2666	0.349 (17/185)	**0.001**
Castanopsis sclerophylla	20	2300	0.455 (8/96)	**0.001**
Camphora officinarum	14	1701	0.464 (7/84)	**0.001**
Quercus glauca	18	989	0.567 (5/60)	**0.001**
Daphniphyllum oldhamii	27	913	0.339 (3/13)	**0.014**
Lithocarpus glaber	38	2567	0.468 (3/36)	**0.001**

'# sf' and '# indiv' indicate the number of seed families and the number of individuals in 2012 in the whole experiment. '*R* value' (0–1) compares the mean of ranked dissimilarities among seed families to the mean of ranked dissimilarities within seed families. A larger *R* value suggests higher dissimilarity among seed families. Numbers in brackets indicate the number of seed families and individuals that were used to test genetic distance ('# sf/# indiv'). '*P* value' indicates the significance of dissimilarities among seed families compared to the mean of ranked dissimilarities within seed families. The bold *P* values indicate significance at $P < 0.05$.

Materials and Methods

Study site and experimental design

This study was carried out in a large-scale forest biodiversity experiment in southeastern China, the Biodiversity–Ecosystem Functioning China Platform (BEF-China, (Bruelheide *et al.*, 2014; Huang *et al.*, 2018)). BEF-China is located close to Xingangshan, Dexing, Jiangxi Province, a region with subtropical forest (29°04′48″ to 29°06′36″N, 117°54′00″ to 117°55′48″E). The recent mean annual temperature in the region was 16.7°C and the mean annual precipitation was 1800 mm (averaged from 1971 to 2000). In 2009 and 2010, 566 plots with a size of 25.8 × 25.8 m (equal to one Chinese area unit of 'mu'; horizontal projection) were planted with monocultures or 2-, 4-, 8-, 16- and 24-species mixtures at two sites, A (2009) and B (2010). Each plot had 400 planting positions in a square design (20 × 20). The present study was carried out at site B, where, for eight species (Table 1), enough saplings raised from seeds collected from known mother trees in the neighboring natural forests had been planted to allow statistically relevant analysis (Table 1; Fig. S1a). Here, we refer to all trees originating from the same mother tree as a seed family. These trees with known seed-family identity were randomly distributed in each plot (Fig. S1b). Furthermore, and as far as possible, members of each seed family were assigned to plots of each species richness level in equal proportion. We omitted data from 24-species plots from the analyses presented in the main text because of the few and spatially contiguous replicates (95 trees from four plots and the plots located in one small portion of the experiment, Fig. S1a). In 2012, 15 637 trees with known seed-family origin were inventoried across 137 plots. A total of 13 435 trees were still found alive in 2021. Members of a seed family may be full- to half-sibs depending on the breeding system of the species (Fig. 1a). We used GBS to confirm the assumption that genetic relatedness was greater within than between seed families (see 'Genotyping' and 'Genetic distance' in the Materials and Methods section). We thus used seed-family identity to indicate genetic identity. Due to variation in the availability of seeds from mother trees, differing responses of species to the common seedling growth conditions, and differential establishment success after transplanting to the diversity plots, the number of seed families and individuals within each family and their distribution across species richness levels was uneven for the set of trees included in the present analyses (Table 1).

Genotyping

To test our assumption that the relatedness within seed families was closer than among seed families, we sampled a subset of seed families (and within those a subset of individuals) that were well represented across the different species richness levels for GBS. Fresh, healthy leaves were collected in the field and stored at −20°C until DNA extraction. In total, 673 out of the 13 435 surviving trees were sampled from different seed families of the eight species (Table 1). The number of seed families per species varied according to variation in their representation in the experiment (see 'Study site and experimental design' in the Materials and Methods). A phenol-chloroform extraction method (Methods S1) was used to extract DNA from frozen leaf tissue. Before library preparation, the quantity and quality of DNA samples were checked using agarose gels, Nanodrop (OD_{260}/OD_{280}), and Qubit® DNA Assay Kit in a Qubit® 2.0 Fluorometer (Life Technologies, Carlsbad, CA, USA). GBS libraries were prepared for the eight species for sequencing (Methods S2); the restriction enzymes used are shown in Table S1. The constructed libraries were sequenced on an Illumina Novaseq using a 150 bp paired-end sequencing strategy (Illumina, San Diego, CA, USA). The original image data generated by Illumina sequencing were transformed into raw data by CASAVA base calling (Illumina). Reads with low quality (the number of low-quality (Qphred ≤ 5) bases in a single-ended sequencing read exceeding 50% of the length of that read), containing adapter sequences, and with > 10% of 'N' base calls (*N* represents an unresolvable base) were removed from the raw data to obtain clean data (raw data QC). Furthermore, effective rates (Clean Base/Raw Base), base error rates, Q20 (Base Count of Qphred > 20), Q30 (Base Count of

Qphred > 30), and GC content (G & C Base Count/Total Base Count) were checked to ensure the accuracy and reliability of the sequencing data. DNA extraction, GBS library preparation, sequencing, and raw data QC were done by Novogene Bioinformatics Technology Co., Ltd (Beijing, China).

Genetic distance

To ensure the quality of downstream analyses, we used FASTP v.0.22.0 (Chen *et al.*, 2018) to trim five bases in front of each read and discarded reads shorter than 100 bp. STACKS v.2.61 (Rochette & Catchen, 2017) was used to detect single nucleotide polymorphisms (SNPs) in individuals. We used the 'denovo_map.pl' program to execute 'ustacks', 'cstacks', 'sstacks', 'tsv2bam', 'gstacks', and 'populations'. We specified the number of mismatches allowed between stacks within individuals as six ($M = 6$), the number of mismatches allowed between stacks between individuals as five ($n = 5$), the minimum number of populations a locus must be present in to process a locus as 1 ($P = 1$), and the minimum percentage of individuals in a population required to process a locus for that population as five ($r = 5$). Seed-family identity was used to indicate the 'population' in detecting SNPs. After SNP detection, we used the R package SNPRELATE v.1.24.0 (Zheng *et al.*, 2012) to calculate the distance among seed families for each of the eight species separately. Then, we used the 'anosim' function in the R package VEGAN (v.2.5.7) (Oksanen *et al.*, 2022) to statistically test whether the distances among seed families were larger than those within seed families.

Tree growth

We used tree cumulative biomass as a proxy for tree growth. In 2012 and 2021, we measured the basal area (BA) and the height (H) of every tree with maternal information ($n = 13\,435$). In addition, every year from 2012 to 2021, we measured the basal area (BA) and the height (H) of trees with maternal information from the center of each plot ($n = 3106$ trees; Fig. S1b). The center of the plot was defined as the central 6×6 planting positions in monoculture and 2-species mixtures or the central 12×12 planting positions in 4-, 8-, and 16-species mixtures. The aboveground biomass (kg) of individual trees was calculated using the equation $H \times BA \times CF$, in which CF is a function of basal area and height and a correction factor for stem shape and wood density specific for the BEF-China experiment (same for all species to avoid circularity when testing species effects). More details about the biomass equation can be found in Huang *et al.* (2018). To correct for the different initial sizes of saplings, we considered their biomass in 2012 as the initial size (following planting in 2010). We calculated the cumulative aboveground biomass (BA) from 2012 to 2021 as aboveground biomass 2021–aboveground biomass 2012 for all 13 435 trees with maternal information across entire plots and from 2012 to 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, and 2021 for the subset of 3106 trees from the plot center; for example, cumulative aboveground biomass 2013 = aboveground biomass 2013–aboveground biomass 2012, cumulative aboveground biomass 2014 = aboveground biomass 2014 – aboveground biomass 2012. In 2016, due to budget limitations, only 6×6 trees were measured across all the species richness plots, resulting in missing values in 2016 for the central plot dataset. Missing tree diameter and height values in 2016 were imputed using the method from Schnabel *et al.* (2021). For this, we established a model of the rate of yearly growth changes from 2015 to 2017 using the trees with complete data. Then, for the trees with missing data, a tree diameter or height in 2016 was imputed as $(v2017 - v2015) \times r2016 + v2015$, where v is the tree diameter or height measured in that year, and r is the rate of change (see Schnabel *et al.*, 2021 for details).

Statistical analyses

We carried out all analyses with the statistical software R v.4.0.5 (www.r-project.org). All generalized linear mixed models (GLMMs) and linear mixed models (LMMs) were conducted using the R package 'ASREML' (v.4.2.0; Butler, 2021) unless otherwise specified.

First, before analyzing the effects of seed-family identity on tree cumulative biomass, we calculated the survival rate for each species from 2012 to 2021. If different seed families had differential survival responses to the species richness gradient, the orthogonality between the terms seed-family identity and species richness would be reduced. To test whether this was the case, we used a GLMM with a complementary log–log link function (cloglog) and binomial distribution (Liu *et al.*, 2022). The survival was presented by binary individual data in 2021 compared with 2012 (1 for survival, 0 for death, $n = 15\,637$ trees). Species richness was $\log_2$-transformed to linearize richness–survivorship relationships (see next paragraph). To explain variation in the dependent variable tree survival, we sequentially fitted species identity (SP), seed-family identity (SF), $\log_2$-transformed species richness (logSR), the interaction between species richness and species identity within species (logSR × SP), and the interaction between species richness and seed-family identity (logSR × SF) as fixed-effects explanatory terms. Plot was included as a random-effects term in the model (plot):

$$\text{Survival}_{ij} \sim \text{Binomial}\left(n_{ij}, \pi_{ij}\right)$$

where Survival_{ij} is the survival for the individual j in plot i and π_{ij} is the probability of survival.

$$\begin{aligned}\text{cloglog}\left(\pi_{ij}\right) \sim\ & \beta_0 + \beta_1 \text{SP}_{ij} + \beta_2 \text{SF}_{ij} + \beta_3 \text{logSR}_i \\ & + \beta_4\left(\text{logSR}_i \times \text{SP}_{ij}\right) + \beta_5\left(\text{logSR}_i \times \text{SF}_{ij}\right) \\ & + u_{\text{plot}_i},\ n = 15637\end{aligned}$$

where β_0 is the intercept, $\beta_1 \text{SP}_{ij}$ is the fixed effect of species identity for individual j in plot i, $\beta_2 \text{SF}_{ij}$ is the fixed effect of seed-family identity for individual j in plot i, $\beta_3 \text{logSR}_i$ is the fixed effect species richness in plot i, $\beta_4(\text{logSR}_i \times \text{SP}_{ij})$ is the

interaction between species richness and species identity for individual j in plot i, $\beta_5(\log SR_i \times SF_{ij})$ is the interaction between species richness and seed-family identity for individual j in plot i, u_{plot_i} is the random effect of plot i and $u_{plot_i} \sim N(0, \sigma_u^2)$. Additionally, to test for biased survival of individuals with different growth, we fitted tree survival against tree cumulative biomass using the function 'lm' in R:

$$Survival_{mean_i} \sim \beta_0 + \beta_1 BM_{mean_i} + \beta_2 SP_i + \beta_3(BM_{mean_i} \times SP_i) + \epsilon_i, n = 180$$

where $Survival_{mean_i}$ is the mean survival rate from 2012 to 2021 of seed family i within each species, β_0 is the intercept, $\beta_1 BM_{mean_i}$ is the fixed effect of mean cumulative biomass from 2012 to 2021 of seed family i, $\beta_2 SP_i$ is the fixed effect of species identity of seed family i, and $\beta_3(BM_{mean_i} \times SP_i)$ is the interaction between mean cumulative biomass and species identity for seed family i.

Second, by using tree cumulative aboveground biomass (BM) from 2012 to 2021 of the 13 435 trees that survived until 2021, we estimated the overall effects of species and seed-family identity on tree individual growth. Species richness was $\log_2$-transformed to linearize species richness–biomass relationships. This is commonly done in biodiversity experiments (see e.g. Schmid *et al.*, 2009; Weisser *et al.*, 2017; Huang *et al.*, 2018) because adding a single species to a community with low species richness is expected to have a larger effect on richness–biomass relationships than adding the same species to a community with high species richness. In an LMM, species identity (SP), seed-family identity (SF), $\log_2$-transformed species richness (logSR), the interaction between species richness and species identity within species (logSR × SP), and the interaction between species richness and seed-family identity (logSR × SF) were sequentially fitted as fixed-effect terms and plot as the random-effects term:

$$BM_{ij} \sim \beta_0 + \beta_1 SP_{ij} + \beta_2 SF_{ij} + \beta_3 \log SR_i + \beta_4(\log SR_i \times SP_{ij}) + \beta_5(\log SR_i \times SF_{ij}) + u_{plot_i} + \epsilon_{ij}, n = 13\,435$$

where BM_{ij} is the cumulative biomass from 2012 to 2021 of individual j in plot i, β_0 is the intercept, $\beta_1 SP_{ij}$ is the fixed effect of species identity for individual j in plot i, $\beta_2 SF_{ij}$ is the fixed effect of seed-family identity for individual j in plot i, $\beta_3 \log SR_i$ is the fixed effect species richness in plot i, $\beta_4(\log SR_i \times SP_{ij})$ is the interaction between species richness and species identity for individual j in plot i, $\beta_5(\log SR_i \times SF_{ij})$ is the interaction between species richness and seed-family identity for individual j in plot i, u_{plot_i} is the random effect of plot i, and ϵ_{ij} is the residual error term for individual j in plot i.

To assess the effects of this and subsequent LMMs, we extracted slopes and their SE for terms including species richness and variance components for terms including seed-family identity. Following the fitting of an LMM, we then used analysis of variance (ANOVA) to assess the significance of these model parameters and used the percentage of sum of squares (% SS) contributed by a term to the total sum of squares of the model as a measure of effect size (Rosenthal & Rosnow, 1985). % SS are increments of multiple R^2 (times 100) as terms are added to the statistical model.

Third, to test our first hypothesis (H1 in Fig. 1c), we plotted the growth reaction norms (Stearns & Koella, 1986) of the different seed families for each species along the species richness gradient and fitted the following LMM for each species separately:

$$BM_{ij} \sim \beta_0 + \beta_1 SF_{ij} + \beta_2 \log SR_i + \beta_3(\log SR_i \times SF_{ij}) + \epsilon_{plot_i} + \epsilon_{plot_i \times SF_{ij}} + \epsilon_{ij}$$

where BM_{ij} is cumulative biomass from 2012 to 2021 of individual j in plot i of a given species (the number of replicate individuals per species is shown in Table 1), β_0 is the intercept, $\beta_1 SF_{ij}$ is the fixed effect of seed-family identity for individual j in plot i, $\beta_2 \log SR_i$ is the fixed effect species richness in plot i, $\beta_3(\log SR_i \times SF_{ij})$ is the interaction between species richness and seed-family identity for individual j in plot i, ϵ_{plot_i} and $\epsilon_{plot_i \times SF_{ij}}$ are errors of plot and the interaction between plot i and seed family for individual j in plot i to test the significance of previous terms in the same way as in ordinary mixed models (Schmid *et al.*, 2017; see Table S2), and ϵ_{ij} is the residual error term for individual j in plot i.

Fourth, to test our second hypothesis (H2 in Fig. 1d), we estimated between- (V_{SF}) and within-seed family (V_{within}) variance components by fitting LMMs without fixed-effect terms for each species in each plot. The dependent variable was the cumulative biomass from 2012 to 2021 of the 13 435 trees surviving until 2021. V_{SF} could be estimated as negative due to too few seed families or too few trees for a given species in a plot, but such negative values cannot be meaningfully interpreted. We therefore only kept the variance components ≥ 0, and data from plots with more than two seed families and > 10 individuals per species for further analysis. We used the estimated variance components to calculate intraclass correlation coefficients ($ICC = V_{SF}/(V_{SF} + V_{within})$) as heritability measures. The ICC is related to broad sense heritability and can range from 0 to 1, with 0 indicating that seed-family identity has no influence at all on variation in tree cumulative biomass and 1 indicating that all variation in tree cumulative biomass is explained by seed-family identity. To obtain broad-sense heritability estimates, it would be possible to divide ICC values by the relatedness among seed-family members (from 1 for fully inbred seed families to 0.5 for perfect full-sibs to 0.25 for perfect half-sibs; see for example Falconer, 1989), but because our genomic data were insufficient to derive relatedness for all seed families, we did not convert ICC values to actual (broad-sense) heritability values. The estimated variance components and ICC values (each with $n = 133$) were then used as response variables in new LMMs with the fixed-effects terms species identity (SP), species richness (logSR), and interaction species richness × species identity (logSR × SP) and the random-effects term plot. To obtain normally distributed

residuals in this analysis, ICCs and variance components were square-root transformed (variances representing squared items). The following LMMs were fitted ($n = 133$):

$$V_{\mathrm{SF}_{ij}} \sim \beta_0 + \beta_1 \mathrm{SP}_j + \beta_2 \mathrm{logSR}_i + \beta_3 \left(\mathrm{logSR}_i \times \mathrm{SP}_j\right) + u_{\mathrm{plot}_i} + \epsilon_{ij}$$

$$V_{\mathrm{within}_{ij}} \sim \beta_0 + \beta_1 \mathrm{SP}_j + \beta_2 \mathrm{logSR}_i + \beta_3 \left(\mathrm{logSR}_i \times \mathrm{SP}_j\right) + u_{\mathrm{plot}_i} + \epsilon_{ij}$$

$$\mathrm{ICC}_{ij} \sim \beta_0 + \beta_1 \mathrm{SP}_j + \beta_2 \mathrm{logSR}_i + \beta_3 \left(\mathrm{logSR}_i \times \mathrm{SP}_j\right) + u_{\mathrm{plot}_i} + \epsilon_{ij}$$

where $V_{\mathrm{SF}_{ij}}$, $V_{\mathrm{within}_{ij}}$, and ICC_{ij} are between-seed family variance component, within-seed family variance component, and ICC of species j, respectively, in plot i, β_0 is the intercept, $\beta_1 \mathrm{SP}_j$ is the fixed effect of species j, $\beta_2 \mathrm{logSR}_i$ is the fixed effect species richness in plot i, $\beta_3(\mathrm{logSR}_i \times \mathrm{SP}_j)$ is the interaction between species richness in plot i and species j, u_{plot_i} is the random effect of plot i, and ϵ_{ij} is the residual error term for species j in plot i.

Fifth, to test our third hypothesis (H3 in Fig. 1d), we used the yearly cumulative biomass data from 2012 to 2013, …, 2020 to 2021 of the 3106 central trees to examine how the contributions to growth variation of seed-family identity and its interaction with species richness changed with stand age. In linear models, we used the 'lm' function in R to sequentially fit species identity (SP), seed-family identity within species (SF), and $\log_2$-transformed species richness (logSR), the interaction between species richness and species identity (logSR × SP), and the interaction between species richness and seed-family identity (logSR × SF) to tree cumulative aboveground biomass:

$$\mathrm{BM}_i \sim \beta_0 + \beta_1 \mathrm{SP}_i + \beta_2 \mathrm{SF}_i + \beta_3 \mathrm{logSR}_i + \beta_4 \left(\mathrm{logSR}_i \times \mathrm{SP}_i\right) + \beta_5 \left(\mathrm{logSR}_i \times \mathrm{SF}_i\right) + \epsilon_i, n = 3106$$

where BM_i is the cumulative biomass of individual i in a given year, β_0 is the intercept, $\beta_1 \mathrm{SP}_i$ is the fixed effect of species identity of individual i, $\beta_2 \mathrm{SF}_i$ is the fixed effect of seed-family identity of individual i, $\beta_3 \mathrm{logSR}_i$ is the fixed effect of species richness of the plot where individual i is located, $\beta_4(\mathrm{logSR}_i \times \mathrm{SP}_i)$ is the interaction between species richness and species identity for individual i, and $\beta_5(\mathrm{logSR}_i \times \mathrm{SF}_i)$ is the interaction between species richness and seed-family identity for individual i. We used the 'aov' function in R to fit this linear model, calculate ANOVA tables, and extract % SS values from these linear models. We then used these yearly effect-size measures (growth variation explained by SP, SF, logSR, logSR × SP, and logSR × SF) as new dependent variables in simple linear models ('lm' function in R). For growth variation explained by SP and SF, we fitted models using stand age and quadratic stand age as explanatory variables. The inclusion of the quadratic term accounts for the nonlinearity of age effects and improved model fit compared to using stand age alone ($\Delta\mathrm{AIC} > 2$):

$$\text{Sum-of-squares}_i \sim \beta_0 + \beta_1 \text{Stand-age}_i + \beta_2 \text{Stand-age}_i^2 + \epsilon_i, n = 9$$

For growth variation explained by logSR, logSR × SP, and logSR × SF, we only used stand age as an explanatory variable because adding a quadratic age term did not improve the model fits ($\Delta\mathrm{AIC} < 2$):

$$\text{Sum-of-squares}_i \sim \beta_0 + \beta_1 \text{Stand-age}_i + \epsilon_i, n = 9$$

where Sum-of-squares_i indicates the sum square of SP, SF, logSR, logSR × SP, or logSR × SF at the stand age i, β_0 is the intercept, $\beta_1 \text{Stand-age}_i$ is the fixed effect of stand age i, and $\beta_2 \text{Stand-age}_i^2$ is the fixed effect of quadratic stand age i.

Results

Seed family as a proxy for genetic identity

Based on 673 genotyped trees, for seven out of the eight species in our experiment, the genetic distances among seed families were significantly larger than those within seed families (Table 1). The only species in which distances between individuals of different families were similar to distances between individuals of the same family was *Castanopsis eyrei*, perhaps due to a high outcrossing rate (Table 1).

Similar survival responses of seed families within species to species richness

Of the 15 637 trees with known seed-family identity, 13 435 survived from 2012 to 2021. Survival rates differed among species and among seed families within species and increased with stand species richness, but the species × species richness and seed family × species richness interactions on survival were not significant (Table S3). The survival of five species increased and that of three species decreased with species richness. These results indicated that differences in individual tree growth presented in the following sections were not confounded by differential survival among seed families along the species richness gradient; that is, the orthogonality between the terms seed-family identity and stand species richness was maintained over the 9-yr observation period. There was no relationship between the mean survival rate and the mean growth of each seed family of the eight species (Fig. S2), suggesting that there was biased survival between seed families with different growth potentials.

Differential growth responses of seed families within species to species richness (H1)

In the 13 435 surviving trees, species identity ($P < 0.001$, SS = 12.8%), seed-family identity ($P < 0.001$, SS = 4.43%), and

species richness ($P = 0.002$, SS = 1.11%) all had significant main effects (Table 2) on 9-yr tree biomass accumulated from 2012 to 2021. In addition, interactions between species identity and seed-family identity with species richness on tree cumulative aboveground biomass were also significant ($P < 0.001$, SS = 1.09% and $P < 0.001$, SS = 2.03%, respectively; Table 2), indicating significant variation in reaction norms along the species-richness gradient among species and within species among seed families. Cumulative biomass responded positively to species richness in all of the eight test species, with slopes ranging from 0.03 ± 0.19 to 5.32 ± 0.47 (Table 2, lower part).

When tested separately, we found that within each species the growth of some seed families showed a negative response to species richness, while that of others showed a positive response (Fig. 2). Testing each species separately has lower statistical power than the combined analysis presented in Table 2. In the separate tests, all eight species showed strong variation in mean growth between seed families (Table S2). In two of the species, *Castanopsis eyrie* ($P = 0.019$) and *Castanopsis fargesii* ($P < 0.001$), the overall positive reaction norms at the species level along species richness were still significant and in three of them, *Alniphyllum fortunei* ($P < 0.001$), *C. fargesii* ($P = 0.001$), and *Lithocarpus glaber* ($P = 0.024$), these reaction norms still differed significantly between seed families.

Increasing contribution of seed-family identity to growth variation with increasing species richness (H2)

Overall, based on the 13 435 surviving trees, the variance component of seed-family identity increased with species richness ($\beta = 0.79 \pm 0.34$, $P = 0.017$; Fig. 3a), but the mean and slopes significantly differed among the eight species ($P < 0.001$). The variance component of the residuals, that is effects of remaining genetic variation within seed families and environmental variation within plots, strongly differed among species ($P < 0.001$; Fig. 3b) but increased only marginally with species richness ($\beta = 0.76 \pm 0.44$, $P = 0.070$; Fig. 3b). The ICC was used to indicate heritability in our study, which ranged from 0 to 0.769 across all species and plots. The ICC increased with increasing species richness for all studied species ($\beta = 0.06 \pm 0.01$, $P < 0.001$; Fig. 3c).

Increasing contribution of seed-family identity and its interaction with species richness on growth variation with increasing stand age (H3)

Based on the 3106 trees in the plot center, we found that although species identity explained the greatest variation in tree cumulative aboveground biomass (ranging from 16.0 to 23.2%),

Table 2 Overall effects of species identity (SP), seed-family identity (SF) within species, species richness (logSR), and their interactions on tree growth from 2012 to 2021, and slopes of species richness–tree growth relations for the eight test species.

Overall effects

Terms	df	dendf	*F* value	*P* value	SS%
SP	7	10137.8	260.2	< **0.001**	12.8
SF (within species)	171	13021.7	2.779	< **0.001**	4.43
logSR	1	121.1	6.587	**0.002**	1.11
SP × logSR	7	2500.9	7.924	< **0.001**	1.09
SF (within species) × logSR	164	13037.7	1.556	< **0.001**	2.03

Means and slopes (for each doubling of species richness) for each species

Species	# sf	# indiv	BM ± SE	$\beta \pm$ SE
Alniphyllum fortunei	22	2924	20.51 ± 0.34	2.55 ± 0.30
Castanopsis eyrei	14	1205	18.72 ± 0.46	3.16 ± 0.48
Castanopsis fargesii	27	2031	26.91 ± 0.56	5.32 ± 0.47
Castanopsis sclerophylla	20	1987	6.980 ± 0.22	0.33 ± 0.19
Camphora officinarum	14	1401	13.23 ± 0.43	0.75 ± 0.38
Quercus glauca	18	876	7.310 ± 0.27	0.03 ± 0.19
Daphniphyllum oldhamii	26	773	21.20 ± 0.46	0.64 ± 0.41
Lithocarpus glaber	38	2238	15.80 ± 0.30	0.93 ± 0.28
Overall	179	13 435	16.95 ± 0.16	0.77 ± 0.13

logSR, $\log_2$-transformed species richness; SF × logSR, interaction between seed-family identity and $\log_2$-transformed species richness; SF, seed-family identity; SP × logSR, interaction between species identity and $\log_2$-transformed species richness; SP, species identity. Fixed effects were fitted sequentially (type I ANOVA) as shown in the table and 'plot' was used as a random effects term. df, numerator degrees of freedom; dendf, denominator degrees of freedom. F value and *P* value indicate *F* ratios and the *P* values of the significance tests, respectively. The bold numbers in '*P* value' indicate $P < 0.05$. % SS, percentage sum of squares, representing the percentage explained variation in the dependent variable, related to increases in multiple R^2 as terms are added to the model. % SS values were extracted from ANOVA tables calculated using simple linear models for the explanatory terms. These species-level parameter estimates were obtained from simple linear regressions of cumulative biomass on species richness per species. #sf, number of seed families, #indiv, number of individuals still alive in 2021, BM ± SE, mean cumulative biomass from 2012 to 2021 (kg) ± SE; $\beta \pm$ SE, slope ± SE against $\log_2$-transformed species richness, that is increase in cumulative biomass (kg) per doubling of species richness.

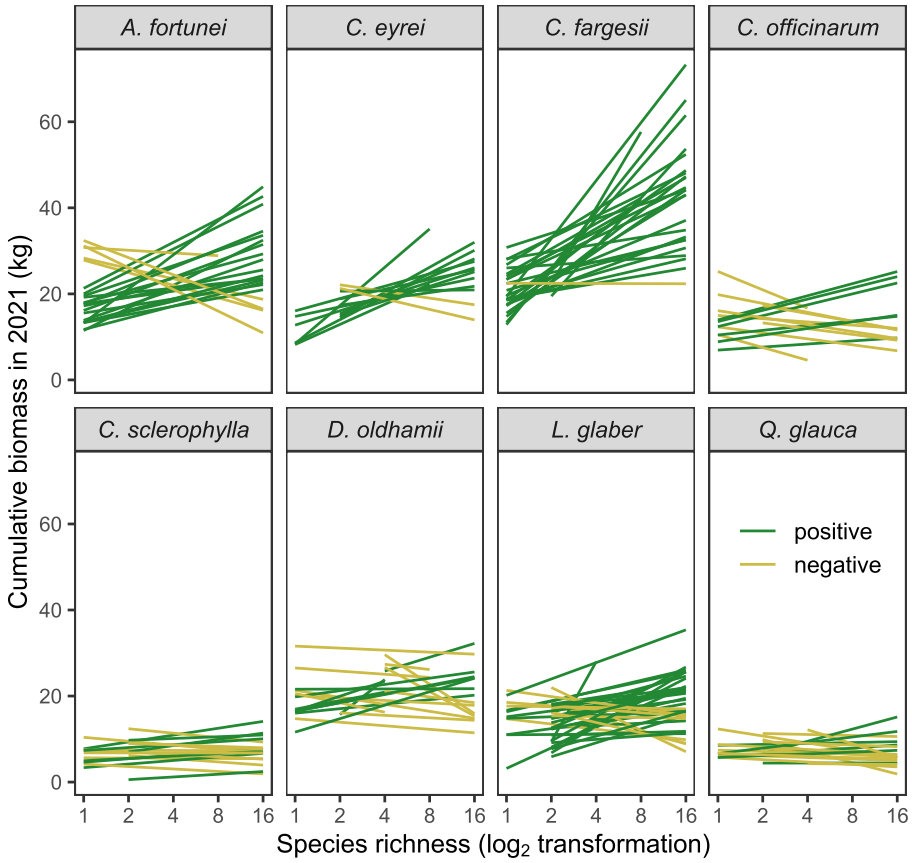

Fig. 2 Growth reaction norms of different seed families along the species-richness gradient in the eight test species. The full species names of the eight species are: *Alniphyllum fortunei*, *Castanopsis eyrei*, *Castanopsis fargesii*, *Camphora officinarum*, *Castanopsis sclerophylla*, *Daphniphyllum oldhamii*, *Lithocarpus glaber* and *Quercus glauca*. The green lines indicate positive responses, and the yellow lines indicate negative responses. Note that the reaction norms vary significantly within species when tested in the overall model presented in Table 2. Separate tests for each species are presented in Supporting Information Table S3.

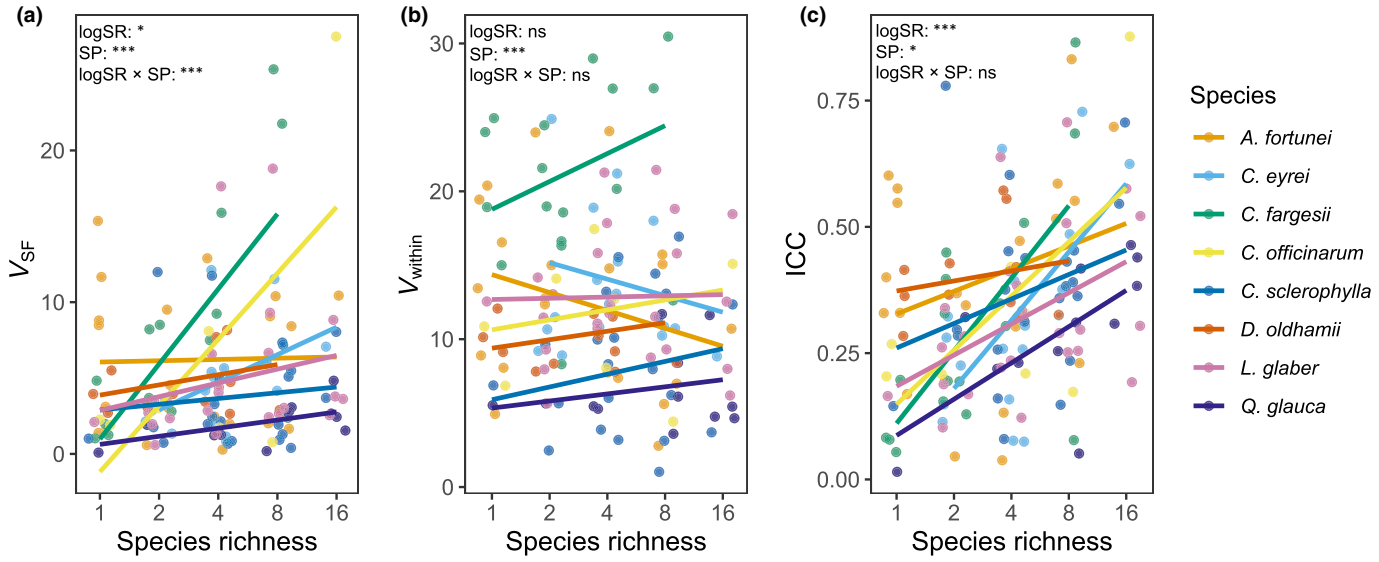

Fig. 3 Between- and within-seed family variance components and the corresponding intraclass correlation coefficient (ICC) as a function of species richness. Positive relationships indicate that the corresponding term has a stronger influence on growth variation in more species-rich communities. (a) Seed-family variance components (V_{SF}) generally increase with species richness. (b) Within-seed family variance components (V_{within}) increase marginally with species richness. (c) Intraclass correlation coefficients (ICC = $V_{SF}/(V_{SF} + V_{within})$, range 0–1) related to within-species growth broad sense heritability generally increase with species richness. Different species are indicated by different colors of data points and regression lines. The full species names of the eight species are: *Alniphyllum fortunei*, *Castanopsis eyrei*, *Castanopsis fargesii*, *Camphora officinarum*, *Castanopsis sclerophylla*, *Daphniphyllum oldhamii*, *Lithocarpus glaber* and *Quercus glauca*. Variance components and ICCs were calculated for each species separately using linear mixed models and then square-root transformed to obtain normally distributed residuals in regression analyses with $\log_2$-transformed species richness (logSR), species identity (SP), and the interaction between these two (SP × logSR) as fixed-effect terms. Their significances are indicated by asterisks in each panel: *, $P < 0.05$; ***, $P < 0.001$; ns, $P \geq 0.05$. Regarding the absolute size of the variance components shown in (a, b), see Table 2 (seed-family identity effect size: SS = 4.43%, $P < 0.001$) and the similar size of seed-family and residual variance components.

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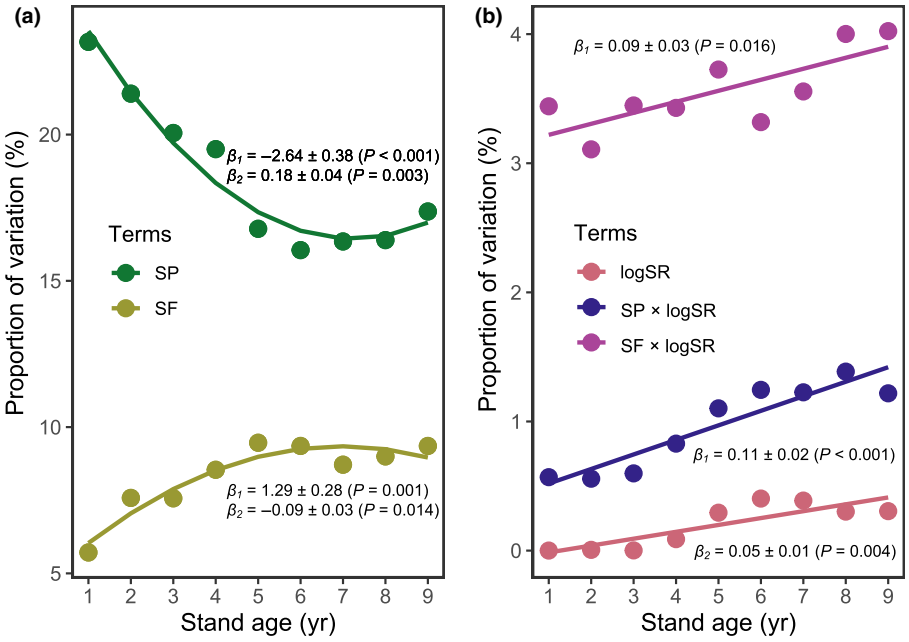

Fig. 4 The relative variation (percentage sum of squares as the effect-size measure) of tree growth is explained by the explanatory terms as a function of stand age. (a) Explanatory terms species identity (SP) and seed-family identity (SF) were modeled with stand age and quadratic stand age, resulting in a better model fit compared to using stand age alone ($\Delta AIC > 2$). (b) Explanatory terms $\log_2$-transformed species richness (logSR), interaction between species identity and $\log_2$-transformed species richness (SP × logSR), and interaction between seed-family identity and $\log_2$-transformed species richness (SF × logSR) were modeled with stand age alone, because adding the quadratic stand age did not improve the model fit ($\Delta AIC \leq 2$). The estimated effect sizes (slopes) of stand age, the quadratic stand age (if applicable), and their SEs ($\beta_1 \pm SE$ and $\beta_2 \pm SE$, respectively), together with the corresponding P values (P), are listed next to each line.

seed-family identity within species also explained a substantial part of this variation (ranging from 5.7 to 9.5%; Fig. 4a). With increasing stand age, the contribution of seed-family identity ($P < 0.001$; Fig. 4a) increased significantly, while the contribution of species identity decreased significantly ($P = 0.001$; Fig. 4a). After 6 yr of age, the contributions of both species identity and seed-family identity stabilized (Fig. 4a). Additionally, the contributions of species richness and the interactions between species richness with species identity, as well as seed-family identity with species richness ($P = 0.016$; Fig. 4b) increased significantly over stand age during the whole 9-yr observation period ($P = 0.004$ and $P < 0.001$, respectively; Fig. 4b).

Discussion

In our study, we used seed-family identity as a proxy for genetic identity in a large-scale forest biodiversity experiment to investigate the impact of genetic identity on tree growth in diverse forests. As predicted, the growth of genetically different trees responded variably to increasing species richness (H1). This finding suggests that artificial selection of seed families can be used to create stands of either monoculture-preferring or mixture-preferring trees in afforestation projects, thereby enhancing ecosystem function (e.g. productivity) at a given species richness level. Furthermore, we observed that while genetic variation increased strongly with species richness, residual variation only increased marginally, leading to a greater contribution of seed-family identity to individual tree growth variation in more species-rich stands (H2). This implies that species-diverse communities enable trees to increase their capacity to achieve the inherited maximum growth-related trait expression, likely due to less stressful competitive environments created by species with different niches. Finally, over 9 yr of forest development, the proportion of tree growth variation explained by seed-family identity within species and its interaction with species richness continually increased (H3). This indicates that genetic differences in growth expression accumulate with stand age, and the importance of intraspecific variation increases over the ontogeny process. Therefore, genetic identity should be considered in afforestation projects aiming for long-term productivity goals.

Maintaining orthogonality between the terms 'seed-family identity' and 'species richness' ensures that the subsequent analysis of the effects of seed family and species richness on tree growth is not confounded by variation in survival rates. Additionally, the survival rate differed among species and among seed families within species and increased with stand species richness. This finding is consistent with previous survival studies across species richness gradients in the same experiment (Liu *et al.*, 2022), which related the differing survival rates among 39 species (including those used in the present study)—and their responses to species richness—to variation in species traits.

Our findings that some seed families responded positively to increased species richness and others had less positive or even negative responses reflect the strong interactions between seed-family identity and community species richness. Our results extend knowledge from previous studies in a grassland biodiversity experiment (the Jena Experiment), which have found that species-rich communities can select mixture-preferring genotypes over multiple generations (Zuppinger-Dingley *et al.*, 2014; van Moorsel *et al.*, 2019). Seed families that show a positive response to species richness may benefit from a species-diverse environment, as these communities are likely to have species occupying different niches, thereby providing a less competitive environment (Kunstler *et al.*, 2016; Fichtner *et al.*, 2018). Conversely, seed families with a less positive or even negative response to species richness may benefit from cooperative interactions with genetically similar neighbors, for example through kin recognition (Dudley *et al.*, 2013; Anten & Chen, 2021) or shared

beneficial microbes resulting in positive plant–soil feedbacks (Zuppinger-Dingley *et al.*, 2016). Standing genetic variation in response to species richness within tree populations may have arisen and been maintained due to genetic random drift or diversifying selection in space and time, favoring positive responses at places and times with high species richness and the opposite at places and times with low richness, for example in monoculture patches (Zuppinger-Dingley *et al.*, 2014). Furthermore, our main finding of crossing reaction norms of seed families along the tree species richness gradient implies that different seed families should be used when high-diversity stands are planted than when monocultures are planted. In other words, across the species tested, seed families that would perform best in monoculture plantations are generally not those that would perform best in mixture plantations. Therefore, when planning afforestation with diverse species mixtures, we recommend using members of seed families with high growth performance in mixtures. Matching specific genetic identities to targeted growth conditions has been regularly applied in crops (reviewed by Elias *et al.*, 2016) or commercial forests (reviewed by Silvertown, 2004) to promote the health, production, and quality of managed ecosystems. With growing interest in managing species richness for afforestation, our study suggests that the establishment success and ecosystem functions of forest stands can be increased by matching seed-family identity with specific species richness environments in afforestation projects.

Tree growth heritability as measured by the ICC increased with species richness of the stand because the increase in the variation among seed families was larger than the corresponding increase in the variation within seed families across species richness. The marginal increase in within-family variation with stand richness indicates that more species-diverse communities may expose trees to a more heterogeneous environment. The increase in the contribution of seed-family identity to growth variation across species richness indicates that compared with less species-diverse communities, more species-diverse communities may provide more opportunities for trees to express trait variation underpinned by genetic variation. In high-diversity communities, plant–plant interactions among trees with different niches are expected to reduce competition and provide a less stressful biotic environment (Silvertown, 2004; Fichtner *et al.*, 2018). Our findings are consistent with previous findings that the contribution of genetic identity to phenotypic variation is higher in less stressful environments (Hoffmann & Merilä, 1999; Merilä & Sheldon, 2001; Shama *et al.*, 2011). Additionally, given that tree growth significantly affects reproductive success (Roff., 2000; Avanzi *et al.*, 2020), our findings suggest that in the long term, the higher growth heritability in species-rich stands may lead to stronger natural selection within species compared to species-poor stands. We suggest that considering the genetic identity of planted trees is particularly important when species-rich stands are designed in afforestation projects.

At the early stage (before age 6), the increasing effect size with stand age of seed-family identity and its interaction with species richness may result from the genetic regulation and the continuous interaction between genetic variation and species richness through ontogeny (reviewed by Barton, 2024; Lawrence-Paul & Lasky, 2024). This enhanced effect of seed-family identity, along with environmental factors such as species richness tested in this study, increasingly masks the relative variation among species, making different species' mean biomass more similar as the stand ages. Initially, trees from different species may exhibit distinct growth patterns due to their species-specific characteristics. However, as trees grow larger and the canopy closes, interspecific interactions become more intense, leading to convergence in height in response to light competition (Tilman, 1982; Novoplansky, 2009; Williams *et al.*, 2017). Moreover, increased interspecific resource-use complementarity as stands age has been observed in the present experiment by Huang *et al.* (2018), and this can contribute to a more balanced utilization of available resources, thereby promoting coexistence and equalizing growth among species. From around stand age 6 yr onward, the effects of seed-family identity and species identity developed in parallel, suggesting that the equalization of species-specific growth may stabilize once the tree canopy closes. This stabilization may arise from convergent allometric allocation patterns of biomass to stems and other organs among different species during ontogenetic development (Müller *et al.*, 2000). As the plants mature, environmental factors and the interactions between genetic identity and the environment continue to play important roles in plant growth. This is further supported by our observations that the effects of community species richness, along with the interactions of species identity and seed-family identity with species richness, persistently increase with stand age, even after 6 yr (Fig. 4b). Our study indicates the increasing importance of intraspecific variation with stand age, which is consistent with other studies that found that within-species trait variation can be comparable in magnitude to variation among species (Siefert *et al.*, 2015) and can substantially contribute to ecological responses such as biomass production (Zeng *et al.*, 2017; Des Roches *et al.*, 2018). However, most of these previous studies quantifying intraspecific variation have been conducted at specific developmental stages, whereas our study suggests that considering stand age is crucial for understanding the contribution of genetic variation to variation in plant performance. Our findings provide evidence that, from a long-term perspective, it is even more important to consider genetic identity across species richness gradients in afforestation projects.

Although the magnitude of intraspecific variation – due to underpinning genetic and environmental variation and the interaction between the two – has been found to be comparable to interspecific variation in many traits and functions (Des Roches *et al.*, 2018), how genetic identity affects tree growth along species richness gradients has rarely been studied. We showed that different seed families responded differently to species richness. Without relying on natural selection, these reaction norms of seed families across species richness can guide artificial selection to further enhance the performance of planted mixed forests. Additionally, we found that seed-family identity explained a substantial proportion of variation in tree aboveground growth, and this proportion increased with species richness and stand age. Given the crucial roles of afforestation in bending the curve of forest loss and maintaining forest ecosystem functions (Bastin

et al., 2019; Chazdon & Brancalion, 2019), our study emphasizes the need to consider the genetic identity of planted trees and their expected biodiversity-specific performance to increase forest establishment success and desired ecosystem functions in long-term afforestation projects.

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Competing interests

None declared.

Author contributions

XL, BS and KM conceptualized the study. SL, GvO, WD and XL performed the investigation. TT, BS, MCS, FJB, SZ and XL contributed to the formal analysis. TT, BS, MCS and XL wrote the original draft. TT, BS, MCS, FJB, YL, SJvM, HB, KM and XL contributed to reviewing and editing the manuscript.

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Data availability

The data and R script in the analyses are available at the Dryad portal (https://datadryad.org/stash/share/Ol5Ia4BJxM12ElyRPXJDVRNga8J0V4U0If1CMCulap8). DNA sequences used in this study have been deposited in the NCBI database (accession no. PRJNA1013695).

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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 The distribution and the number of trees with maternal information within the experimental site and in an example plot.

Fig. S2 Regressions of mean cumulative biomass on mean survival rate per seed family for the eight test species from 2012 to 2021.

Methods S1 DNA extraction protocol.

Methods S2 GBS library preparation.

Table S1 Restriction enzymes used to digest the genomic DNA of the eight species.

Table S2 Summary of linear mixed models of the effects of seed-family identity, species richness, and their interactions on tree cumulative biomass for the eight tree species in 2021.

Table S3 Overall effects of species identity, seed-family identity within species, species richness, and their interactions on tree survival from 2012 to 2021, and slopes of species richness–tree growth relations for the eight test species.

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