FOREST ECOLOGY

Impacts of species richness on productivity in a large-scale subtropical forest experiment

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Biodiversity experiments have shown that species loss reduces ecosystem functioning in grassland. To test whether this result can be extrapolated to forests, the main contributors to terrestrial primary productivity, requires large-scale experiments. We manipulated tree species richness by planting more than 150,000 trees in plots with 1 to 16 species. Simulating multiple extinction scenarios, we found that richness strongly increased stand-level productivity. After 8 years, 16-species mixtures had accumulated over twice the amount of carbon found in average monocultures and similar amounts as those of two commercial monocultures. Species richness effects were strongly associated with functional and phylogenetic diversity. A shrub addition treatment reduced tree productivity, but this reduction was smaller at high shrub species richness. Our results encourage multispecies afforestation strategies to restore biodiversity and mitigate climate change.

Forest ecosystems harbor around two-thirds of all terrestrial plant species. Observational studies suggest that species-rich forests exceed the productivity of less diverse forests (1–3), but covarying factors [such as spatial heterogeneity in abiotic environment (1), species composition (2), and successional stages (2)] make assigning causation difficult. Systematic experimental manipulations of plant species composition in grassland (4–6) have shown that plant diversity promotes community productivity through niche partitioning among species, specifically with respect to abiotic resources (7) or interactions with enemies (8), or through increasing the contribution of highly productive species in more diverse communities (9). These two types of biological mechanisms are thought to be captured by the complementarity and selection effects calculated by the additive partitioning of net biodiversity effects (10). Complementarity effects are large and positive when most species in a mixture contribute more than expected on the basis of their monoculture values to community values, and negative when most species in a mixture contribute less than expected, whereas selection effects are large when a single or few species show a disproportionate contribution to community values (10). It has been postulated that biodiversity effects may be weak or absent in forests, especially in those of high species richness, because the coexistence of so many species may require similar niches and competitive abilities (1, 11–13).

Several forest biodiversity experiments have recently been initiated (14, 15), mostly in the temperate zone or in small plots with limited species richness gradients (16–22). Here, we report results of the "BEF-China" experiment (BEF, biodiversity–ecosystem functioning) that was established in a highly diverse subtropical forest in southeast China (23). The experiment is characterized by a large species richness gradient, multiple simulated extinction scenarios, high replication, and extended duration (2009 to present). We studied how changing tree species richness affected stand-level development of tree basal area, aboveground volume, and aboveground carbon (C) from 2013 to 2017 (24). The experiment was implemented at two sites (site A and site B) of ~20 ha each, with communities assembled from six partially overlapping species pools (three per site). A complete pool represented a 16-species community, which was repeatedly divided to yield reduced richness levels of eight, four, two, and one species; in addition, 24-species communities were created by combining species of all three pools present at each site (fig. S1) (24). Of the 42 tree species used in the experiment (table S1), 40 occurred with the same frequency at each richness level. The remaining two species were typical plantation species in the area and were established in reference monocultures. A special feature of the design is that within each pool, communities form nested series that simulate different trajectories of trait-based species extinctions (fig. S2 and table S2). We analyzed trajectories related to

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means and diversities of the three functional traits leaf duration (LD), specific leaf area (SLA), and wood density (WD). These traits are often used to characterize plant-growth strategies (25) and are potentially related to extinction probabilities under environmental change (26). In 2009 (site A) and 2010 (site B), communities of 400 trees were planted on square plots 0.067 ha in size, which equals the Chinese area unit of 1 mu.

Communities of pools A2, A3, B2, and B3 (fig. S1) were established in single 1-mu plots. Each community of pools A1 and B1 was replicated in five 1-mu plots, four of which formed a larger square plot of 4 mu; these four plots received an understory shrub species richness treatment factorially crossed with the tree species richness gradient: Plots had zero, two, four, or eight shrub species randomly selected from a pool of 18

species, with shrubs planted at the same density as the trees.

We found significant positive effects of the logarithm of tree species richness on stand basal area and stand volume as well as on the annual increments of these two variables (Table 1, Fig. 1, and figs. S3 and S4). These effects grew steadily through time (changes in stand volume per doubling of species, with standard errors, were 0.74 ± 0.58, 1.47 ± 0.85, 2.98 ± 1.29, 4.91 ± 1.83, and 6.99 ± 2.24 m^3 ha^{-1} from 2013 to 2017). Mean volume increments were larger in wetter years ($F_{1,99.1} = 7.58$, $P = 0.007$), but richness effects on volume increments were not affected by annual precipitation ($F_{1,91.7} = 2.25$, $P = 0.137$). After 8 years of growth (site A), the average 16-species mixture stored 31.5 Mg C ha^{-1} above ground [95% Bayesian credible interval (CI), 25.5 to 37.6] (24), which is more than double the amount found in monocultures (11.9 Mg C ha^{-1}; CI, 10.6 to 13.5) (fig. S5) and similar to the C storage of monocultures of the commercial plantation species *Cunninghamia lanceolata* (26.3 Mg C ha^{-1}; CI, 19.0 to 33.2) and *Pinus massoniana* (28.5 Mg C ha^{-1}; CI, 20.8 to 36.1) (fig. S5). These strong positive effects of tree species richness must have been driven by faster growth of live trees in more diverse stands because tree survival rate did not increase with species richness (fig. S6). This is in contrast to findings in a large grassland biodiversity experiment in which positive diversity effects on productivity were mediated by a greater number rather than larger size of individuals in high-diversity plots (27).

The net biodiversity effect (10) on stand volume increased through time for mixtures of all species-richness levels (year as linear term with $F_{1,38.6} = 29.15$, $P < 0.001$) (Fig. 2) and was driven by increases in complementarity effects (year as linear term with $F_{1,52.4} = 9.23$, $P = 0.004$) (Fig. 2). Selection effects were on average negative ($F_{1,37.8} = 8.75$, $P = 0.005$) because some species with relatively high monoculture stand volume had lower performance in mixtures, and some with relatively low monoculture stand volume had higher performance. This was corroborated by negative species-level selection effects (fig. S7).

We tested whether the observed species-richness effects could be explained by functional or phylogenetic diversity. For this, we calculated functional diversity (FD) and functional dispersion (FDis) (24) on the basis of the seven plant
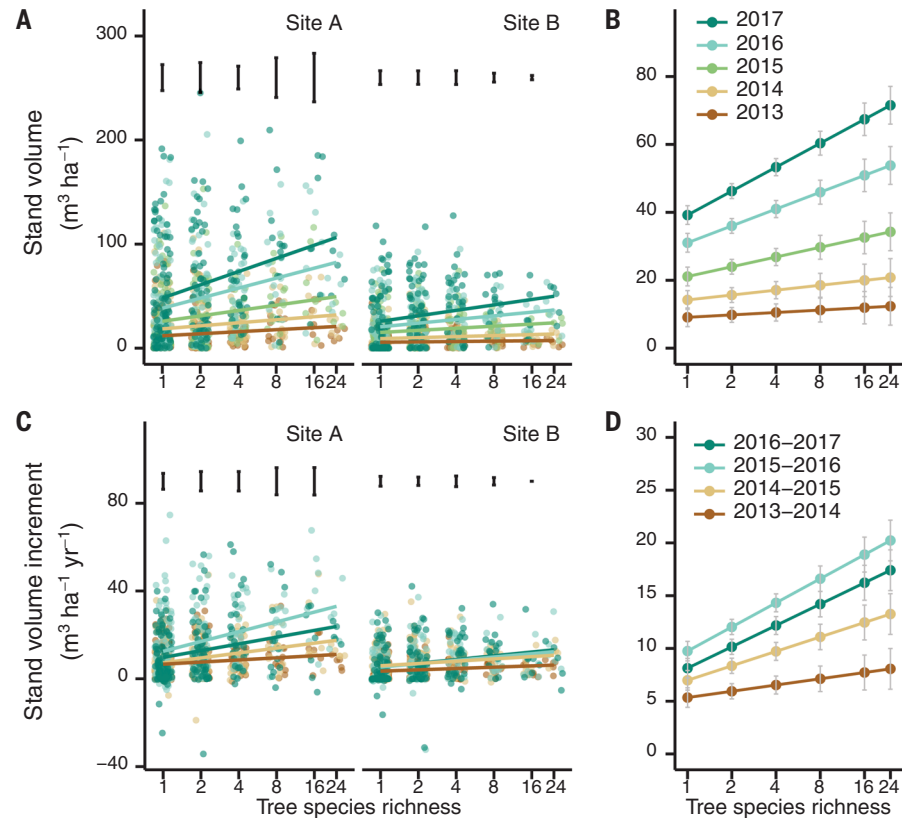

Fig. 1. Stand-level tree volume and its increment as a function of tree species richness from 2013 to 2017. (**A** and **B**) Stand-level tree volume. (**C** and **D**) Stand-level tree volume increment. In (A) and (C), raw data points and regression lines are shown for each year. (B) and (D) show predicted means and standard errors based on mixed-effects models (Table 1). The extremes of the point cloud taper off toward higher diversity levels because of decreasing sample size; quantile regressions show qualitatively the same positive relationships for the largest 10% of values at each diversity level (fig. S4). Standard deviations of species compositions (square root of corresponding between-composition variance components), shown as black error bars above the raw data, indicate that there is no variance-reduction effect of increasing species richness.

Table 1. Mixed-effects models for effects of site, tree species richness (logSR), year, and interactions on stand-level tree basal area and volume and their increments. Fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table [random terms are provided in (24)]. n, numbers of plots; df, numerator degrees of freedom; ddf, denominator degrees of freedom; and logSR, log$_2$(tree species richness). F and P indicate F ratios and the P value of the significance test, respectively.

Source of variation	df	ddf	F	P	df	ddf	F	P	df	ddf	F	P	df	ddf	F	P
	Basal area (n = 387)				Volume (n = 387)				Basal area increment (n = 387)				Volume increment (n = 387)			
Site	1	120.0	14.35	<0.001	1	100.0	20.79	<0.001	1	121.5	8.12	0.005	1	101.3	20.79	<0.001
LogSR	1	111.9	7.45	0.007	1	88.9	6.62	0.012	1	113.8	15.58	<0.001	1	91.2	12.41	<0.001
Year	4	489.4	309.0	<0.001	4	402.3	197.10	<0.001	3	287.5	9.90	<0.001	3	281.8	35.05	<0.001
Site × year	4	488.3	7.75	<0.001	4	410.4	20.92	<0.001	3	301.0	9.43	<0.001	3	309.0	19.62	<0.001
LogSR × year	4	456.2	15.21	<0.001	4	368.9	11.98	<0.001	3	265.6	3.82	0.010	3	259.0	6.18	<0.001

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Fig. 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 in mixed-species plots. *N* = 65 to 77, 50 to 52, 28, and 14 plots for two-, four-, eight-, and 16-species mixtures, respectively. The figure shows means ± SEs. The *y* axis is square root–scaled to reflect the quadratic nature of biodiversity effects (*10*).
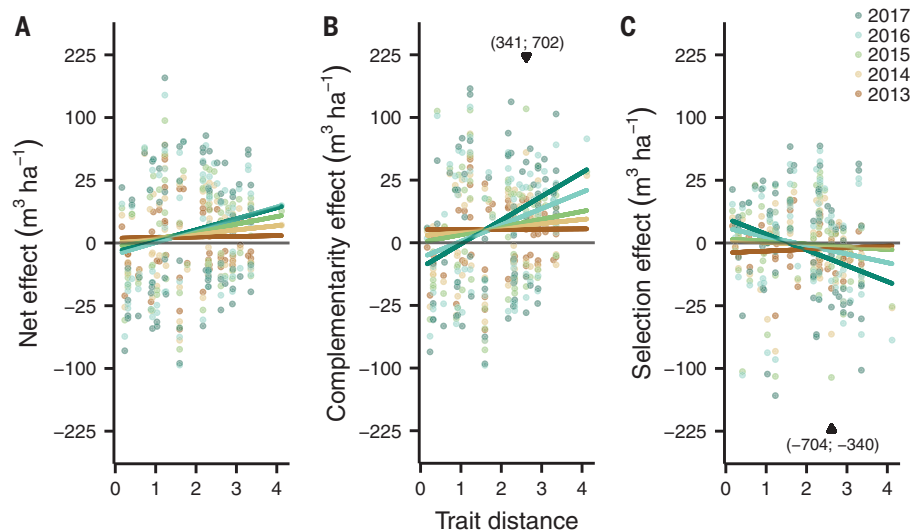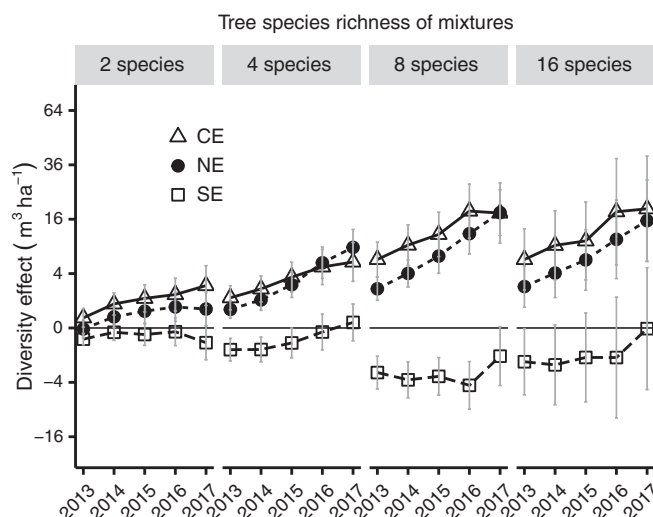

Fig. 3. Relationship between functional trait distance and biodiversity effects on stand volume in two-species mixtures across years. (**A** to **C**) Each point represents a plot in a year (*n* = 65 to 77 plots). Regression lines are based on mixed-effects models (*24*). Euclidean trait distances were calculated with the three *z*-transformed traits LD, SLA, and WD. The *y* axes are square root–scaled to reflect the quadratic nature of biodiversity effects (*10*). Two extreme *y* values are moved to the plot margin and given as numbers.

functional traits LD (deciduous or evergreen), SLA, WD, leaf dry matter content, leaf nitrogen, leaf phosphorus, and leaf thickness or the first three of these (LD, SLA, and WD), which contributed most to explanatory power. We also calculated phylogenetic diversity (PD) and mean phylogenetic distance (MPD) for each community (*24*). All measures of functional and phylogenetic diversity had similar explanatory power as that of species richness for stand-level productivity measures; differences between species-richness levels in stand volume could also be explained by associated differences in functional or phylogenetic diversity (fitted before species richness in model 1 in tables S3 and S4, respectively). However, none of the functional or phylogenetic diversity measures could explain additional variation among communities of the same richness level (when

fitted after species richness in model 2 in tables S3 and S4, respectively). This finding is consistent with similar reports from large-scale grassland biodiversity experiments (*28*). It is conceivable that for each particular species mixture with high stand-level productivity, a particular combination of functional traits causes the observed biodiversity effect; this cannot be captured by using the same functional diversity measure for all species mixtures.

Earlier studies have suggested that positive biodiversity effects in forests might originate from denser crown packing and enhanced light interception in mixed-species canopies (*21, 29, 30*). We measured the vertical crown extent of all trees in 2016 and 2017 and tested whether plots with less crown overlap produced greater stand-level volume (*24*), which was not the case ($F_{1,446.8} = 1.73$,

P = 0.189). A reason for the absence of such a correlation might be that depending on the particular species combination, crown dissimilarity can result from light competition (*18*) or from complementary light use among species.

Despite the absence of general effects of functional diversity beyond species richness, we found some specific effects along the multiple extinction scenarios inherent in our experimental design (fig. S2A) (*24*). Changes in FD with each halving of species richness were negatively correlated with stand-volume changes at high but positively correlated at low species richness (fig. S8A), suggesting that FD captured beneficial differences between species at low but not at high diversity. We then focused on mixtures of two species because for these, the highest number of distinct species compositions were available. We found that a positive correlation of net biodiversity and complementarity effects with functional-trait distances developed over the 5 years of measurements (Fig. 3 and table S5). This was also the case for the diversity of the trait LD, indicating that mixtures of a shade-tolerant evergreen and a shade-intolerant deciduous broad-leaved species captured more light than did species pairs with uniform leaf duration.

Extinction sequences that differed in trajectories of community-weighted means for LD, SLA, or WD (fig. S2, B to D) did not show any significant variation in species-richness effects on stand-level productivity (fig. S8, B to D). This suggests that effects of trait-based extinctions, at least the ones tested and often considered most important (*25, 26*), may not differ much from effects of random extinction. Different results might have been obtained with other trait-based extinction scenarios, either ones that we did not analyze (for example, based on root traits) or ones that we did not simulate.

Plots additionally planted with shrubs (*24*) had reduced stand-level tree volume ($F_{1,234.5} = 7.30$, *P* = 0.007), which is consistent with other findings that shrub removal in forests can increase tree growth (*31*). However, the effect of shrub competition decreased with increasing shrub species richness (log shrub richness $F_{1,191.9} = 6.57$, *P* = 0.011), even though stand-level basal area of shrubs did not decrease (fig. S9). The reduced competition between shrubs and trees at higher shrub diversity suggests that complementarity effects extend to tree interactions with shrubs.

Our results provide strong evidence for a positive effect of tree species richness on tree productivity at stand level in establishing subtropical forest ecosystems and support the idea that co-occurring species in highly diverse subtropical forest can differ in niches and competitive abilities. At the end of the observation period, mixed stands with 16 species had accumulated about 1.7 times the amount of C found in the average monoculture (fig. S5). This effect is, on a relative scale, similar to the 1.8-fold average increase in aboveground stand biomass from monocultures to 16-species mixtures in a multisite grassland biodiversity experiment (*4*). Given that plant biomass is higher in forests, and that the largest

fraction of tree C is bound in relatively persistent woody biomass, these effects translate into large diversity-mediated rates of C accumulation. Specifically, after 8 years of growth at site A, we found an extra 19.5 (95% CI, 14.1 to 25.1) Mg C ha^{-1} accumulated in 16-species mixtures relative to the average monoculture. The biodiversity-productivity effects that we found did not differ between 1-mu and 4-mu plots ($F_{1,118.5} = 0.07$, $P > 0.5$ for interaction log tree species richness × plot size). However, biodiversity effects might be even larger at spatial scales beyond the ones that we tested experimentally because environmental heterogeneity might promote spatial insurance effects (32). Our first-order extrapolation to the global scale indicated that a 10% decrease in tree species richness would lead to a 2.7% decrease in forest productivity on average (24), which is within the range of productivity decreases (2.1 to 3.1%) reported for the same tree species loss scenario in a recent observational study that used plot data covering a large part of the global forests (3). In that study, it was estimated that such a loss would correspond to around $20 billion per year of commercial wood production.

Substantial forest areas are managed worldwide, with large afforestation programs underway (33, 34); in China, the total forested area increased by 1.5×10^6 ha year^{-1} from 2010 to 2015, mainly because of new monoculture plantation of species with high short-term productivity (35). Our experimental findings suggest that a similar or potentially even higher productivity can be achieved with mixed plantations of native species. Such strategies would yield cobenefits (2) in terms of active biodiversity management and likely higher levels of stability of productivity and ecosystem services under adverse conditions such as pathogen infestation or future climate change, including extreme events.

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Science

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Tree diversity improves forest productivity

Experimental studies in grasslands have shown that the loss of species has negative consequences for ecosystem functioning. Is the same true for forests? Huang *et al.* report the first results from a large biodiversity experiment in a subtropical forest in China. The study combines many replicates, realistic tree densities, and large plot sizes with a wide range of species richness levels. After 8 years of the experiment, the findings suggest strong positive effects of tree diversity on forest productivity and carbon accumulation. Thus, changing from monocultures to more mixed forests could benefit both restoration of biodiversity and mitigation of climate change.
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