FORESTRY

Multispecies forest plantations outyield monocultures across a broad range of conditions

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Multispecies tree planting has long been applied in forestry and landscape restoration in the hope of providing better timber production and ecosystem services; however, a systematic assessment of its effectiveness is lacking. We compiled a global dataset of matched single-species and multispecies plantations to evaluate the impact of multispecies planting on stand growth. Average tree height, diameter at breast height, and aboveground biomass were 5.4, 6.8, and 25.5% higher, respectively, in multispecies stands compared with single-species stands. These positive effects were mainly the result of interspecific complementarity and were modulated by differences in leaf morphology and leaf life span, stand age, planting density, and temperature. Our results have implications for designing afforestation and reforestation strategies and bridging experimental studies of biodiversity–ecosystem functioning relationships with real-world practices.

Forest plantations are an important means of restoring degraded land, supplying ecosystem services, and mitigating climate change (*1*–*4*). In recent years, several global initiatives, such as the Bonn Challenge (*5*), the New York Declaration on Forests (*6*), and the United Nations (UN) Decade on Ecosystem Restoration (*7*), have been launched to restore degraded ecosystems and provide nature-based solutions to mitigate climate change by increasing global forest cover in the coming decades. In the context of these global initiatives, there is an urgent need to understand the factors that promote the functions and services of forest plantations to ensure effective strategic planning of afforestation and reforestation practices.

In the hope of maximizing the benefits of plantations, early foresters explored various forest plantation strategies (*8*, *9*). One strategy was to plant several tree species with different traits, such as legume and nonlegume species or conifer and broad-leaved trees—i.e., multispecies plantations (*9*, *10*). Ecological theory and experiments predict that multiple species growing together will create more biomass, called the biodiversity–ecosystem functioning (BEF) relationship (*11*, *12*). Biodiversity can increase biomass production because of either niche differentiation among species (complementarity effects) or an increased likelihood that highly productive species are present (selection effects) (*12*). Field experiments in both grasslands (*12*, *13*) and forests (*14*–*16*) have revealed that complementarity effects generally contribute more than selection effects to the observed positive BEF relationships and that these effects change with traits of species, time, planting density, and environmental conditions. The positive effect of biodiversity on ecosystem productivity has also been documented by global and regional observational studies (*17*, *18*). The long history of multispecies plantation practices (*10*, *19*, *20*) and the growing experimental research on tree diversity effects [e.g., the global network of tree diversity experiments, TreeDivNet (*16*, *21*)] provide an opportunity for a systematic assessment of the effects of species mixing in forest plantations and the mechanisms that underpin them. Here, we hypothesize that, as in BEF experiments with random species selection, multispecies plantations established by foresters can also increase tree growth and biomass production through complementarity effects and that these effects are modulated by biotic and abiotic factors.

To test our hypotheses, we assembled a global dataset (Global MixTrees) of single-species (monocultures) and multispecies stands (mixtures or mixed stands) matched by age and planting density at 255 sites from 273 publications (*22*) (figs. S1 and S2). The dataset contains 243 tree species with diverse functional traits, wide ranges of stand age and

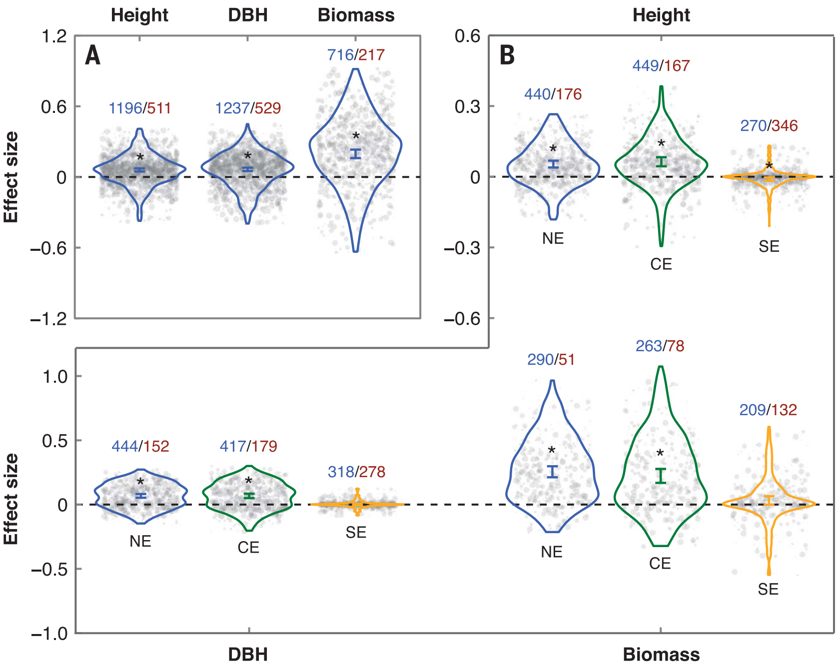

Fig. 1. Effect sizes of species mixing on height, DBH, and aboveground biomass. (**A**) Effect sizes at the species level. (**B**) Effect sizes at the whole-stand level. In (B), net effect (NE), complementarity effect (CE), and selection effect (SE) are shown in blue, green, and yellow colors, respectively. Gray bubbles show the original sample effect size, and the two numbers above each subset graph indicate the number of samples with effect sizes greater than (blue) or smaller than (red) zero. The colored bars represent the 95% confidence intervals of mean effect size across samples. *$P < 0.05$.

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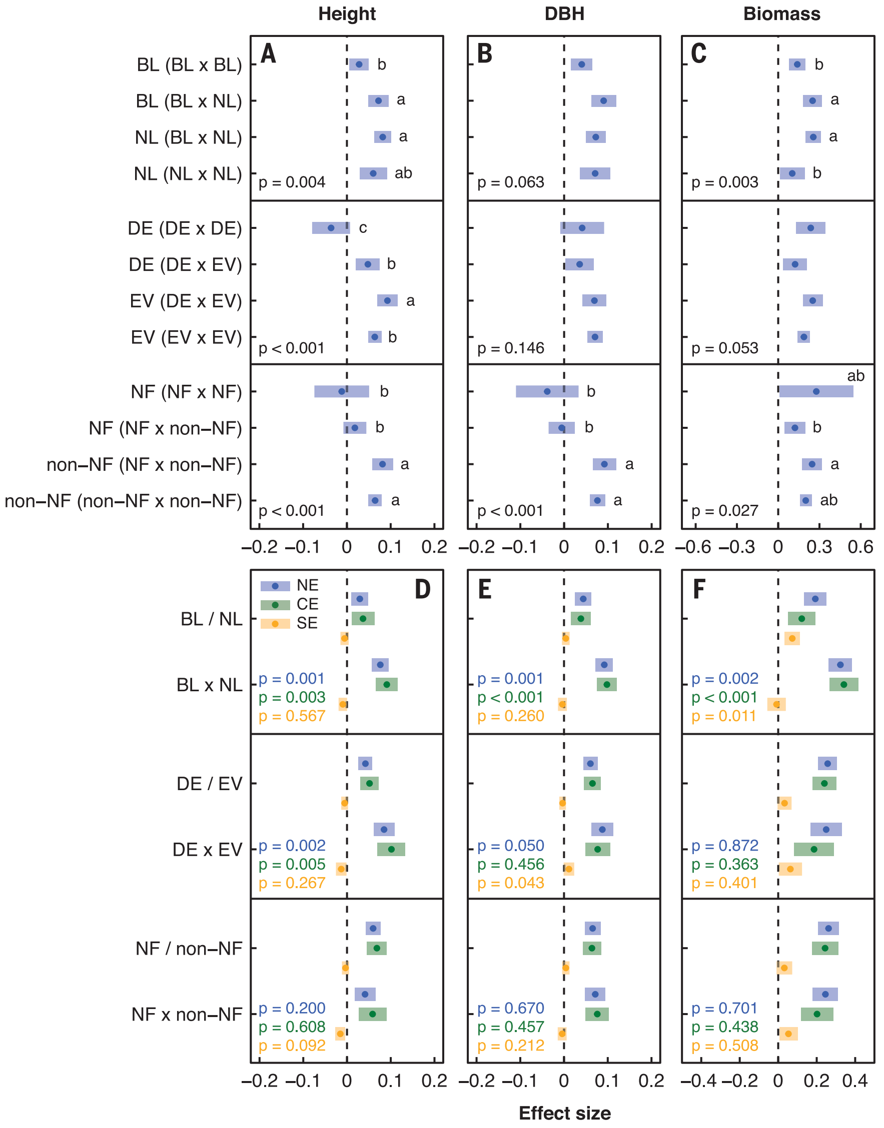

Fig. 2. Impacts of functional trait composition on the effect sizes of species mixing. (**A** to **C**) Impacts at the species level. (**D** to **F**) Impacts at the whole-stand level. (A and D) Tree height. (B and E) DBH. (C and F) Aboveground biomass. Functional traits are divided into three categories: leaf morphology [broad-leaved (BL) versus needle-leaved (NL)], leaf life span [deciduous (DE) versus evergreen (EV)], and nitrogen acquisition strategy [nitrogen-fixing (NF) versus non–nitrogen-fixing (non-NF)]. In (A) to (C), "BL (BL × NL)" denotes the effect size for the BL species in the mixed stands consisting of BL and NL species; in (D) to (F), "BL / NL" denotes the mixed stands consisting of only BL or only NL species, and "BL × NL" denotes the mixed stands consisting of both BL and NL species. Other notations are similarly defined. Colored dots and shaded bars represent the mean effect sizes and their 95% confidence intervals, respectively. *P* values are derived from likelihood ratio tests (*22*). In (A) to (C), different letters denote significant differences in the mean effect size between groups. In (D) to (F), NE, CE, and SE are shown in blue, green, and yellow colors, respectively.

planting density, and spanning a broad climatic gradient. It includes information on three major stand-level growth variables: mean tree height (in meters), mean diameter at breast height (DBH) (in centimeters), and aboveground biomass (in metric tons per hectare) (data S1 and S2). We defined a sample as a set of matched monocultures and mixed stands from the same site and with the same stand age, planting density, and mixing ratio (i.e., percentage of each species at planting) (figs. S3 and S4). Each sample typically had three to six replicates, which we used to characterize spatial environmental heterogeneity and estimate the variation of species mixing effects within the site. In total, our dataset consisted of 5959 samples, including 2323 samples for mean height, 2362 samples for mean DBH, and 1274 samples for aboveground biomass. Most samples had mixed stands consisting of two species (5439 samples), and the remaining had 3 to 16 species (520 samples) (fig. S5). We conducted our analyses at both the species (i.e., the single target species) and community (i.e., the whole stand) levels. For species-level analyses, 4406 samples were used to compare the growth of a target species in mixed stands with its growth in monocultures (fig. S3); for whole-stand–level analyses, the remaining 1553 samples were used to compare the growth of the whole mixed stands with that of the corresponding monocultures (fig. S4).

Using this dataset, we examined the effects of species mixing on three growth variables (tree height, DBH, and aboveground biomass) and explored how biotic (i.e., functional traits, stand age, and planting density) and abiotic (i.e., temperature and precipitation) factors influenced the effects of species mixing. For each growth variable, we quantified the effect size of species mixing at the species level using the logarithmic ratio of the growth variable in mixed stands versus monocultures of the target species [eqs. S7 and S8 (*22*, *23*)] and at the whole-stand level using the relative difference between the growth variable in mixed stands and the average of this variable in the monocultures of the component species [eqs. S9 and S10 (*22*)]. At the whole-stand level, we further partitioned the effect size of species mixing (also called net effect) additively into complementarity and selection effect to disentangle whether the mixing effect was caused by niche differentiation or the presence of specific species (*13*). Then, we pooled all effect sizes across samples to derive an overall effect size of species mixing at both species and whole-stand levels, as well as for complementarity and selection effects (*23*). For all analyses, we conducted tests of robustness using samples with two-species mixed stands and found that all results were qualitatively similar (figs. S6 to S9). We also tested whether effect sizes increased with species richness beyond two species.

Our analyses showed that, at the species level, the mean values of the three growth variables were all larger in multispecies stands than in monocultures (Fig. 1A). The mean effect sizes for height, DBH, and biomass were 0.060 (95% confidence interval, 0.047 to 0.073), 0.065 (0.050 to 0.079), and 0.196 (0.160 to 0.232), respectively, corresponding to a relative increase of 6.2% (4.8 to 7.6%), 6.7% (5.1 to 8.2%), and 21.7% (17.3 to 26.1%), respectively. Positive effect sizes for these variables occurred in 70.1, 70.0, and 76.7% of all samples, respectively (Fig. 1A and fig. S10, A to C). The effect sizes of these growth variables tended to increase with species richness (fig. S11, A to C).

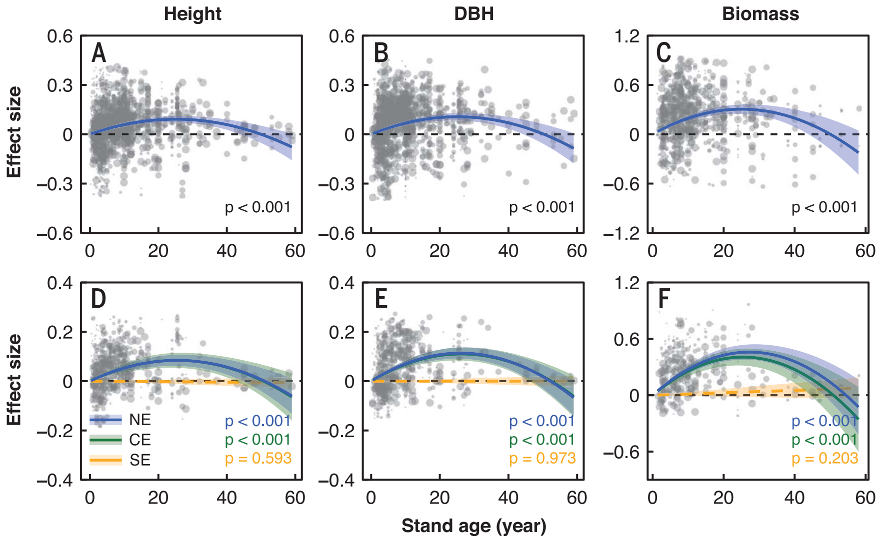

Fig. 3. Changes in the mixing effects with stand age. (**A** to **C**) Changes at the species level. (**D** to **F**) Changes at the whole-stand level. (A and D) Tree height. (B and E) DBH. (C and F) Aboveground biomass. Both linear and quadratic mixed-effects models were fit, and the optimal fits are shown according to the likelihood ratio tests (*22*). Shaded areas are 95% confidence intervals of fitted curves, with dashed lines indicating $P > 0.05$. Bubble sizes are proportional to the weights of samples. In (D) to (F), NE, CE, and SE are shown in blue, green, and yellow colors, respectively.

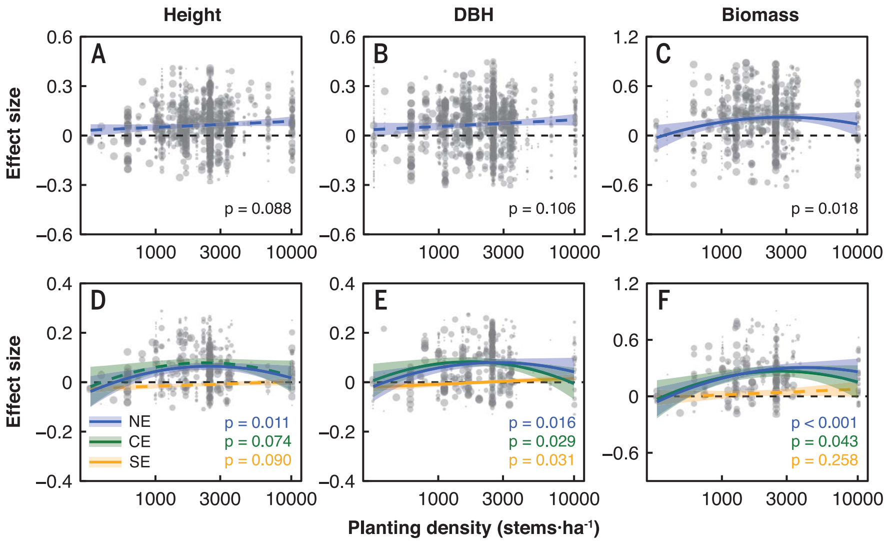

Fig. 4. Changes in the mixing effects with tree density. (**A** to **C**) Changes at the species level. (**D** to **F**) Changes at the whole-stand level. (A and D) Tree height. (B and E) DBH. (C and F) Aboveground biomass. The upper limit of planting density is set to 10,000 stems ha^{-1}, and the density values are $\log_{10}$-transformed before statistical analyses to avoid bias as a result of high leverage of a few sites with very high densities. In (D) to (F), NE, CE, and SE are shown in blue, green, and yellow colors, respectively. For other explanations, see the caption of Fig. 3.

At the whole-stand level, the three growth variables were also higher in multispecies stands than in monocultures (Fig. 1B), with an increase of 5.4% (3.9 to 6.8%) in height, 6.8% (5.3 to 8.2%) in DBH, and 25.5% (21.2 to 29.8%) in biomass. Positive net effects of these variables occurred in 71.4, 74.5, and 85.0% of all samples, respectively (Fig. 1B and fig. S10, D to F). These positive net effects were mainly the result of complementarity rather than selection effects (which were close to zero or even negative) (Fig. 1B and fig. S10, G to L). These small selection effects can be understood by the fact that foresters deliberately use highly productive tree species (*24*) and thus exclude low-performing species that probably represent most of the species in BEF experiments with random species selection (*14*) (if component species have equal performance in monoculture, then selection effects are zero by definition). As at the species level, the net and complementarity effects of the growth variables increased with species richness beyond two species (fig. S11, D to F), which supports the conclusions of previous experimental and observational studies (*14*, *17*, *18*).

To disentangle the mechanisms underpinning the positive effects of species mixing, we investigated how combinations of tree species with different functional traits influenced tree size or biomass in multispecies plantations. We focused our analysis on three groupings of species according to functional traits: leaf morphology (i.e., broad-leaved versus needle-leaved species), leaf life span (i.e., deciduous versus evergreen species), and nitrogen acquisition strategy (i.e., nitrogen-fixing versus non–nitrogen-fixing species). For each of these three groupings, multispecies plantations with opposite functional traits may produce higher complementarity effects through niche partitioning: Broad-leaved and needle-leaved species can partition space in the canopy (*25*), deciduous and evergreen species can partition seasonal time (*26*), and non–nitrogen-fixing species and nitrogen-fixing species can partition the source of nitrogen nutrition (*27*).

At the species level, target species tended to benefit more in one or more growth variables when growing with species in the opposite functional trait categories compared with those growing with species with similar traits (fig. S12). Both broad- and needle-leaved species grew taller and produced more biomass when growing with species of the other functional group than when growing with species of the same functional group (Fig. 2, A and C). Deciduous and evergreen species also grew taller when growing with species of the other compared with species of the same functional group (Fig. 2A). However, nitrogen-fixing and non–nitrogen-fixing species performed similarly when growing with species of the other or with species of the same functional group (Fig. 2, A to C). Analyses at the whole-stand level corroborated these species-level results. Multispecies stands containing both broad- and needle-leaved species had larger net and complementarity effects on all three growth variables than multispecies stands containing only broad-leaved or only needle-leaved species (Fig. 2, D to F, and fig. S13). Multispecies stands containing both deciduous and evergreen species had larger net and complementarity effects on height and DBH than multispecies stands containing only deciduous or only evergreen species (Fig. 2, D and E). However, multispecies stands containing both nitrogen-fixing and non–nitrogen-fixing species performed similarly to multispecies stands containing only nitrogen-fixing or only non–nitrogen-fixing species (Fig. 2, D to F). Overall, our results suggest that functional differences in leaf morphology and leaf life span—but notably not in nitrogen acquisition strategy—underpin stronger complementarity effects in mixed stands (*15*, *28*).

Next, we examined whether stand characteristics (stand age and planting density) modified the effects of species mixing. At both the species and whole-stand levels, the effect sizes of species mixing on height, DBH, and biomass all showed unimodal relationships when plotted against stand age, which peaked at ~25 years (Fig. 3). These unimodal patterns were mainly driven by time-dependent complementarity effects, which first increased and then decreased with stand age (Fig. 3, D to F). Previous BEF experiments have revealed increasing complementarity and biodiversity effects with experimental duration but were limited to a relatively short time span [e.g., <15 years (*14*, *29*)]. Our results corroborate findings from these short-term experiments, but they also suggest that as stands develop further, complementarity effects may subsequently decrease, possibly as a result of enhanced interspecific competition for light or soil resources (*30*).

Along a gradient of tree planting density, the species-level effect sizes for height and DBH showed increasing trends (Fig. 4, A and B), but that for biomass showed a unimodal pattern, peaking at a density of ~2860 stems ha^{-1} (Fig. 4C). At the whole-stand level, the effect sizes for all three growth variables showed similar unimodal patterns along a gradient of tree density, peaking at ~2500, 2700, and 4100 stems ha^{-1}, respectively (Fig. 4, D to F). These results support previous findings that the effect of species mixing increases with planting density within low-density ranges [e.g., <2000 stems ha^{-1} (*31*)] but that negative effects can emerge at high densities (*32*). In other words, the benefits of multispecies plantations may be reduced at both very low densities, where individuals are far apart and thus do not interact, and very high densities, where intense competition may inhibit the operation of complementarity (*30*).

Climate (temperature and precipitation) may be a factor that influences the effects of species mixing (*20*). At both the species and whole-stand levels, the effect sizes for the three growth variables all showed increasing trends along a gradient of mean annual temperature [fig. S14; see (*22*) for climatic data]. This increase was largely the result of interspecific complementarity, whereas selection effects were negligible at the whole-stand level. This suggests that warmer climates could benefit tree growth in multispecies stands more than in monocultures, which may be because of longer growing seasons that promote complementarity in time (*33*). Compared with temperature, mean annual precipitation did not significantly influence the mixing effect sizes (fig. S15), probably because forest plantations mainly occurred in humid areas where precipitation may not be a limiting factor (*34*).

Our study demonstrates substantial benefits of multispecies plantations, which corroborates and generalizes findings from forest BEF experiments (*14*, *16*, *21*) and helps to show their implications for real-world forestry applications. Our analyses offer predictions that go beyond the conclusions of short-term BEF experiments with random species selection and call for more long-term experiments with deliberate species selection to reveal the time dependency of biodiversity effects. Our findings also have direct implications for forest management and afforestation and reforestation practices. Foresters often prefer monoculture plantations because of their lower planting and management costs, targeted special uses of trees (e.g., kind and amount of timber production and economic value) (*35*), and the difficulty in identifying the site characteristics that will give the best result for a given multispecies plantation (*30*, *35*). However, a growing body of research is revealing the benefits of multispecies plantations in terms of productivity (this study), stability (*16*, *36*), community structure (*15*), and biodiversity (*4*). Therefore, we advocate a multifunctional cost-benefit analysis framework to identify planting strategies that optimize the benefits of forest plantations for restoration, conservation, and climate change mitigation.

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ACKNOWLEDGMENTS

The authors thank three anonymous reviewers for their constructive comments, which improved the quality of earlier versions of the manuscript. **Funding:** This study was funded by National Natural Science Foundation of China 31988102 (to J.F.) and 32122053 (to S.W.), Basic Research Program of Yunnan Province grant 202101BC070000 (to J.F.), and TULIP Laboratory of Excellence grant ANR-10-LABX-41 (to M.L.). **Author contributions:** Conceptualization: J.F.; Methodology: Y.F., Jianx.Z., Jiang.Z., X.X., J.X., and Z.T.; Investigation: Y.F., S.W., B.S., P.H., H.S., C.J., and Y.S.; Visualization: Y.F. and H.S.; Funding acquisition: J.F., S.W., and M.L.; Project administration: J.F. and Jiang.Z.; Supervision: J.F.; Writing – original draft: Y.F., S.W., and J.F.; Writing – review and editing: S.W., J.F., Y.F., B.S., D.I.F., M.L., S.F., and all other other authors. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** The data used in this study (i.e., the Global MixTrees dataset) are uploaded as online content (data S1 and S2). All code can be accessed at Zenodo (*37*).

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abm6363
Materials and Methods
Figs. S1 to S16
Tables S1 to S11
References (*38*–*54*)
MDAR Reproducibility Checklist
Data S1 and S2

Submitted 24 October 2021; accepted 25 April 2022
10.1126/science.abm6363

Science

Multispecies forest plantations outyield monocultures across a broad range of conditions

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Science, 376 (6595), • DOI: 10.1126/science.abm6363

Diversity boosts plantation biomass
Across experimental and natural systems, more diverse plant communities often have higher primary productivity. This effect can be due to complementarity between different species, which can more effectively use resources together, or a higher likelihood of more productive species being present. Feng *et al*. used data from 255 sites to test whether forest plantations with multiple species have greater productivity than monocultures (see the Perspective by Gurevitch). They found that multispecies plantings, on average, have taller and thicker trees and greater aboveground biomass accumulation than monocultures. This effect was mainly due to complementary between species, with greatest benefits from pairing species with different traits. —BEL

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