1 Strong positive biodiversity–productivity relationships in a subtropical forest 2 experiment

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147 **Forest ecosystems contribute substantially to global terrestrial primary**
148 **productivity and climate regulation, but, in contrast to grasslands, experimental**
149 **evidence for a positive biodiversity–productivity relationship in highly diverse**
150 **forests is still lacking¹. Here, we provide such evidence from a large forest**
151 **biodiversity experiment with a novel design² in subtropical China. Productivity**
152 **(stand-level tree basal area, aboveground volume and carbon and their annual**
153 **increment) increased linearly with the logarithm of tree species richness.**
154 **Additive partitioning³ showed that increasing positive complementarity effects**
155 **combined with weakening negative selection effects caused a strengthening of the**
156 **relationship over time. In 2-species mixed stands, complementary effects**
157 **increased with functional distance and selection effects with vertical crown**
158 **dissimilarity between species. Understorey shrubs reduced stand-level tree**
159 **productivity, but this effect of competition was attenuated by shrub species**
160 **richness, indicating that a diverse understorey may facilitate overall ecosystem**
161 **functioning. Identical biodiversity–productivity relationships were found in plots**
162 **of different size, suggesting that extrapolation to larger scales is possible. Our**
163 **results highlight the potential of multi-species afforestation strategies to**
164 **simultaneously contribute to mitigation of climate change and biodiversity**
165 **restoration.**

166 Forest ecosystems harbor around two thirds of all terrestrial plant species, but
167 currently lose biodiversity at high rates which may threaten the production of timber,
168 fiber, fuel and other services beneficial to humans⁴. Observational studies suggest that
169 species-rich forests exceed the productivity of less diverse forests^{5,6}, but co-varying
170 factors (e.g. spatial heterogeneity in abiotic environment, species composition and
171 successional stages; interventions by forest management) make assigning causation

difficult. Systematic experimental manipulations of plant species composition in grassland communities⁷⁻⁹ have demonstrated that plant diversity promotes community productivity. This effect has been attributed to positive effects of niche partitioning between species, specifically to complementarity in the use of abiotic resources¹⁰ or interactions with enemies¹¹, or to an increasing contribution of highly productive species in more diverse communities¹². These two types of mechanisms have been related to statistical complementarity and selection effects obtained by additive partitioning³. However, these mechanisms may differ in species-rich forests in which neutral processes may be important^{13,14} and where “diffuse” coevolution may result in niche convergence toward generalist strategies¹⁵. Furthermore, trees have large and persistent vertical structures that support the long-term accumulation of biomass. Several forest experiments have recently been initiated^{16,17}, but these are mainly in the temperate zone or implemented in small plots with a limited species richness gradients¹⁸⁻²³. To close these critical gaps in knowledge¹, controlled experiments in which the diversity of tree species is systematically manipulated are needed. The largest such study concerning numbers of treatments and plots has been established in 2009/2010 in subtropical south-east China and is referred to as the BEF-China experiment².

Here, we report how stand-level productivity in the BEF-China experiment 3–7 years after planting was related to species richness and how variation within species-richness levels was related to trait differences among species. Experimental forest communities were constructed systematically from a pool of 40 tree (Extended Data Table 1) and 20 shrub species, and were established in plots at two hilly sites (in 2009 at site A and in 2010 at site B). By the time of our later measurements the tree communities were well established with some canopies exceeding 12 m in height in

2016. The design of previous biodiversity experiments had been criticised because not all species were found at all diversity levels, and because the compositions of the experimental communities that were realized were not nested as would be expected with sequential extinction²⁴. We adopted a novel design that avoided these caveats² (see Methods, Extended Data Fig. 1, Extended Data Table 2). In brief, we first created three pools of 16 species per site. These were then repeatedly split into halves, resulting in nested, non-overlapping subsets of 8, 4, 2 and 1 species. We used these sets, and in addition also the full sets of 24 species per site, to plant tree communities comprising 1 to 24 species. We further established plots with two sizes: 0.067 ha (equivalent to the Chinese area unit of 1 mu; 400 individual trees) and 0.267 ha (4 mu; 1600 individuals). The larger plots were established for one of the three 16-species pools at each site and included a split-plot treatment that consisted of understorey shrubs planted in the centre of the quadrats formed by four neighbouring trees. Shrubs were planted at a species richness of 0 (no shrubs), 2, 4 or 8, in factorial combination with the tree species-richness treatment. We assessed stand-level tree productivity in all 1-mu plots (including all 1-mu subplots of the larger plots) non-destructively by measuring stem basal area and height of the 16 central trees every year from 2013–2016 in September/October. We used these data, together with data from separately harvested trees to obtain conversion factors, to calculate tree volume and aggregated the individual volume data of live trees to the stand level. To characterize annual stand growth, we further derived yearly increments of stand volume from successive inventories. Using the same method, we determined the same metrics at the population-level (stand-level data separated into species).

We found significantly positive effects of the logarithm of tree species richness on both stand volume and annual stand volume increment of trees ($F_{1, 89} = 5.26$, $P =$

0.024 and $F_{1,94} = 9.34$, $P = 0.003$, respectively; Fig. 1 and Extended Data Fig. 2, Table 1). The size of these effects increased over time ($F_{1,95} = 10.83$, $P = 0.001$ and $F_{1,95} = 12.01$, $P < 0.001$, respectively, for interaction species richness $\times$ year). Similar results were obtained for stand basal area and its increment (Extended Data Fig. 3, Table 1). In 2016, at the end of our measuring period, stand basal area increased on average by $1.65 \text{ m}^2 \text{ ha}^{-1}$ and stand volume by $5.09 \text{ m}^3 \text{ ha}^{-1}$ with each doubling of tree species richness. After seven years of growth, the average 16-species mixture stored $22.0 \pm 4.5 \text{ Mg C ha}^{-1}$ above ground, which is double the amount found in monocultures ($9.4 \pm 1.1 \text{ Mg ha}^{-1}$, Extended Data Fig. 4) and similar to the productivity of monocultures of commercial plantation species *Cunninghamia lanceolata* ($22.4 \pm 10.7 \text{ Mg C ha}^{-1}$) and *Pinus massoniana* ($21.0 \pm 3.0 \text{ Mg C ha}^{-1}$) that we had planted for reference at the same site (Extended Data Fig. 4, Extended Data Table 4). System-level C sequestration likely is higher, given that additional C will have been allocated to belowground tree organs²⁵ and in part transferred to persistent soil pools important for long-term carbon sequestration. These strong positive effects of tree species richness were driven by faster growth of live trees in more diverse stands, and were unrelated to tree survival rate, which was independent of species richness; if anything, there was a trend towards lower survival at higher richness (Extended Data Fig. 5).

The net biodiversity effect²⁶ on productivity increased through time for mixtures of all species-richness levels (Fig. 2, $F_{1,48} = 23.61$, $P < 0.001$). The positive effects of tree species richness on productivity were also reflected in a higher frequency of mixtures that overyielded relative to the ones that underyielded and in many cases of transgressive overyielding²⁶ (Extended Data Table 5). Additive partitioning revealed that the increases of net biodiversity effects were primarily driven by increases in complementarity effects (Extended Data Table 6, $F_{1,31} = 9.61$, $P = 0.004$) and

247 weakening negative selection effects (Extended Data Table 6, $F_{1,37} = 4.61$, $P = 0.038$).
 248 In the last year of measurements, selection effects were no longer significantly
 249 different from zero (Fig. 2, $F_{1,31} = 3.40$, $P = 0.075$).

250 We observed considerable variation in overyielding among communities of the
 251 same species-richness level. Some of this variation was explained by functional
 252 diversity but phylogenetic diversity had low explanatory power. For the 48 different
 253 2-species mixtures, complementarity effects were positively correlated with the
 254 functional distance and selection effects with vertical crown dissimilarity, also
 255 referred to as crown complementarity between species (Fig. 3, Extended Data Table
 256 7). That vertical crown complementarity²² contributed to overyielding via selection
 257 rather than complementarity effects indicated that it was due to asymmetric light
 258 competition²⁷ and is consistent with the “competition-trait hierarchy hypothesis”²⁸.

259 Species with high monoculture productivity (Fig. 4a) explained large amounts
 260 of variation in stand-level productivity (Fig. 4b), but their contribution was not always
 261 positive, as demonstrated by several negative species-level selection effects (Fig. 4c).
 262 Despite the positive effect of species richness on community productivity, the
 263 population-level responses of each species to species richness varied from positive to
 264 neutral to negative (Fig. 4d). These responses did not differ between evergreen and
 265 deciduous species (Fig. 4d, $F_{1,159} = 0.89$, $P = 0.347$). A similar decoupling between
 266 community- and population-level responses has previously been reported from
 267 grassland biodiversity experiments⁸ and indicates that a few positive population-level
 268 responses can overcompensate a larger number of negative population-level
 269 responses. Nevertheless, the number of species with positive responses to community
 270 diversity and the magnitude of their responses increased with time (Fig. 4d).

271 Competition by understorey shrubs planted in the gaps between the trees
 272 reduced stand-level tree volume (Extended Data Table 8, $F_{1,234} = 4.80$, $P = 0.029$), but
 273 this effect decreased with shrub species richness (Extended Data Table 8, $F_{1,199} =$
 274 5.40 , $P = 0.022$) and was negligible when mixtures of 8 shrub species were planted
 275 (Extended Data Fig. 6), indicating reduced competition between shrubs and trees at
 276 higher shrub diversity levels. The diversity–productivity relationships we found were
 277 scale-independent, i.e. they did not differ between 1- and 4-mu plots (Extended Data
 278 Table 8, $F_{1,114} = 0.20$, $P = 0.694$ for interaction species richness $\times$ plot size).

279 Our results provide strong evidence for a positive effect of tree species richness
 280 on tree productivity at stand-level in establishing subtropical forest ecosystems, and
 281 support the idea that highly diverse subtropical forest ecosystems are niche-
 282 structured^{22,27}. Seven-year old mixed-species stands can produce an estimated
 283 additional aboveground wood volume of $25 \text{ m}^3 \text{ ha}^{-1}$ relative to the average
 284 monoculture, which translates to the sequestration of approximately an extra 10 Mg C
 285 ha^{-1} (Fig. 1, Extended Data Fig.4). We expect this effect to grow further, given that we
 286 did not observed any signs of a deceleration over the present measurement period.
 287 The size of the biodiversity effects we found for these forests is similar to biodiversity
 288 effects reported from grassland studies^{8,9}. Given that plant biomass is higher in
 289 forests, and that the largest fraction of tree carbon is bound in relatively persistent
 290 woody biomass, these effects translate into significant diversity-mediated rates of
 291 carbon sequestration. Substantial forest areas are managed world-wide, with large
 292 afforestation programs underway in many countries. In China, huge economic efforts
 293 are made for afforestation, with a net growth of total forested area by $1.5 \times 10^6 \text{ ha yr}^{-1}$
 294 achieved from 2010 to 2015²⁹. However, the overwhelming fraction of newly
 295 established forests are monoculture plantations of species with highest productivity in

296 the short term³⁰. Our analysis suggests that a similar productivity could be achieved
 297 with mixed plantations of native species, which would result in co-benefits in the
 298 form of biodiversity management and a likely higher level and stability of ecosystem
 299 services in the longer term.

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301 **Online content** Methods, along with additional Extended Data display items and
 302 Source Data, are available in the online version of the paper; references unique to
 303 these sections appear only in the online paper.

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381

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398 METHODS

399 Study site and experimental design

400 The BEF-China experimental platform was established in Jiangxi Province, China
 401 (29°08'–29°11'N, 117°90'–117°93'E). Climate at the site is subtropical, with mean
 402 annual temperature and precipitation of 16.7°C and 1800 mm, respectively (averaged
 403 from 1971–2000)³¹. A large-scale tree biodiversity experiment was established in
 404 2009–2010 on two sites (A and B) of approximately 20 ha each, with a total of
 405 226'400 individual trees planted. Here, we use all plots in which random species-loss
 406 scenarios were simulated. The species pool contains 40 tree species (Extended Data
 407 Table 1), 24 for each site (of which eight are shared between sites). The 24 species at
 408 each site were divided into three 8-species sets. By combining these 8-species sets in all
 409 possible ways, three pools of 16 species were created. The species in each 16-species
 410 pool were put in random sequence and then repeatedly divided in halves until
 411 monocultures were obtained. This procedure resulted in 70 unique species
 412 compositions per site (Extended Data Table 2) and ensured that each tree species
 413 occurred in equal overall proportion at each diversity level. We further included
 414 monoculture plots with two commercially important tree species, *Pinus massoniana*
 415 and *Cunninghamia lanceolata*, as reference, with 5 replicate plots per species and site.
 416 Each plot was 25.8 × 25.8 m in size and planted with 400 tree individuals arranged on
 417 a rectangular 20 × 20 grid with 1.29 m spacing between rows and columns. To
 418 minimize edge effects, plots were established adjacent to each other, with trees thus
 419 forming a continuous cover across the entire site. Site A was planted in 2009, site B in
 420 2010.

421 Plots of one species pool per site (pools A1 and B1 at sites A and B,
 422 respectively, Extended Table 2) were additionally replicated in plots that were four

423 times larger and thus contained 1600 trees. These large plots were subdivided into
424 four quadrants in which a factorial understorey shrub-diversity treatment was
425 established. These four subplots either had no shrub understorey (0 species), or shrubs
426 planted in all the centers between 4 adjacent trees, at a diversity of 2, 4 or 8 shrub
427 species (Fig. 1a).

428 The design we use here consisted of 140 small plots (1 mu) and 64 large plots
429 (4 mu). Out of this total of 396 1-mu sized (sub)plots, nine had to be excluded
430 because these were not established due to a lack of sapling material or high initial
431 mortality. All plots were weeded annually to remove emerging herbs and woody
432 species that were not part of the planting design.

433

434 **Tree measurements**

435 We assessed stand-level and population-level tree growth by measuring the height of
436 trees and maximum and minimum stem diameter at 5 cm above ground to calculate
437 basal area. We focused on the central $4 \times 4 = 16$ trees of each 1-mu (sub)plot to avoid
438 edge effects. These measurements were repeated annually in September/October from
439 2013 to 2016. We aggregated these tree-level data at the species (i.e. population) and
440 stand level.

441 We further calculated a cylindrical tree volume as the product of basal area and
442 height. The true volume was then obtained by multiplying this proxy with a form
443 factor determined by a complete harvest of 154 trees in natural forest near the
444 experimental sites. The total volume of each harvested trees was calculated as ratio of
445 total aboveground dry biomass and average wood density. Similarly, tree biomass was
446 determined by multiplying the cylindrical volume of each experimental tree with a

447 biomass conversion factor determined based on the harvested trees (Extended Data).

448 Biomass was converted to carbon content³² by multiplying with 0.474 g C g⁻¹.

449

450 **Complementarity effect and selection effect**

451 We used the additive partitioning method of Loreau & Hector³ to decompose net

452 biodiversity effects (NEs) of productivity measures into complementarity (CEs) and

453 selection effects (SEs), separately for each year and diversity level. CEs and SEs

454 depend on relative yields of species, which we calculated using monoculture biomass

455 as denominator. If a species failed to establish in monoculture (which was the case for

456 *Meliosma flexuosa*, *Castanopsis eyrei* and *Machilus grijsii*), or had a mortality

457 exceeding 80% (*Quercus phillyreoides*, *Phoebe bournei*), it was excluded from the set

458 of target species in the corresponding mixtures³³. Formally, CEs and SEs are related

459 to (co)variances and therefore were square-root transformed with sign reconstruction

460 $(\text{sign}(y)\sqrt{|y|})$ prior to analysis, which improved the normality of residuals³.

461

462 **Overyielding and underyielding**

463 Overyielding describes the case where the productivity of a mixture exceeds the

464 average productivity of monocultures of component trees²⁶. Conversely,

465 underyielding identifies a lower yield of the mixture relative to monocultures.

466 Transgressive overyielding indicates that the productivity of a mixture exceeds the

467 productivity of the monoculture of the most productive component species.

468 Transgressive underyielding is defined similarly. We determined overyielding and

469 underyielding of all mixtures relative to monocultures. Capitalizing on the nested

470 nature of our design, we further determined the same metrics using the two mixtures

471 with half the set of species as reference, instead of monocultures, i.e. we tested

whether combining communities with two sets of species resulted in a community that produced more or less biomass than expected on the assumption of no interactions among the sets (overyielding) or that community productivity would be determined by the more productive set of species alone (transgressive overyielding).

Vertical crown complementarity

We quantified the interspecific complementarity in vertical crown extent of trees in 2016. The crown extent was determined as interval between the lowest side-branch and the top of a tree in monocultures. These data were averaged across all surviving trees of the 16 central individuals planted in a plot. We then calculated vertical crown complementarity in 2-species mixtures as proportional dissimilarity of the crown extents between the two species:

$$PDS_{A,B} = \frac{x_{A \setminus B} + x_{B \setminus A}}{x_{A \cup B}}$$

where $x_{A \setminus B}$ indicates the vertical extent (in meters) that is occupied by A but not by B (vice versa for $x_{B \setminus A}$), and $x_{A \cup B}$ indicates the extent occupied by at least one of the species. This index is equivalent to one minus the proportional similarity index proposed by Colwell and Futuyma³⁴.

Statistical analysis

We used analysis of variance based on type-I sum of squares linear mixed-effects models to assess the effects of tree species richness (and additional design variables) on productivity³⁵. All analyses were done in R 3.3.2 and ASReml-R³⁶. The models included the fixed effects site, tree species richness (log₂-transformed), year (continuous variable, centered over our observation period), the interaction log₂(tree species richness) × year, and the interaction site × year. Random effects were species

497 composition (with a separate variance component for each site), plot (with a separate
498 variance component for each site), subplot, and the interactions of all these random
499 terms with year. Model residuals were checked for normality and homogeneity of
500 variances.

501 For the analyses of shrub diversity effects, the model contained the additional
502 fixed effects shrub presence (a two-level factor: 0 vs. 2, 4 or 8 shrub species), plot
503 size (a two-level factor: 1 vs. 4 mu), log₂ of shrub species richness (for shrub-species
504 richness >0), and the interactions of all these terms with log₂(tree species richness)
505 and with year. Random effects were species composition (with a separate variance
506 component for each site), plot (with a separate variance component for each site),
507 subplot, and the interactions of all these random terms with year (Extended Data
508 Table 6). The interaction of year and site and the site-specific variance terms
509 estimated for some random terms accounted for the fact that site B was established
510 one year after site A and that trees at site B were therefore smaller.

511

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529

530 **Data availability statement**

531 The data supporting the findings of this study will be deposited in Pangaea with the
532 accession code <https://doi.pangaea.de/xxxxxxxxxxxxxx>.

533

Figure 1 | Stand-level tree volume (a), and its annual increment (b) as a function of tree species richness from 2013–2016. The figure shows predicted means and standard errors based on fitted mixed models (Table 1). Effects of species richness were significantly positive and increased significantly throughout the observation period.

Figure 2 | Changes over time in the net biodiversity effect (NE) and its additive components, complementarity effect (CE) and selection effect (SE), on stand-level tree volume. The figure shows means and standard errors. In (a), diversity effects were calculated with monocultures as reference (Extended Data Table 6), in (b) with component mixtures of half the number of species as reference. The y-axes are square root-scaled to reflect the quadratic nature of biodiversity effects.

550

551 **Figure 3 | Relationships between biodiversity effects and (a) functional trait**

552 **distance and (b) vertical crown complementarity (proportional dissimilarity of**

553 **monoculture vertical crown extent) in 2016 ($n = 108$). Regression lines and**

554 **confidence bands (indicating $\pm$ standard error of predicted values) are based on**

555 **mixed models (Extended Data Table 7). The y-axes are square root-scaled to reflect**

556 **the quadratic nature of biodiversity effects. Four extreme y-values are moved to the**

557 **plot margin and given as numbers.**

558

559
560 **Figure 4 | Monoculture stand-level tree volume of species in 2016 (a) and the**
561 **fraction of stand-level tree volume sum of squares explained by the presence of**
562 **each species in a plot (b), their species-specific selection effects (SEs) on stand-**
563 **level tree volume (c) and their tree-level volume response to species richness (d).**
564 Bars indicate standard errors. For (d) the volume of each species, standardized for the
565 number of originally planted individuals of that particular species, was linearly
566 regressed against $\log_2(\text{tree species richness})$ with the data from (sub)plots without
567 shrub species.

568

Table 1 | Mixed-effects models for effects of site, tree species richness (logSR), time (year) and interactions on stand-level tree basal area, stand-level tree volume and their increments.

	Basal area (n = 387)				Volume (n = 387)			
Source of variation	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	120.0	13.80	<0.001	1	100.8	19.21	<0.001
LogSR	1	111.2	6.00	0.016	1	88.7	5.26	0.024
Year	1	125.5	359.90	<0.001	1	103.0	206.30	<0.001
Site × year	1	125.3	5.80	0.018	1	103.7	18.80	<0.001
LogSR × year	1	117.8	16.00	<0.001	1	94.8	10.83	0.001
	Basal area increment (n = 387)				Volume increment (n = 387)			
Source of variation	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	123.5	5.10	0.025	1	104.0	14.54	<0.001
LogSR	1	115.7	13.30	<0.001	1	93.9	9.34	0.003
Year	1	111.4	20.90	<0.001	1	104.2	68.85	<0.001
Site × year	1	115.2	4.40	0.037	1	109.2	27.50	<0.001
LogSR × year	1	102.1	10.20	0.002	1	95.1	12.01	<0.001

572

573 Notes:

574 Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table

575 (random terms were community composition, plot, subplot and the interaction of

576 these with year, with site-specific variance components for species composition and

577 plot). Abbreviations: n = numbers of plots in analysis; df = nominator degree of

578 freedom; ddf = denominator degree of freedom; logSR = log₂(tree species richness). *F*

579 and *P* indicate F-ratios and the P-value of the significance test.

EXTENDED DATA

Conversion factors for volume, biomass and carbon content

We harvested 154 trees in a natural forest in 2010 near the experimental sites to determine conversion factors from cylindrical volume (tree basal area $\times$ height) to true volume and biomass. The trees belonged to eight common species and three life forms (evergreen, deciduous and coniferous) and were chosen to represent a naturally occurring size span of young trees.

Trees were separated into large woody parts (stems and large branches with a diameter $\geq$ 3 cm), twigs (the apical part of the stem and large branches plus side branches with a diameter $<$ 3 cm), and dead attached material (large dead branches or twigs). Branches were divided into segments of typically about 1 m length. The volume of large woody parts and twigs was determined geometrically, approximating the parts as truncated cone (large woody parts, $V = \frac{1}{3}\pi(r_1^2 + r_1r_2 + r_2^2) \times l$ where l is the length and r_1 and r_2 are the end radius), or cone (twigs, as above but $r_2=0$). The density of these fractions was determined by oven-drying a representative subsample of stem and branch discs or twigs.

These geometric and density data were then scaled up to total aboveground tree biomass using a Bayesian framework, modeling twig mass and density in dependence of branch positions within tree crowns³⁷.

Conversion factors from cylindrical volume to true volume (and mass) were determined as total tree volume (and tree mass, including leaves) divided by cylindrical volume. We analyzed the variation of these conversion factors with tree size and species life form using mixed effects models with species identity as random term. We found that large trees deviated from the linear relationship of form factor and cylindrical volume, and we therefore removed trees with a cylindrical volume $\geq$ 500 liter from the form factor calibration, leaving a set of 119 trees. Within this set, there was only a small variance among species and no

significant effect of life form on the form factor; the form factor decreased linearly with the cylindrical volume of harvested trees (Extended Data Table 3). We therefore used a form factor of $0.5412 \text{ m}^3 \text{ m}^{-3} - 0.1985 \text{ m}^3 \cdot \text{BA} \cdot \text{h}$ (with basal area BA in m^2 and height h in m). The intercept of $0.5412 \text{ m}^3 \text{ m}^{-3}$ is the weighted average form factor of evergreen and deciduous species at size zero (in our study, 19 of 40 species were evergreen and 21 deciduous). Biomass factors were determined similarly, yielding a conversion factor of $269.13 \text{ kg m}^{-3} - 141.96 \text{ kg m}^{-3} \cdot \text{BA} \cdot \text{h}$. For the two coniferous species that were planted for comparison in monocultures only, we used separate equations obtained from the harvested trees of the same species *Pinus massoniana* and *Cunninghamia lanceolata*. Here the form factor was $0.5083 \text{ m}^3 \text{ m}^{-3} - 0.1985 \text{ m}^3 \cdot \text{BA} \cdot \text{h}$ and the biomass factor was $216.79 \text{ kg m}^{-3} - 141.96 \text{ kg m}^{-3} \cdot \text{BA} \cdot \text{h}$.

Functional trait and phylogenetic distances

We used four functional traits related to the resource-use strategies of tree species: specific leaf area³⁸, branch-wood density³⁸, relative volume growth rate (RGR) and life form (deciduous or evergreen). These traits were determined in plots that were part of the experiment. RGR was calculated as the log-transformed relative difference in stand volume of monocultures between seven (2015 for site A and 2016 for site B) and five years (2013 for site A and 2014 for site B) after planting. We selected the monocultures without shrub treatments. We used site-specific RGR because of the large variation in growth rates between sites A and B. We calculated functional trait distances among species pairs in 2-species communities as Euclidean distances in standardized multivariate trait space (using the four traits as axes).

We calculated phylogenetic distances among species pairs as their cophenetic distance in a node age-calibrated phylogenetic tree³⁹.

We assessed the effects of trait and phylogenetic distances on different components of diversity effects of two-species mixtures with linear mixed-effects models, where we set site and trait/phylogenetic distance as fixed effects, community composition and plot as random effect (with a separate variance component for each site). Measures of diversity effects were square-root transformed with sign reconstruction to improve normality of model residuals.

Extended Data Figure 1 | Map of BEF-China position and experimental plots of random extinction scenarios and economic trees (a). Results from species pool A1 to illustrate the “broken stick” design (b). Letters represent different species (A= *Cyclobalanopsis glauca*; B = *Quercus fabri*; C = *Rhus chinensis*; D = *Schima superba*; E = *Castanopsis eyrei*; F = *Cyclobalanopsis myrsinifolia*; G = *Koelreuteria bipinnata*; H = *Lithocarpus glaber*; I = *Castanea henryi*; J = *Nyssa sinensis*; K = *Liquidambar formosana*; L = *Sapindus saponaria*; M = *Castanopsis sclerophylla*; N = *Quercus serrata*; O = *Choerospondias axillaris*; P = *Triadica sebifera*). Solid lines represent overyielding, while dashed lines represent underyielding.

Extended Data Figure 2 | Stand-level tree volume (a) and its increment (b) as a function of tree species richness from 2013–2016. Positive effects of tree species richness increase with time. Raw data points, regression lines and 95% confidence bands are shown for each year. Note that the extremes of the point cloud necessarily taper off towards higher diversity levels for statistical rather than biological reasons; this is due to the fact that for a given diversity level extreme values are more extreme the larger the sample size is²⁶.

Extended Data Figure 3 | Stand-level tree basal area (a) and its annual increment (b) as a function of tree species richness from 2013–2016. The figure shows predicted means and standard errors based on fitted mixed models (Table 1). Effects of species richness were significantly positive and increased throughout the observation period.

Extended Data Figure 4 | Aboveground stand-level tree carbon (a) and its annual increment (b) as a function of tree species richness from 2013–2016. Raw data points, regression lines and 95% confidence bands are shown. On the left of each panel means $\pm$ standard errors for the two economic tree species (PiMa = *Pinus massoniana*; CuLa = *Cunninghamia lanceolata*) are inserted. Note that the extremes of the point cloud necessarily taper off towards higher diversity levels for statistical reasons; this is due to the fact that for a given diversity level extreme values are more extreme the larger the sample size is²⁶.

Extended Data Figure 5 | Stand density as a function of tree species richness from 2013–

2016. Raw data points together with non-significant regression lines (dashed) are shown.

Density indicates the number of surviving trees out of 16 planted in the central area of each plot.

Extended Data Figure 6 | Effects of shrub diversity on average stand-level tree volume

in species pools A1 and B1. Data are from 4mu plots. The figure shows predicted means and standard errors based on a fitted mixed model (Extended Data Table 8).

Extended Data Table 1 | List of tree species used in the BEF-China experiment according to the Flora of China (<http://www.efloras.org> and <http://frps.eflora.cn>).

Species	Abbreviation	Site	Type
<i>Acer davidii</i> Franchet	AcDa	A	Deciduous
<i>Ailanthus altissima</i> (Miller) Swingle	AiAl	B	Deciduous
<i>Alniphyllum fortunei</i> (Hemsley) Makino	AlFo	B	Deciduous
<i>Betula luminifera</i> H. Winkler in Engler	BeLu	B	Deciduous
<i>Castanea henryi</i> (Skan) Rehd. et Wils.	CaHe	A	Deciduous
<i>Castanopsis carlesii</i> (Hemsley) Hayata	CaCa	A	Evergreen
<i>Castanopsis eyrei</i> (Champion ex Benth) Tutchet	CaEy	AB	Evergreen
<i>Castanopsis fargesii</i> Franchet	CaFa	B	Evergreen
<i>Castanopsis sclerophylla</i> (Lindley & Paxton) Schottky	CaSc	AB	Evergreen
<i>Celtis biondii</i> Pampanini	CeBi	B	Deciduous
<i>Choerospondias axillaris</i> (Roxb.) Burt et Hill	ChAx	A	Deciduous
<i>Cinnamomum camphora</i> (Linnaeus) J. Presl in Berchtold & J. Presl	CiCa	AB	Evergreen
<i>Cunninghamia lanceolata</i> (Lamb.) Hook.	CuLa	AB	Evergreen
<i>Cyclobalanopsis glauca</i> (Thunberg) Oersted	CyGl	AB	Evergreen
<i>Cyclobalanopsis myrsinifolia</i> (Blume) Oersted	CyMy	A	Evergreen
<i>Daphniphyllum oldhamii</i> (Hemsley) K. Rosenthal in Engler	DaOl	AB	Evergreen
<i>Diospyros japonica</i> Siebold & Zuccarini	DiJa	AB	Deciduous
<i>Elaeocarpus chinensis</i> (Gardner & Champion) J. D. Hooker ex Benth	ElCh	B	Evergreen
<i>Elaeocarpus glabripetalus</i> Merrill	ElGl	B	Evergreen
<i>Elaeocarpus japonicus</i> Siebold & Zuccarini	ElJa	B	Evergreen
<i>Idesia polycarpa</i> Maximowicz	IdPo	B	Deciduous
<i>Koelreuteria bipinnata</i> Franch.	KoBi	A	Deciduous
<i>Liquidambar formosana</i> Hance	LiFo	A	Deciduous
<i>Lithocarpus glaber</i> (Thunb.) Nakai	LiGl	AB	Evergreen
<i>Machilus grijsii</i> Hance	MaGr	B	Evergreen

<i>Machilus leptophylla</i> Handel-Mazzetti	MaLe	B	Evergreen
<i>Machilus thunbergii</i> Siebold & Zuccarini	MaTh	B	Evergreen
<i>Manglietia fordiana</i> Oliver	MaFo	B	Evergreen
<i>Melia azedarach</i> Linnaeus	MeAz	A	Deciduous
<i>Meliosma flexuosa</i> Pampanini	MeFl	B	Deciduous
<i>Nyssa sinensis</i> Oliver	NySi	A	Deciduous
<i>Phoebe bournei</i> (Hemsley) Yen C. Yang	PhBo	B	Evergreen
<i>Pinus massoniana</i> Lamb.	PiMa	AB	Deciduous
<i>Quercus acutissima</i> Carruthers	QuAc	A	Deciduous
<i>Quercus fabri</i> Hance	QuFa	A	Deciduous
<i>Quercus phillyreoides</i> A. Gray	QuPh	B	Evergreen
<i>Quercus serrata</i> Murray	QuSe	A	Deciduous
<i>Rhus chinensis</i> Mill.	RhCh	A	Deciduous
<i>Sapindus saponaria</i> Linnaeus	SaSa	A	Deciduous
<i>Schima superba</i> Gardn. et Champ.	ScSu	AB	Evergreen
<i>Triadica cochinchinensis</i> Loureiro	TrCo	A	Deciduous
<i>Triadica sebifera</i> (L.) Small	TrSe	A	Deciduous

684

685 Notes:

686 The site column shows the experimental site (A, B) where the species was planted. The type

687 column shows species life form (D = deciduous species; E = evergreen species).

688

Extended Data Table 2 | Experimental design

Site	Pool	Species richness	Plot size	Shrubs	Species composition
A	A1	16	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEyCyMyKoBi LiGl CaHeNySi LiFo SaSa CaSc QuSe ChAx TrSe
		8	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEyCyMyKoBi LiGl CaHeNySi LiFo SaSa CaSc QuSe ChAx TrSe
		4	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEyCyMyKoBi LiGl CaHeNySi LiFo SaSa CaSc QuSe ChAx TrSe
		2	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEyCyMyKoBi LiGl CaHeNySi LiFo SaSa CaSc QuSe ChAx TrSe
		1	4mu/1mu	yes	CyGl QuFa RhCh ScSu CaEyCyMyKoBi LiGl CaHeNySi LiFo SaSa CaSc QuSe ChAx TrSe
	A2	16	1mu	no	CaCa LiGl AcDaMeAzCaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		8	1mu	no	CaCa LiGl AcDaMeAzCaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		4	1mu	no	CaCa LiGl AcDaMeAzCaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		2	1mu	no	CaCa LiGl AcDaMeAzCaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
		1	1mu	no	CaCa LiGl AcDaMeAzCaEy KoBi CiCa CyMy DiJa NySi TrCo ScSu DaOl QuFa QuAc SaSa
	A3	16	1mu	no	AcDaQuAc CaHe RhCh CaSc CiCa LiFo MeAzCaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		8	1mu	no	AcDaQuAc CaHe RhCh CaSc CiCa LiFo MeAzCaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		4	1mu	no	AcDaQuAc CaHe RhCh CaSc CiCa LiFo MeAzCaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		2	1mu	no	AcDaQuAc CaHe RhCh CaSc CiCa LiFo MeAzCaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
		1	1mu	no	AcDaQuAc CaHe RhCh CaSc CiCa LiFo MeAzCaCa CyGl TrCo TrSe ChAx DiJa DaOl QuSe
B	B1	16	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLuCaFaMaFo QuPh ElCh MaTh AlFo MaLe
		8	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLuCaFaMaFo QuPh ElCh MaTh AlFo MaLe
		4	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLuCaFaMaFo QuPh ElCh MaTh AlFo MaLe
		2	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLuCaFaMaFo QuPh ElCh MaTh AlFo MaLe
		1	4mu/1mu	yes	AiAl MeFl IdPo MaGr CeBi ElGl ElJa PhBo BeLuCaFaMaFo QuPh ElCh MaTh AlFo MaLe
	B2	16	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		8	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		4	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		2	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
		1	1mu	no	CaEy CeBi MaLe PhBo DiJa LiGl ElGl MaTh AiAl AlFo CaFa CaSc CyGl ScSu CiCa DaOl
	B3	16	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		8	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		4	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		2	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu
		1	1mu	no	BeLu DaOl CaEy QuPh CyGl MaGr ElJa LiGl CaSc IdPo ElCh MaFo CiCa DiJa MeFl ScSu

Note:

See Extended Data Table 1 for species abbreviations.

Extended Data Table 3 | Mixed-effects model for the effects of cylindrical volume and life form on form and biomass factors.

	Form factor				Biomass factor			
	Df	ddf	<i>F</i>	<i>P</i>	ddf	denDF	<i>F</i>	<i>P</i>
(Intercept)	1	4.4	2418	<0.001	1	4.8	828.9	<0.001
Cylindrical volume	1	105.7	8	0.007	1	114.7	11.2	0.001
Life form	2	4.7	20	0.005	2	4.9	22.1	0.004
Variance components	Component		s.e.	z-ratio	Component		s.e.	z-ratio
Species identity	0.00002		0.00058	0.043	257.90		356.87	0.723
Residual	0.01237		0.00169	7.321	4384.52		590.66	7.423

Notes:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (the random term was species identity). Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom; s.e. = standard error; *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 4 | Mixed-effects models for the effects of site, tree species richness (logSR), time (year) and interactions on aboveground stand-level tree carbon and its increment.

Source of variation	Aboveground carbon				Aboveground carbon increment			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Site	1	101.30	19.12	<0.001	1	104.70	14.42	<0.001
LogSR	1	89.20	5.16	0.026	1	94.60	9.11	0.003
Year	1	104.20	209.50	<0.001	1	106.20	70.30	<0.001
Site × year	1	104.80	18.47	<0.001	1	110.60	26.78	<0.001
LogSR × year	1	95.90	10.54	0.002	1	97.00	11.63	<0.001

Notes:

Fixed effects were fitted sequentially (type I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot). Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom; logSR = $\log_2$ (tree species richness). *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 5a | Average number of 1-mu (sub)plots with overyielding (Over) and underyielding (Under) for stand-level tree volume in 2016 across richness levels.

Reference	Target ->	All plots			Transgressive plots		
		<i>P</i>			<i>P</i>		
	reference	Over	Under	(over>under)	Over	Under	(over>under)
Component monocultures	2->1	65	47	0.088	43	21	0.005
	4->1	39	17	0.003	14	0	<0.001
	8->1	21	7	0.007	3	0	0.041
	16->1	9	5	0.280	1	0	0.239
	total	134	76	<0.001	62	21	<0.001
Component mixtures with half the number of species	2->1	65	47	0.088	43	22	0.009
	4->2	32	24	0.284	20	9	0.039
	8->4	17	11	0.250	10	6	0.315
	16->8	7	7	1.000	6	5	0.763
	total	121	89	0.027	79	42	<0.001

Extended Data Table 5b | Average number of 1-mu (sub)plots with overyielding (Over) and underyielding (Under) for stand-level tree volume in different years.

Reference	Year	All plots			Transgressive plots		
		Over	Under	<i>P</i> (over>under)	Over	Under	<i>P</i> (over>under)
Component monocultures	2013	126	84	0.004	50	20	<0.001
	2014	128	82	0.001	61	21	<0.001
	2015	133	77	<0.001	60	24	<0.001
	2016	134	76	<0.001	61	21	<0.001
Component mixtures with half the number of species	2013	112	98	0.33	69	37	0.002
	2014	111	99	0.41	74	40	0.001
	2015	115	95	0.17	73	43	0.005
	2016	121	89	0.027	79	42	<0.001

Notes:

P-values indicate significance of differences between the numbers of overyielding vs. underyielding plots (χ^2 -test), or between transgressively overyielding vs. transgressively underyielding plots.

Extended Data Table 6 | Mixed-effects models for the effects of site, tree species richness (logSR), time (year) and the interaction of the latter two on the biodiversity effects NE, CE and SE.

	NE				CE				SE			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
Intercept	1	60.7	20.43	<0.001	1	50.7	43.54	<0.001	1	52.7	9.29	0.004
Site	1	64.5	0.18	0.675	1	58.9	2.69	0.107	1	59.7	3.74	0.058
LogSR	1	60.5	4.58	0.036	1	50.6	9.79	0.003	1	52.6	5.89	0.019
Year	1	47.7	23.61	<0.001	1	31.3	9.61	0.004	1	37.3	4.61	0.038
LogSR × year	1	47.1	0.81	0.374	1	31.1	0.26	0.617	1	37.0	0.24	0.627

Notes:

Biodiversity effects were square-root transformed with sign reconstruction ($\text{sign}(y)\sqrt{|y|}$).

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table

(random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot).

Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom. *F*

and *P* indicate F-ratios and P-values of the significance tests. The first line “Intercept” shows

that the overall mean for all biodiversity effects differs significantly from zero (positively for

NE and CE, negatively for SE).

Extended Data Table 7 | Mixed-effects models for the effects of functional distance (FD), phylogenetic distance (PD) or vertical crown complementarity (PDS) on the biodiversity effects NE, CE and SE in 2-species tree stands.

	NE				CE				SE			
	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>	df	ddf	<i>F</i>	<i>P</i>
FD	1	34.6	4.34	0.045	1	17.3	5.09	0.037	1	94	0.28	0.600
PD	1	58.4	0.92	0.342	1	76.3	0.07	0.787	1	39.4	0.67	0.420
PDS	1	22.5	3.43	0.077	1	56.5	0.20	0.659	1	8.2	26.43	< 0.001

Notes:

Biodiversity effects were square-root transformed with sign reconstruction ($\text{sign}(y)\sqrt{|y|}$). The effects of FD, PD and PDS were fitted after site (random terms were species composition and plot, considering a separate variance component for each site). Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom. *F* and *P* indicate F-ratios and P-values of the significance tests.

Extended Data Table 8 | Mixed-effects model for the effects of site, tree species richness (logSR), shrub presence, plot size, shrub species richness (logShrubSR), time (year) and interactions on stand-level tree volume. Data are from species pool A1 and B1, which include a shrub treatment in the planting design.

Source of variation	df	ddf	<i>F</i>	<i>P</i>
Site	1	46.2	12.20	0.001
LogSR	1	45.0	3.70	0.059
Shrub presence	1	233.5	4.80	0.029
Plot size	1	116.2	0.90	0.353
LogShrubSR	1	198.8	5.40	0.022
Year	1	46.9	86.80	<0.001
LogSR × shrub presence	1	232.2	0.80	0.380
LogSR × plot size	1	114.2	0.20	0.694
LogSR × logShrubSR	1	198.8	0.30	0.606
LogSR × year	1	46.9	7.20	0.010
Shrub presence × year	1	235.1	9.50	0.002
Plot size × year	1	128.7	0.00	0.942
LogShrubSR × year	1	197.1	3.30	0.069

Notes:

Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table (random terms were community composition, plot, subplot and the interaction of these with year, with site-specific variance components for species composition and plot).
Abbreviations: df= nominator degree of freedom; ddf = denominator degree of freedom;
logSR = log₂(tree species richness); logShrubSR= log₂(shrubs species richness—this term is

764 aliased with shrub presence and plot size and therefore fitted after these to only test for
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