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Title: Strong Impacts of Biodiversity in a Large-Scale Forest Experiment

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One Sentence Summary: Complementary interactions among tree species lead to faster stand growth and greater carbon accumulation in diverse forests.

Abstract: Biodiversity experiments have shown that species loss reduces ecosystem functioning in grassland, but to test if these results can be extrapolated to forests, the main contributors to terrestrial primary productivity, requires large-scale experiments. We manipulated tree species richness by planting over 150000 trees in plots to simulate multiple extinction scenarios. Tree species richness strongly increased stand-level productivity and, after 8 years, 16-species mixtures had accumulated over twice the amount of carbon found in average monocultures. Functional or phylogenetic diversity measures explained richness effects but little additional productivity variation. Competition by shrubs reduced tree productivity, but less so at high shrub species richness, indicating complementarity both within and among canopy strata. Our results encourage multi-species afforestation strategies to simultaneously restore biodiversity and mitigate climate change.

Main Text: 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 (*2-4*), but co-varying factors [e.g. spatial heterogeneity in abiotic environment (*2*), species composition (*3*) and successional stages (*3*)] make assigning causation difficult. Systematic experimental manipulations of plant species composition in grassland (*5-7*) have shown that plant diversity promotes community productivity by niche partitioning among species, specifically with respect to abiotic resources (*8*) or interactions with enemies (*9*), or by increasing the contribution of highly productive species in more diverse communities (*10*). These two types of biological mechanisms are thought to be captured by the complementarity and selection effects calculated for the additive partitioning of net biodiversity effects (*11*). Complementarity effects are large (positive or negative) when most species in a mixture contribute more (or less) than expected based on their monoculture values to community values, whereas selection effects are large when a single or few species show a disproportionate contribution to community values (*11*). 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 (*2, 12-14*).

Several forest biodiversity experiments have recently been initiated (*15, 16*), mostly in the temperate zone or in small plots with limited species richness gradients (*17-23*). Here we report results of an experiment, here referred to as "BEF-China" (*24*), that is characterized by a large species richness gradient, multiple simulated extinction scenarios, high replication, extended duration (2009–present) in a highly diverse subtropical forest in south-east China.We studied how changing tree species richness along the different functional-trait trajectories of simulated

extinction scenarios in BEF-China affected the stand-level development of tree basal area, aboveground volume and aboveground carbon from 2013–2017 (*25*). These productivity-related variables were derived from direct measurements of tree basal diameter and height, using allometric equations determined by complete aboveground harvests of young trees in a forest near the experimental area (*25*). The experiment was implemented at two sites (A and B) of approximately 20 ha each, with communities assembled from six partially overlapping species pools (three per site), which we randomly halved. Applying this procedure repeatedly resulted in plots with species richness levels of 16, 8, 4, 2 and 1; in addition, 24-species communities were created by combining species of all three pools present at each site (Fig. 1). Special features of this design are that (i) all 40 tree species used in the experiment (Table S1) occur with the same frequency in communities that make up the different species-richness levels; (ii) there is no overlap between species compositions within richness level and pool; and (iii) each composition is part of a nested extinction sequence linking all richness levels from 16 to 1 without gaps [(*25*), Fig. S1 and Table S2]. This latter feature allowed us to examine effects of species extinctions that are trait-biased with regard to three functional traits often used to describe plant growth strategies (*26*), namely leaf duration, specific leaf area (SLA) and wood density (WD). Specifically, we wanted to know whether particularly slow or rapid loss of variation in these traits went along with low or high productivity losses. The overall design consisted of 396 square plots each 0.067 ha in size, equivalent to the Chinese area unit of 1 mu, each planted with 400 trees. Communities at the two sites A and B were planted in 2009 and
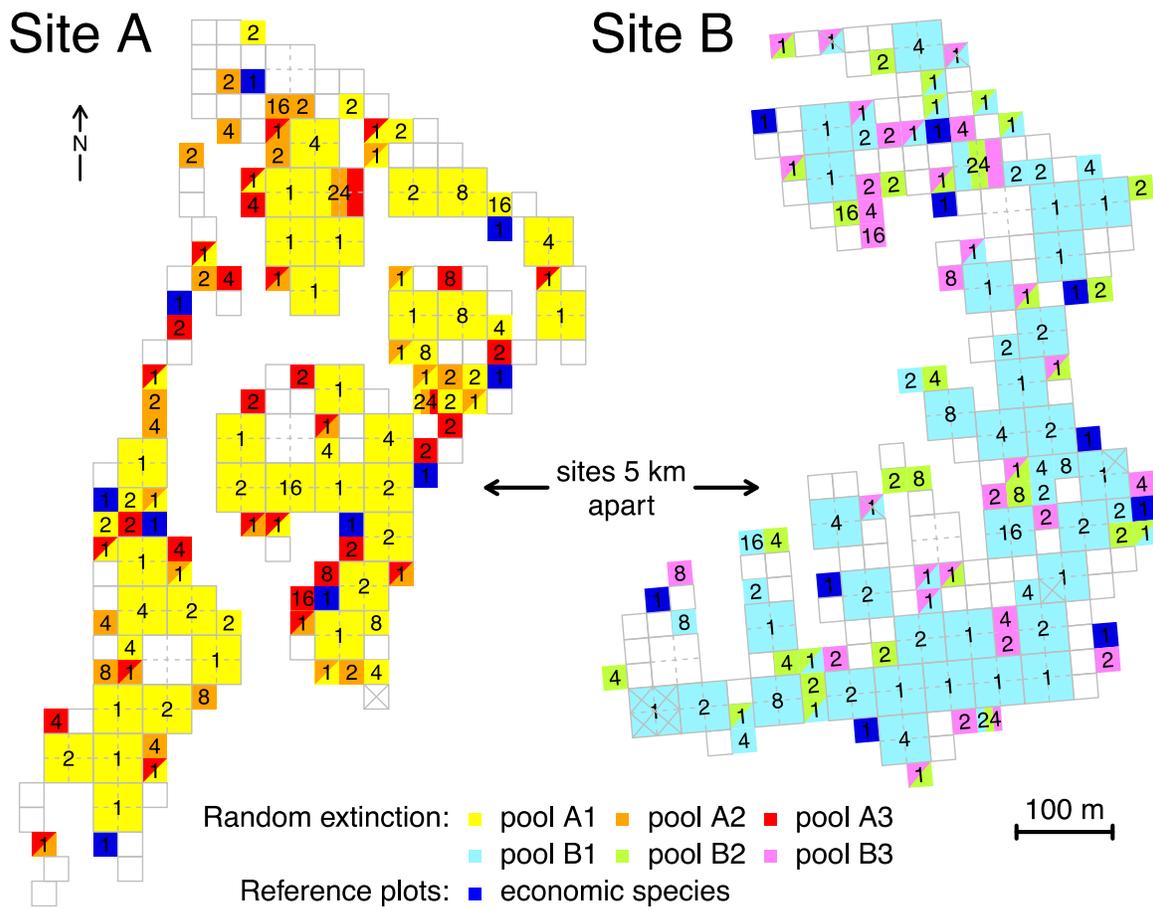
Fig. 1. Map of BEF-China experimental plots analysed in this paper. Numbers indicate planted tree species richness and colours represent different species pools (Tables S1, S2). Note that some monocultures were shared between two pools (diagonal colouring).

2010. Communities of pools A2, A3, B2 and B3 (Fig. 1) were established in single 1-mu plots. Communities of pools A1 and B1were established 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 0, 2, 4 or

8 shrub species randomly selected from a pool of 18 species and 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. 2, Figs. S2 and S3). 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, 6.99 ± 2.24 m^3 ha^{-1} from 2013 to 2017). After eight years of growth (site A), the average 16-species mixture stored 31.5 Mg C ha^{-1} above ground [95% Bayesian credible interval (CI): 25.5–37.6] (*25*), which is more than double the amount found in monocultures (11.9 Mg C ha^{-1}, CI: 10.6–13.5; Fig. S4) and similar to the C storage of monocultures of the commercial plantation species *Cunninghamia lanceolata* (26.3 Mg C ha^{-1}; CI: 19.0–33.2) and *Pinus massoniana* (28.5 Mg C ha^{-1}; CI: 20.8–36.1) that we had planted in reference plots at the same sites (Fig. S4). 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. S5). This is in contrast to findings in a large grassland biodiversity experiment, where 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 (*11*) on stand volume increased through time for mixtures of all species-richness levels (Fig. 3, year as linear term with $F_{1,38.6} = 29.15$, $P < 0.001$). The positive effects of tree species richness on stand volume were reflected in more mixtures that overyielded than underyielded; in many cases, mixtures transgressively overyielded (*28*), i.e.
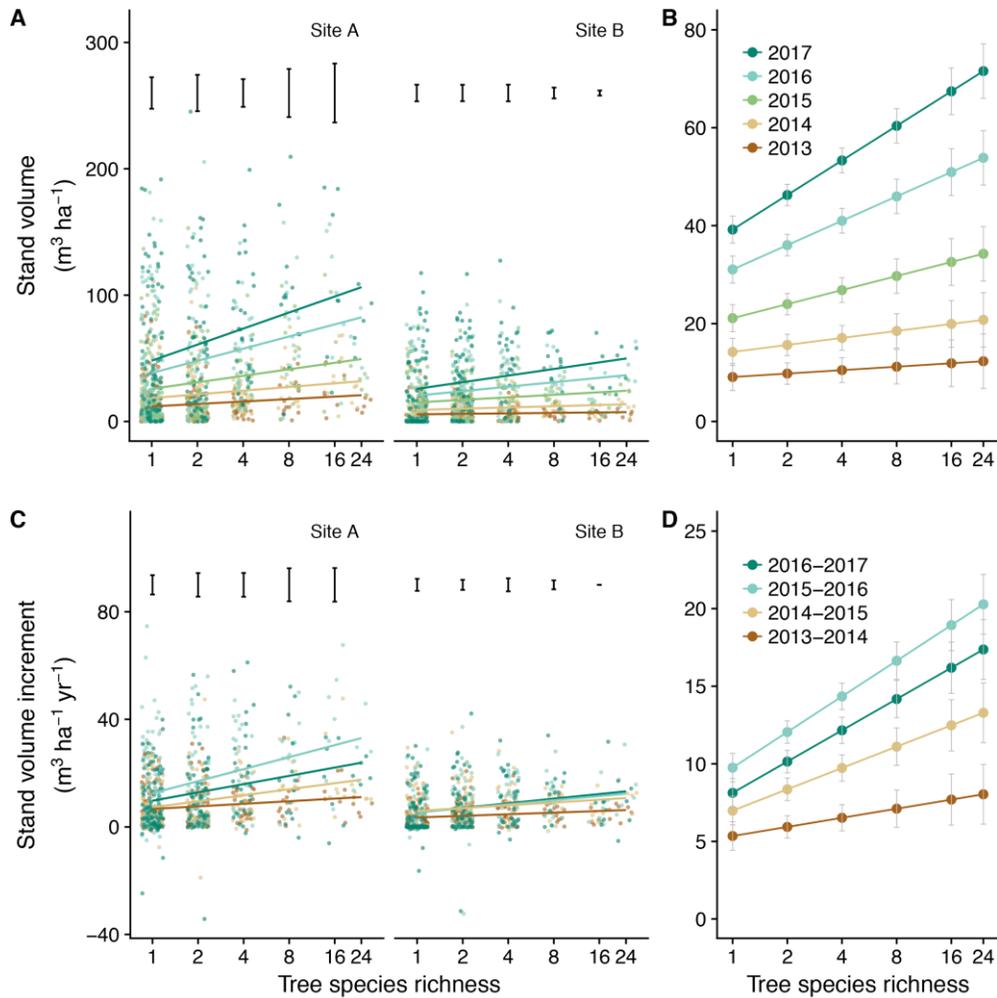
Fig. 2. Stand-level tree volume (A, B) and its increment (C, D) as a function of tree species richness from 2013–2017. In panels A and C, raw data points and regression lines are shown for each year. Panels B and D show predicted means and standard errors based on mixed-effects models (Table 1). Note that the extremes of the point cloud taper off towards higher diversity levels because of decreasing sample size (*28*); quantile regressions show qualitatively the same positive relationships for the largest 10% of values at each diversity level (Fig. S3). 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.

Source of variation	Basal area ($n = 387$)				Volume ($n = 387$)			
	df	ddf	F	*P*	df	ddf	F	*P*
Site	1	120.0	14.35	<0.001	1	100.0	20.79	<0.001
LogSR	1	111.9	7.45	0.007	1	88.9	6.62	0.012
Year	4	489.4	309.0	<0.001	4	402.3	197.10	<0.001
Site × year	4	488.3	7.75	<0.001	4	410.4	20.92	<0.001
LogSR × year	4	456.2	15.21	<0.001	4	368.9	11.98	<0.001

Source of variation	Basal area increment ($n = 387$)				Volume increment ($n = 387$)			
	df	ddf	F	*P*	df	ddf	F	*P*
Site	1	121.5	8.12	0.005	1	101.3	20.79	<0.001
LogSR	1	113.8	15.58	<0.001	1	91.2	12.41	<0.001
Year	3	287.5	9.90	<0.001	3	281.8	35.05	<0.001
Site × year	3	301.0	9.43	<0.001	3	309.0	19.62	<0.001
LogSR × year	3	265.6	3.82	0.010	3	259.0	6.18	<0.001

Notes: fixed effects were fitted sequentially (type-I sum of squares) as indicated in the table [for random terms see (*25*)]. Abbreviations: n = numbers of plots; df = nominator degrees of freedom; ddf = denominator degrees of freedom; logSR = log$_2$(tree species richness). F and *P* indicate F-ratios and the *P*-value of the significance test, respectively.

they were more productive than all component monocultures (Table S3). Additive partitioning

revealed that the increases of net biodiversity effects were primarily driven by increases in

complementarity effects (Fig. 3, year as linear term with $F_{1,52.4} = 9.23$, $P = 0.004$). Selection

effects were on average negative ($F_{1,37.8} = 8.75$, $P = 0.005$) because some species with relatively

high (low) monoculture stand volume underyielded (overyielded) in mixtures, e.g. *Cinnamomum*

camphora, Castanea henryi (*Castanopsis eyrei, Koelreuteria bipinnata*) and *Alniphyllum*
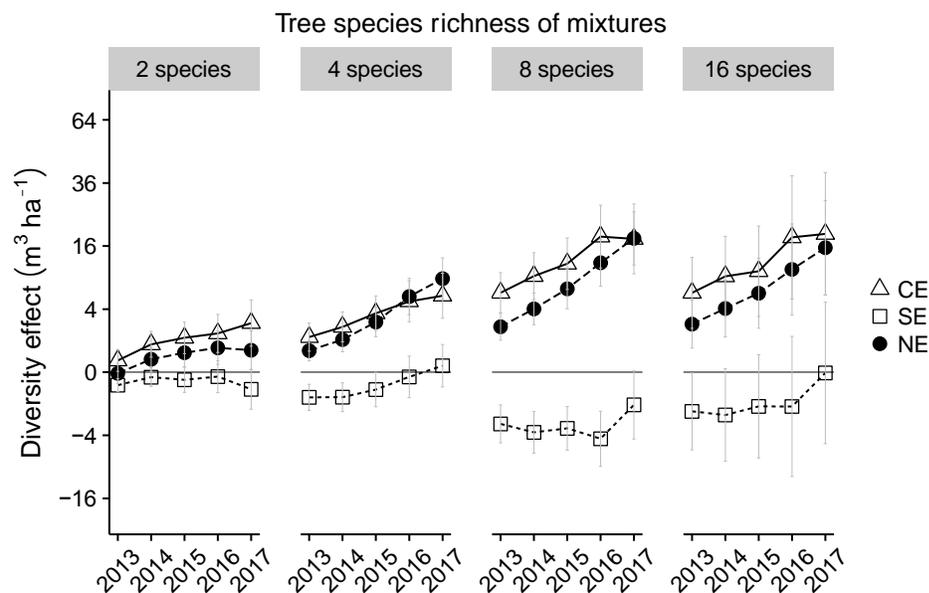
Fig. 3. Changes over time in the net biodiversity effect (NE) and its additive components,

complementarity effect (CE) and selection effect (SE), on stand-level tree volume in mixed-

species plots of increasing diversity level from left to right. Sample sizes from low diversity

level to high diversity level were 65–77, 50–52, 28 and 14, respectively. The figure shows means

± standard errors. The y-axis is square root-scaled to reflect the quadratic nature of biodiversity

effects (*11*).

fortunei, Elaeocarpus sp. (*Machilus* sp.*, Ailanthus altissima*) at sites A and B, respectively. This was corroborated by negative species-level selection effects (Fig. S6).

We tested if the observed species-richness effects and variation among communities of the same species richness could be explained by functional or phylogenetic diversity measures. For this we calculated functional diversity (FD) (*29*) and functional dispersion (FDis) (*29, 30*) based on the seven plant functional traits leaf duration (LD, deciduous or evergreen), SLA, WD, leaf dry matter content, leaf nitrogen, leaf phosphorus and leaf thickness and based on the first three of these, which had highest explanatory power (*25*). We also calculated phylogenetic diversity (PD) and mean phylogenetic distance (MPD) for each community (*31*). These measures can serve as proxy of functional differences when traits are conserved through evolution. All measures of functional and phylogenetic diversity had similar explanatory power as species richness for stand-level productivity measures, i.e. differences between species richness levels in stand volume could also be explained by concurrent differences in functional or phylogenetic diversity (fitted before species richness in model 1 in Tables S4 and S5, respectively). However, none of the functional or phylogenetic diversity measures could explain additional variation among communities of the same richness level (i.e. when fitted after species richness in model 2 in Table S4 and S5). This finding is consistent with similar reports from large-scale grassland biodiversity experiments (*32*). It is conceivable that different combinations of functional traits increase or decrease stand-level productivity of communities with particular species composition above or below the average of the corresponding species richness level, which would require community-specific selection of traits into functional diversity measures and larger replication of particular species compositions than in the present experiment.

Despite the absence of general effects of functional diversity measures beyond species richness, we found some specific effects along the multiple extinction scenarios inherent in our experimental design (Fig. S1A). Changes with each halving of species richness in the FD measure based on three functional traits were negatively correlated with volume changes at high species richness but positively correlated at low species richness (Fig. S7A), suggesting that FD captured more beneficial differences between species at low diversity but less beneficial differences at high diversity. Focusing in on the two-species mixtures, where we had the highest number of communities besides the monocultures, we could find that net biodiversity effects and complementarity effects developed positive correlations with functional-trait distances over the five years of measurements (Fig. 4 and Table S6).
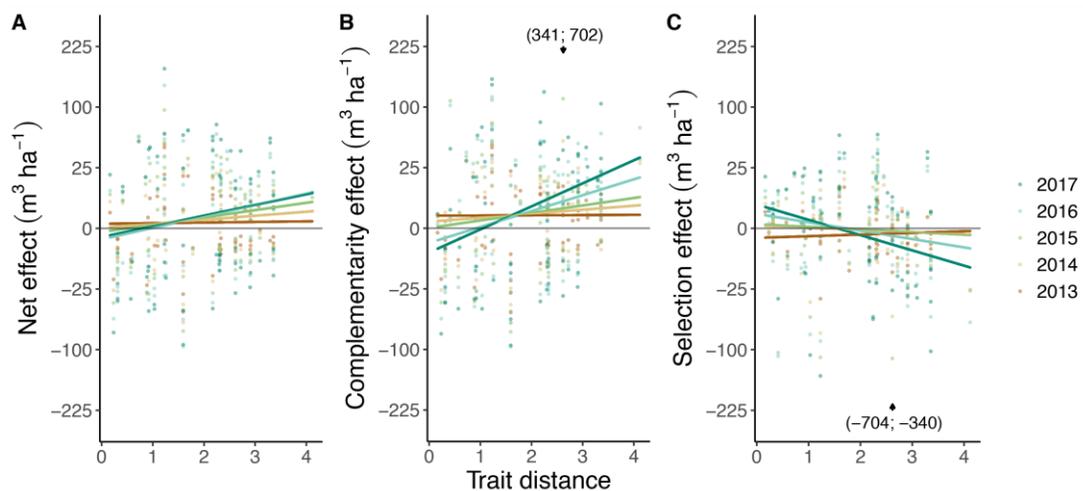
Fig. 4. Relationship between functional trait distance and biodiversity effects on stand volume in two-species mixtures across years (n = 65–77 plots). Regression lines are based on mixed-effects models (*25*). Trait distance was calculated as Euclidean distance with the three z-transformed traits leaf duration, SLA and WD (therefore no units). The y-axes are square root-scaled to reflect the quadratic nature of biodiversity effects (*11*). Two extreme y-values are moved to the plot margin and given as numbers.

Extinction sequences which differed in trajectories of community-weighted means for LD (i.e. proportion of evergreen species in a community), SLA or WD (Figs S1B to S1D) did not show any significant variation in species-richness effects on stand-level productivity (Figs S7B to S7D). This suggests that effects of trait-biased extinctions may not differ much from effects of random extinction. Although between-species variation in these traits is considered as particularly important for biodiversity complementarity effects (*33*) and together could well explain species-richness effects (Table S4), their community-weighted means could not be used to predict consequences of species loss for stand-level productivity in the species-rich forests studied here.

Competition by understory shrubs planted in the gaps between the trees reduced stand-level tree volume (shrub presence with $F_{1,234.6} = 7.10$, $P = 0.008$), but this effect decreased with shrub species richness (log shrub richness with $F_{1,198.1} = 5.61$, $P = 0.019$) and was negligible when mixtures of eight shrub species were planted (Fig. S8). Apparently, although stand-level basal area of shrubs did not decrease with shrub richness, competition between shrubs and trees was reduced at higher shrub diversity, indicating that a diverse understory may facilitate overall ecosystem functioning.

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. S4). 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 multi-site grassland biodiversity experiment (*5*). Given

that plant biomass is higher in forests, and that the largest fraction of tree carbon is bound in relatively persistent woody biomass, these effects translate into large diversity-mediated rates of carbon accumulation. Specifically, after eight years of growth at site A we found an extra 19.5 (95% CI: 14.1–25.1) Mg C ha^{-1} accumulated in 16-species mixtures relative to the average monoculture. The diversity–productivity effects 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 (*34*). 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 *(35)*, which is within the range of productivity decreases (2.1–3.1%) reported for the same tree species loss scenario in a recent observational study using plot data covering a large part of the global forests (*4*). In that study it was estimated that such a loss would correspond to around 20 billion dollars per year of commercial wood production.

Substantial forest areas are managed world-wide, with large afforestation programs underway; in China, the total forested area increased by 1.5×10^6 ha yr^{-1} from 2010 to 2015 (*36*), mainly due to new monoculture plantation of species with high short-term productivity (*37*). 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 co-benefits (*3*) 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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Supplementary Materials:

Materials and Methods

Supplementary Text

Figures S1-S8

Tables S1-S5

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