



Drought resistance enhanced by tree species diversity in global forests

Dan Liu¹, Tao Wang¹✉, Josep Peñuelas^{2,3} and Shilong Piao^{1,4}

Restoring species diversity is proposed as a strategy to improve ecosystem resistance to extreme droughts, but the impact of species diversity on resistance has not been evaluated across global forests. Here we compile a database that contains tree species richness from more than 0.7 million forest plots and satellite-based estimation of drought resistance. Using this database, we provide a spatially explicit map of species diversity effect on drought resistance. We found that higher species diversity could notably enhance drought resistance in about half of global forests but was spatially highly variable. Drought regimes (frequency and intensity) and climatic water deficit were important determinants of differences in the extent that species diversity could enhance forest drought resistance among regions, with such benefits being larger in dry and drought-prone forests. According to a predictive model of species diversity effect, the conversion of current monoculture to mixed-species tree plantations could improve drought resistance, with the large increase in dry forests. Our findings provide evidence that species diversity could buffer global forests against droughts. Restoration of species diversity could then be an effective way to mitigate the impact of extreme droughts on large scales, especially in dry and drought-prone regions.

Forests account for approximately half of the gross primary productivity of terrestrial ecosystems on Earth, and shifts in forest growth would either mitigate or accelerate global warming by affecting the CO₂ level in the atmosphere¹. Extreme drought is the most widespread factor that could notably decrease forest growth at regional and continental scales^{2–4}. The capacity of forest to maintain its functioning (for example, tree growth and ecosystem production) under droughts, referred to as drought resistance, is a key variable that measures the ability of forest ecosystems to continually provide ecosystem services that depend on productivity under drought conditions.

Species-rich ecosystems are generally considered to provide insurance against severe droughts compared with species-poor ecosystems because species can vary in their resistance to severe climatic disturbances^{5,6}. Evidence of such a positive effect of species diversity on resistance comes primarily from experiments conducted in grassland communities exposed to mildly fluctuating climatic conditions⁷. In contrast to grasslands, the effect of species diversity on resistance in forest ecosystems is still unclear⁸. Case studies of tropical tree seedlings⁹ and temperate forests in Europe^{10–12} indicate that high species diversity has a positive effect in mitigating the impacts of drought on forests, but other studies have found neutral¹² and even negative¹³ effects. Studies have focused on limited cases under specific environmental conditions and differ in scale (tree versus ecosystem level) and methodology (experimental versus natural settings), so comparing their results across space and time is difficult⁸. These studies have helped to identify the mechanisms of inter-specific interactions that may drive the impacts of species diversity on forest resistance during droughts but have not tested whether species diversity could stabilize productivity in extreme droughts for different forest types around the globe.

In this Article, we amassed a global tree species richness database from over 0.7 million plots, together with the drought resistance estimated using satellite-derived normalized difference vegetation

index (NDVI), to decipher the species diversity effect on drought resistance at the forest ecoregion level. We then extrapolated the species diversity effect to global forest ecoregions using a predictive model linking the species diversity effect to environmental variables. On the basis of this estimated species diversity effect across global forests, we further evaluated to what extent increasing species diversity could enhance forest resistance in the face of extreme droughts across different forest ecosystems.

Deciphering species diversity effect at ecoregion level

We used gradients of natural forest species diversity to quantify the relationship between species diversity and drought resistance in global forests. We compiled a global dataset of in situ tree species richness from the Global Forest Biodiversity Initiative (GFBFI) and the Botanical Information and Ecology Network (BIEN). This dataset contains >0.7 million plots covering most global forest types and includes a wide range of gradients of species richness, with the number of species varying from 1 to 405. We defined droughts as months when the value of the Standardized Precipitation–Evapotranspiration Index (SPEI) was below the threshold value of –0.67, corresponding to drought events occurring at least once in four years⁶. The resistance of forest productivity to drought was calculated as the ratio of vegetation indices (as a surrogate of productivity) under normal conditions to the reduction of productivity induced by drought at each 0.05° grid cell (Methods). Drought resistance was highest in species-rich forests, such as moist tropical broadleaf forests, where the average number of tree species (*S*) was 65, and was lowest in species-poor forests such as xeric woodlands and Mediterranean forests (*S* = 2) (Fig. 1), indicating the potential impact of tree species richness on drought resistance.

In biodiversity experiments, the tree species diversity is controlled and the effect of species diversity on resistance can then be directly obtained. But when using natural gradients of tree species diversity, the influence of tree species diversity on resistance can be

¹State Key Laboratory of Tibetan Plateau Earth System, Resources and Environment (TPESRE), Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China. ²CSIC, Global Ecology Unit CREA-FCM-UAB, Bellaterra, Spain. ³CREAF, Cerdanyola del Vallès, Spain. ⁴Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing, China. ✉e-mail: twang@itpcas.ac.cn

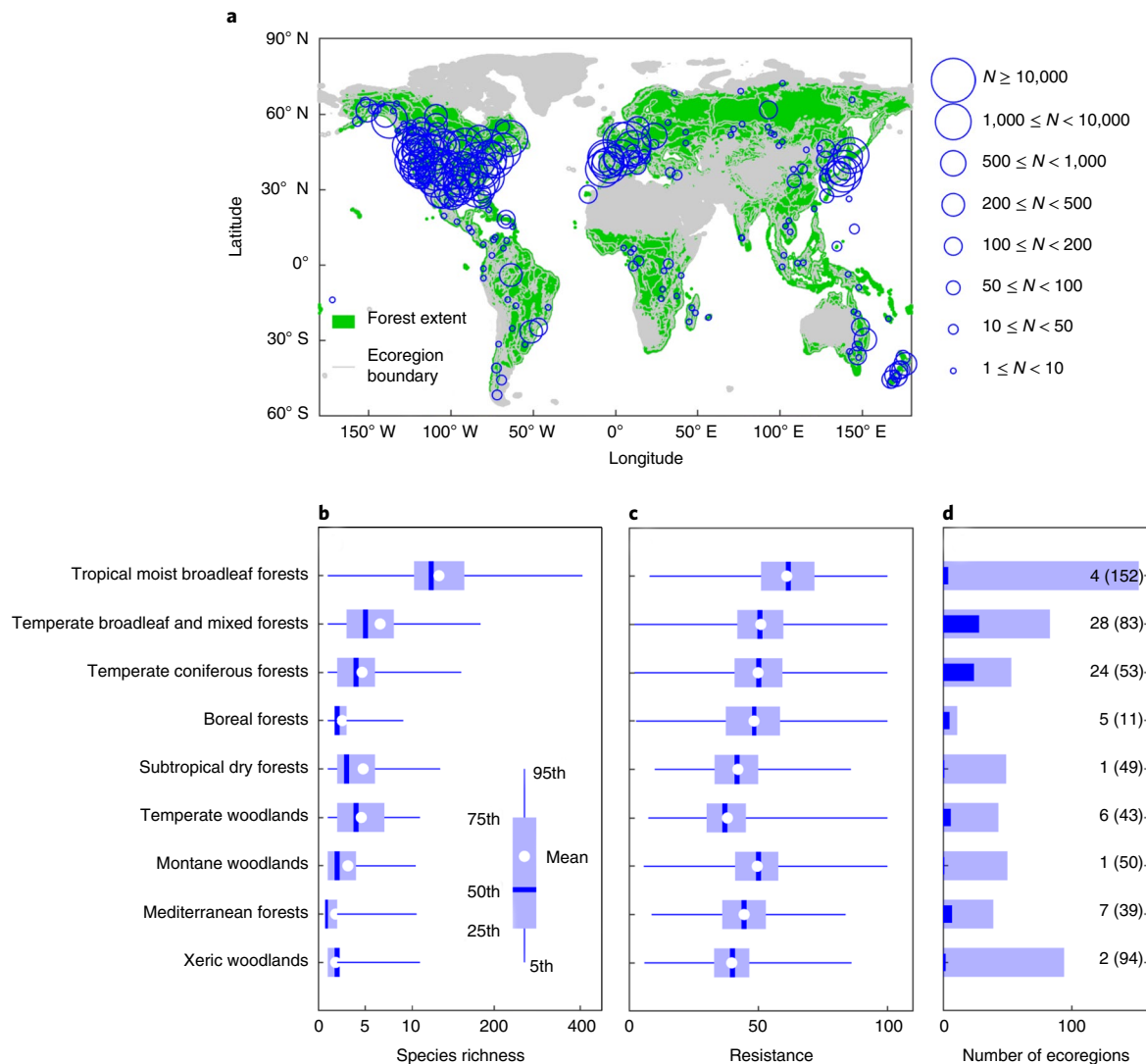


Fig. 1 | Distribution of tree species richness and associated drought resistance. a, Ecoregional distribution of forest plots from the GFBII and BIEN datasets. The grey lines show the ecoregion boundaries, and the circles show the number (N) of plots within each forest ecoregion. **b, c**, The box plots illustrate species richness, i.e., the number of tree species within the sample plot (**b**) and forest drought resistance (**c**) across all forest plots within each forest biome. The forest drought resistance was calculated as the ratio of productivity under normal conditions to reduction in productivity induced by drought, and larger values suggest stronger forest resistance to droughts. The boxes and whiskers show the 5th, 25th, median, 75th and 95th percentiles, and the white dots show the mean value of the data. **d**, Number of ecoregions for each biome. The total number of ecoregions and the number of ecoregions that was used for estimating the species diversity effect are marked with light blue bars (numbers in brackets) and dark blue bars (numbers out of brackets), respectively.

confounded by the effects of covariates of abiotic (for example, climate and drought frequency) and biotic (for example, forest age) factors. For example, species-rich forests were generally distributed in more-humid environments, which have less-intense and less-frequent extreme droughts (Extended Data Fig. 1) that might have a smaller impact on productivity and so lead to higher values of drought resistance. We overcame this issue by adopting different types of regression analyses (multiple regression, sequential regression and structural equation modelling) to separate the effect of species diversity from impacts of other potential covariates on resistance (θ) at the ecoregional level (Methods). We used pooled plots within each ecoregion to calculate θ using forest drought resistance as the response variable and relative species richness, plus environmental variables, representing drought patterns, climate, soil properties, topography, forest age and forest management status (Supplementary Table 1), as potential independent variables.

This dimensionless measure of θ allows the comparison of forest ecosystems with different levels of species diversity. A positive θ suggested that increasing species richness could enhance forest resistance to drought, with larger values indicating greater enhancement. We found that the estimates of θ were comparable among different regression techniques at the ecoregional level (Extended Data Figs. 2 and 3), and species richness generally enhanced resistance, but the magnitude of the enhancement differed greatly across forest ecoregions (Extended Data Fig. 4).

Drivers of global pattern of species diversity effect

Next we analysed how the difference in θ across ecoregions could be explained by gradients in abiotic and biotic factors. We showed that drought regimes (drought frequency and intensity) and annual climatic water deficit (CWD) were important determinants of the observed global pattern of θ (Fig. 2). Drought frequency was

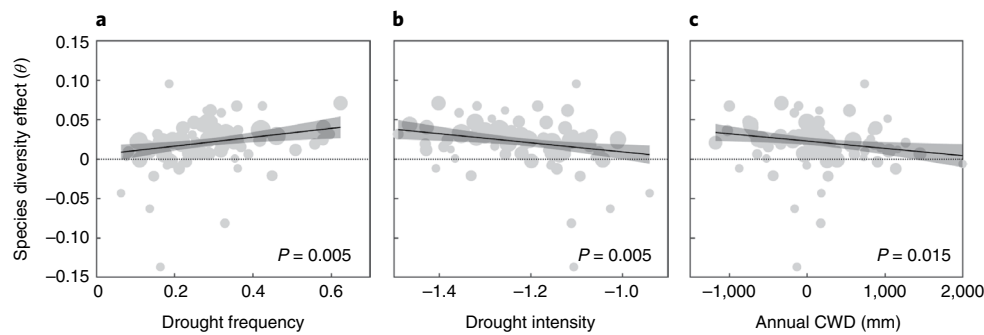


Fig. 2 | The relationships between species diversity effect on drought resistance and the main environmental variables across forest ecoregions. a–c. The relationship of species diversity effect on drought resistance (θ) with drought frequency (**a**), drought intensity (**b**) and annual CWD (**c**). The drought frequency, which is calculated as the ratio of the number of drought months to the total number of months during a growing season, varies between 0 and 1. A robust regression analysis was performed between θ and main environmental variables. The black line denotes the regression line, and the range of the error bands shows the 95% confidence intervals of the estimations of the regression model. The significance was based on the *t* statistics using a two-tailed test with sample size of 79 ecoregions. The size of the dots show the sample size of forest plots within an ecoregion, with larger dots representing ecoregions with more data points.

an important factor that could significantly explain the spatial variability of θ across forest ecoregions. The value of θ increased with increasing drought frequency (Fig. 2a, $P < 0.01$), suggesting stronger species diversity effect on resistance in drought-prone ecoregions. Drought intensity could also contribute to the spatial variation in θ , and the value of θ increases as the drought intensity increases from -1.07 (once in 9 years) to -1.48 (once in 24 years) (Fig. 2b, $P < 0.01$), suggesting a stronger positive species diversity effect under a more severe drought event. In addition to drought regimes, the value of θ gradually increased as the value of annual CWD decreased from $2,000 \text{ mm yr}^{-1}$ to $-1,000 \text{ mm yr}^{-1}$ (Fig. 2c). The CWD was calculated as annual precipitation minus potential evapotranspiration, and a more-negative value of CWD suggests more severe water deficit. This finding suggested that species diversity would generally enhance drought resistance to a larger extent in drier environments.

We found that species diversity promotes forest drought resistance to a larger extent in dry and drought-prone regions. These results are in accord with the insurance hypothesis that drought-tolerant species would be favoured in a drought-prone region via historical selective pressure, and an increase in species diversity would increase the probability of finding a species well adapted to drought conditions^{14,15}, thereby insuring forest ecosystems against large decreases in productivity by compensatory effects among species. Another possible mechanism is the reduction of water stress during droughts via enhanced positive complementary interactions among species in drier environments. The stress-gradient hypothesis suggests that positive complementarity occurs more frequently under drier conditions¹⁶, and such complementary interactions include facilitative processes such as hydraulic redistribution through plant roots—soil water transported by the root system of a species from deep to upper soil layers¹⁷ and a reduction in competition due to temporal or spatial stratification in the uptake or use of soil water¹⁸.

It is worthwhile to mention that the value of θ did not vary significantly along the gradient of the age of forest stands (Supplementary Fig. 1j), implying that the species diversity effect would not vary greatly with stand age. In addition, we did not find a significant change in the value of θ along the gradient from natural to severely managed forests (Supplementary Fig. 1m), tentatively suggesting that the enhancement in forest drought resistance through increasing species diversity might not differ largely between natural and managed forests. These results indicated that the common use of experiments of biodiversity in young tree plantations⁹ to inform the effect of species diversity in natural forests was meaningful.

Global mapping of species diversity effect

We generated a predictive model that explained 73% of the variation in θ on the basis of the relationships between environmental predictors and θ (Supplementary Fig. 2). This predictive model enabled us to extrapolate θ across global forest ecoregions (Fig. 3). To have a qualitative understanding of the relative strength of θ in the predicted map, θ values were classified into three classes (weak, moderate and strong species diversity effect) on the basis of the probability of θ being significant at the level of 0.05 (Methods). We found that nearly 44% of global forest ecoregions, mainly from temperate and tropical forest biomes, have a moderate and strong positive species diversity effect on drought resistance. By contrast, the species diversity effect is quite weak for ecoregions from boreal forests in Alaska, northern Canada and Siberia, suggesting that species diversity in these regions has only a limited beneficial effect in buffering the reduction in forest production, or even slightly exacerbates it during droughts (Fig. 3a). At the biome level, forests that normally have drier climates tended to have larger values of θ , with the largest values of θ being found in xeric woodlands (0.071 ± 0.040), subtropical dry forests (0.047 ± 0.014) and Mediterranean forests (0.029 ± 0.016) (Fig. 3b). Forests in drier and more drought-prone climates, which had lower drought resistance (Fig. 1), instead had a larger species diversity effect on drought resistance than those in wetter regions.

To compare our predicted species diversity effect with those documented from previous field-based studies (Supplementary Table 2), we amassed the species diversity effects from 24 sites with forest types ranging from subtropical and tropical (three sites), temperate (17 sites) and Mediterranean (two sites) to boreal (two sites) forest. A documented positive effect occurred at 13 of the 24 sites, and at 9 of the 17 temperate forest sites, 1 of the 2 Mediterranean forest sites and at all 3 subtropical and tropical forest sites. Ten sites, with seven temperate forests, two boreal forests and one Mediterranean forest, were reported to have a neutral effect. One site has a mixed effect. Our predicted θ generally matches geographically with these documented tree species diversity effects from field-based studies in terms of the sign, with the sign consistency found at 14 of the 24 sites (Extended Data Fig. 5). However, there is still sign inconsistency when pooling field-based studies into the two categories: the studies that used the increase in carbon isotope composition ($\delta^{13}\text{C}$) of plant material (e.g., late wood) from wet to dry years to measure drought resistance at the tree-level or ecosystem scale and studies that used changes in annual tree rings to measure drought resistance at tree scale (Extended Data Fig. 5). First, changes in $\delta^{13}\text{C}$ under

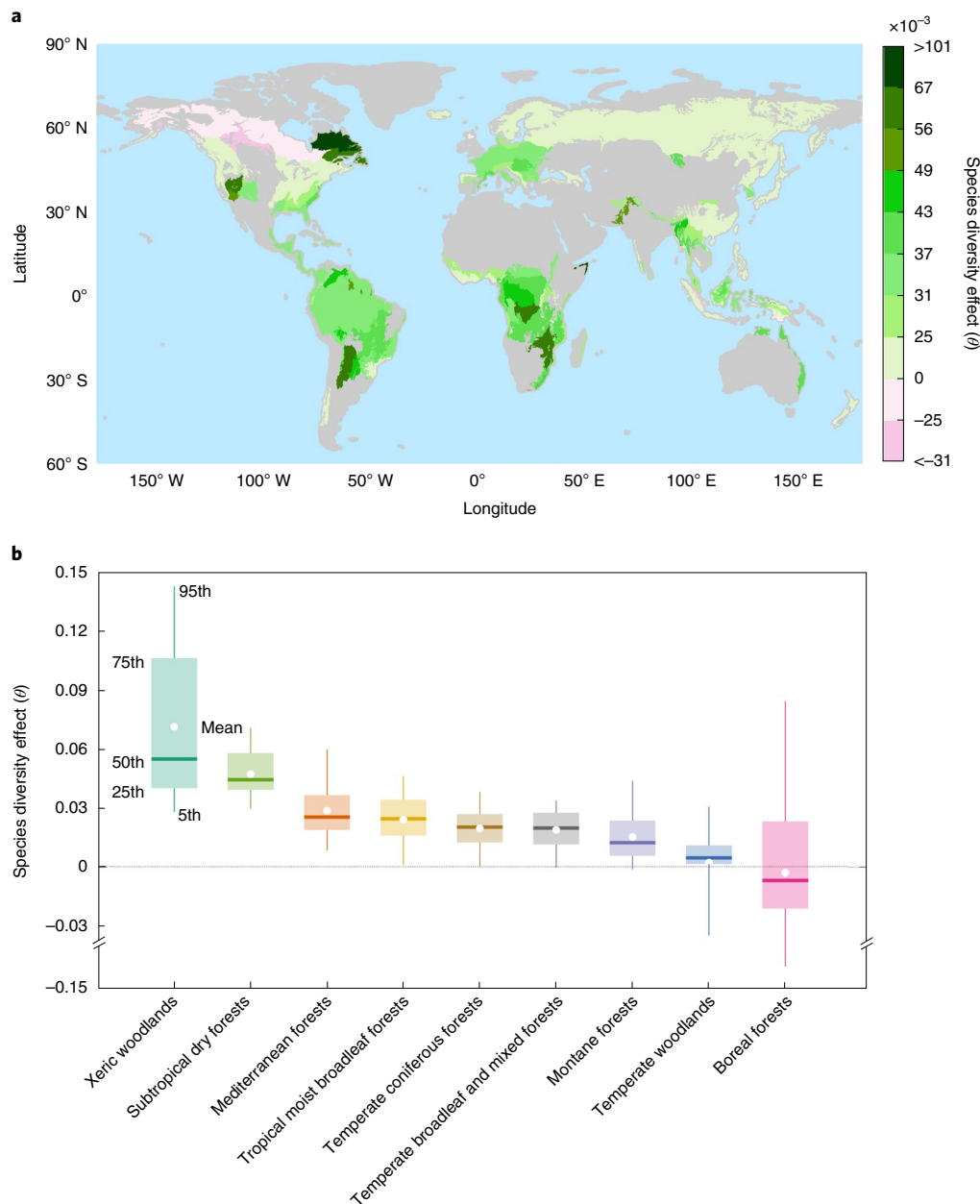


Fig. 3 | Predicted species diversity effect on drought resistance across global forest ecoregions. a, Global distribution of predicted species diversity effect on drought resistance (θ) at the ecoregion level. The labels on the colour bar with $\theta = \pm 0.025$, $\theta = \pm 0.031$, $\theta = 0.037$, $\theta = 0.043$ and $\theta > 0.101$ correspond to the 30%, 40%, 50% and 100% probability of θ to be significant at the level of 0.05 (Methods). The absolute value of θ smaller than 0.025, marked with light green (positive) or light red (negative) colours, indicates the weak species diversity effect; the values of θ between 0.025 and 0.049, marked with bright green colours, indicate moderate species diversity effect; and values of θ above 0.049, marked with dark green colours, suggest strong species diversity effect. **b**, Box plots illustrate θ from all ecoregions within each biome, with the whiskers and boxes showing the 5th, 25th, median, 75th and 95th percentiles and the white dots showing the mean value of θ .

drought conditions are affected to a greater extent by reduction in stomatal conductance than in net CO_2 assimilation and are widely adopted to represent the intensity of drought exposure in trees¹³. Such enhanced drought exposure, however, does not always translate into a decline in tree growth because of other processes such as carbon allocation¹³, thereby leading to a sign inconsistency with our estimation at some sites. Second, the species diversity effect at the tree scale could be highly context dependent, and a different species composition at one site might yield different outcomes¹⁹, contributing to the sign inconsistency with our estimation performed at the ecosystem scale. By contrast, our predicted θ is consistent with

that from field-based studies performed at the ecosystem scale. Our results highlighted the necessity of generating a spatially explicit θ that allows for comparison across space.

Implications for global tree plantation campaigns

Our findings have notable implications for large-scale afforestation and reforestation policies. Planted forests currently account for about 7% of global forest cover and are mostly intensively managed plantations composed of only one or two tree species of equal age. Although some planted forests resemble natural forests at stand maturity, they also usually consist of a very limited number of

species^{20,21}. On the basis of our global map of θ and a map of current plantation distribution²², we estimated that the conversion of current plantations from monocultures to a mixture of four species could increase the drought resistance of global plantation forests by 3.2% (Extended Data Fig. 6). Such an increase in drought resistance could buffer ecosystem productivity reduction by 3.9 TgC yr⁻¹ in response to extreme droughts during 2001–2015, which is 6.3% of the total carbon sink (62.7 TgC yr⁻¹) for global plantations²³. The benefits of mixed-species plantations were especially prominent for dry forests. The enhancement of forest drought resistance introduced by the conversion from monocultures to plantations with four species increased from 2.9% for temperate coniferous forests to 6.4% for subtropical dry forests (Extended Data Fig. 6). This finding indicated the large potential of mixed-species plantations as a management tool for enhancing forest stability under climate change, especially in the vast subtropical dry forests.

In summary, we generated a global map of the species diversity effect on forest resistance to drought and found that increasing species richness could broadly enhance drought resistance. This finding means that restoring species diversity can be justified as a valuable strategy to increase the resistance of forests against frequent and intense droughts under global warming. The positive effect of species diversity was most prominent in dry forests such as xeric woodlands, subtropical dry forests and Mediterranean forests, suggesting that these dry forest biomes should be emphasized as priorities in the current framework of planning the conservation of biodiversity²⁴. Our findings also provide guidelines for managing forest plantations and highlight the necessity to reassess current forestry policies by considering the potential benefits of increasing species diversity to reduce the vulnerability of plantations to extreme droughts. However, our data-driven extrapolation of the species diversity effect to global forests is still subject to uncertainties due to the potential omission of more extreme (for example, megadrought) events based on the short-term satellite era²⁵, and the use of taxonomy-based species diversity (in terms of species richness) instead of the functional trait-based species diversity²⁶. By including more field observations especially from undersampled regions such as tropical and boreal forests, and deploying a global network of coordinated biodiversity experiments for mechanistic understanding of macroecological gradients in the species diversity effect, similar data-driven studies are likely to provide further value to this area of research.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41561-022-01026-w>.

Received: 24 February 2021; Accepted: 9 August 2022;

Published online: 19 September 2022

References

- Beer, C. et al. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* **329**, 834 (2010).
- Anderegg, W. R. L. et al. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**, 528–532 (2015).
- Ciais, P. et al. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529–533 (2005).
- Peñuelas, J. et al. Shifting from a fertilization-dominated to a warming-dominated period. *Nat. Ecol. Evol.* **1**, 1438–1445 (2017).
- Morin, X. et al. Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecol. Lett.* **17**, 1526–1535 (2014).
- Isbell, F. et al. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574 (2015).
- De Boeck, H. J. et al. Patterns and drivers of biodiversity–stability relationships under climate extremes. *J. Ecol.* **106**, 890–902 (2018).
- Grossiord, C. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *N. Phytol.* **228**, 42–49 (2020).
- O'Brien, M. J. et al. Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. *Nat. Ecol. Evol.* **1**, 1643–1648 (2017).
- Gazol, A. & Camarero, J. J. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* **104**, 1063–1075 (2016).
- Pretzsch, H., Schütze, G. & Uhl, E. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* **15**, 483–495 (2013).
- Grossiord, C. et al. Tree diversity does not always improve resistance of forest ecosystems to drought. *P. Natl Acad. Sci. USA* **111**, 14812–14815 (2014).
- Grossiord, C. et al. Does drought influence the relationship between biodiversity and ecosystem functioning in boreal forests. *Ecosystems* **17**, 394–404 (2014).
- Loreau, M., Mouquet, N. & Gonzalez, A. Biodiversity as spatial insurance in heterogeneous landscapes. *P. Natl Acad. Sci. USA* **100**, 12765 (2003).
- Lloret, F. et al. Woody plant richness and NDVI response to drought events in Catalanian (northeastern Spain) forests. *Ecology* **88**, 2270–2279 (2007).
- He, Q. & Bertness, M. D. Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology* **95**, 1437–1443 (2014).
- Hafner, B. D. et al. Hydraulic redistribution under moderate drought among English oak, European beech and Norway spruce determined by deuterium isotope labeling in a split-root experiment. *Tree Physiol.* **37**, 950–960 (2017).
- Forrester, D. I. & Bausch, J. A review of processes behind diversity–productivity relationships in forests. *Curr. For. Rep.* **2**, 45–61 (2016).
- Vitali, V., Forrester, D. I. & Bausch, J. Know your neighbours: drought response of Norway spruce, silver fir and Douglas fir in mixed forests depends on species identity and diversity of tree neighbourhoods. *Ecosystems* **21**, 1215–1229 (2018).
- The State of the World's Forests 2020: Forests, Biodiversity and People* (FAO and UNEP, 2020).
- Zhang, J., Fu, B., Stafford-Smith, M., Wang, S. & Zhao, W. Improve forest restoration initiatives to meet Sustainable Development Goal 15. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-020-01332-9> (2020).
- Schulze, K., Malek, Z. & Verburg, P. H. Towards better mapping of forest management patterns: a global allocation approach. *For. Ecol. Manage.* **432**, 776–785 (2019).
- Harris, N. L. et al. Global maps of twenty-first century forest carbon fluxes. *Nat. Clim. Change* <https://doi.org/10.1038/s41558-020-00976-6> (2021).
- Maxwell, S. L. et al. Area-based conservation in the twenty-first century. *Nature* **586**, 217–227 (2020).
- Williams, A. P. et al. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* **368**, 314–318 (2020).
- Blackman, C. et al. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *N. Phytol.* **188**, 1113–1123 (2010).

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

© The Author(s), under exclusive licence to Springer Nature Limited 2022

Methods

Species-richness data. Records of species richness were derived from the GFBI dataset²⁷ and the BIEN dataset²⁸. The BIEN dataset provides measurements of species richness for 355 forest plots with standard plot size of 1,000 m², most of which are located in the tropics²⁸. The GFBI dataset provides measurements of tree species richness from 773,100 permanent sample plots, with 99.4% of the data plots from national forest inventories (NFIs) over nearly 20 countries²⁷. The public version of the GFBI dataset provides only the level of plot size (0–500 m², 500–1,000 m², 1,000–5,000 m² and ≥10,000 m²)²⁷. However, the plot area could still be inferred from the sampling design of the NFI of each country²⁹. The plots in the GFBI dataset from the United States (73.8% of GFBI plots) have a radius of 7.3 m (167.4 m²), and those from France (8.7% of GFBI plots), Germany (5.8% of GFBI plots) and Spain (3.9% of GFBI plots) have a radius of 25 m for field survey of species richness (1963.5 m²). By contrast, relatively small plots with fixed area are found in Japan (600 m²), Portugal (500 m²) and the Netherlands (300 m²), with contribution to GFBI plots being 1.5%, 0.8% and 0.1%, respectively. Note that the NFIs are designed to provide a holistic assessment of forest services with multiple objectives, including biodiversity monitoring³⁰. Since a comprehensive assessment for all aspects of biodiversity is not realistic, compromises have been made to balance the need for accurate estimation of species diversity and the constraints in time and cost, which would underestimate rare species in the current NFIs³¹. Nevertheless, these plots could well represent the common species and are acting as a rich and comprehensive data source for forest biodiversity research^{30,31}.

The combination of the GFBI and BIEN datasets covered most of the global forested area (Fig. 1). Moist tropical broadleaf forests were the most species-rich forests, with an average number of 65 species at the plot scale. Temperate broadleaf and mixed forests, temperate coniferous forests and temperate woodlands had about four to seven species for each plot, with only two or three species in boreal forests, Mediterranean forests and xeric woodlands.

Some forest plots present in GFBI and BIEN datasets, particularly in the United States and Europe, have been managed, but the information on the management status is not available in the public version of datasets. Here we resorted to satellite-derived global forest management data³². These data present the type of forest managed states (primary forest, naturally regenerating forests with signs of human activities, planted forest, short-rotation plantations for timber, oil palm plantations or agroforestry) for the year 2015 at a spatial resolution of 100 m². For each forest plot, we represented its forest management status using the fraction of managed forests, which is computed as the sum of the fraction of planted forest, short-rotation plantations for timber, oil palm plantation and agroforestry within a 0.05° pixel centred on the plot. Among all forest plots, only 9.5% are severely managed forests with a fraction of managed forests over 0.5, which are located mainly in the southeastern United States, Europe and Japan. Seventy-three percent are considered as natural forest (19.4%), with the fraction of managed forest being equal to zero, and slightly managed forests (53.6%), with the fraction of managed forest below 0.2 (Supplementary Fig. 3). It should be noted that the satellite-inferred forest management status at a relatively coarse spatial resolution would differ from realistic management practices (for example, harvesting and thinning) at the plot scale.

Climatic data. We used the SPEI (version 2.6) to define droughts at a monthly timescale. SPEI denotes the magnitude of drought conditions relative to average long-term conditions, with more-negative values indicating more-severe droughts³³. SPEI has a range of integration times from months to years. We used 12-month SPEI, which integrates the water status over the previous 12 months, with values <−0.67 (at least once every four years) indicating drought months.

Forest-extent and vegetation indices. We mapped forested areas at a spatial resolution of 0.05° using a global forest-change dataset³⁴. Forests were defined as those with canopy coverages >10% following the Food and Agriculture Organization definition³⁵. Net forest change was the sum of the 'loss' and 'gain' of canopy coverage. Forest extent was then obtained by summing net forest change into treecover2000 (tree canopy cover for 2000). We also used a map of forest plantations at a spatial resolution of 1 km (ref. 22). This dataset scales down national and subnational forest data to map global forest management and classifies global forests into primary, naturally regrown and planted forests. Pixels marked as planted forests were used to generate a mask of forest plantations.

We used satellite-based vegetation indices to estimate ecosystem resistance to droughts. The monthly NDVI for 2001–2016 was derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) MOD13C2 Collection 6 product. This latest version of the MODIS product resolves the problem of sensor degradation present in the Collection 5 product, providing more-accurate monitoring of terrestrial vegetation growth³⁶. We focused only on droughts in the growing season and defined the start and end of the growing season using a dataset of satellite-derived phenologies (VIPPHEN_EVI2 v004) for 2001–2016³⁷. To estimate the effect of increasing species diversity in monocultured plantations on buffering ecosystem production perturbations during droughts, we also used data for gross primary production for 2001–2015 derived from the MODIS MOD17A2 product.

Calculating forest resistance to extreme drought. The resistance of forests to drought was calculated using MODIS NDVI, a proxy for ecosystem productivity. It was defined as the ratio of productivity under normal conditions to the reduction in productivity induced by drought:

$$R_t = \frac{Y_{\text{ref}}}{Y_{\text{ref}} - Y_e} \quad (1)$$

where R_t represents forest resistance to drought, Y_{ref} is productivity under normal conditions (reference productivity) and Y_e is productivity during a drought. We calculated R_t at monthly time step, and considered only months when productivity declines in response to droughts. We used the average productivity for a given month over all the years for 2001–2016 to represent Y_{ref} . The change in productivity induced by drought ($Y_{\text{ref}} - Y_e$) is equivalent to the detrended and deseasonalized anomaly of productivity for the drought months of each year. An R_t value of 10, for example, indicates that a drought led to a 1/10 decrease of productivity relative to the multiyear average productivity during a specific month. A larger R_t indicates a smaller decline in productivity and a higher resistance to drought.

Mapping the species diversity effect on resistance across global forest ecoregions

Here we estimated the species diversity effect on drought resistance at the ecoregion level using the regression technique that could remove the confounded effect from environmental covariates. The boundaries of ecoregions were derived from the Terrestrial Ecoregions of the World³⁸, which is a biogeographic regionalization of the terrestrial biotas of Earth under the classification framework of biogeographic realms and biomes. This map subdivides the 14 terrestrial biomes of the world into 827 ecoregions. We selected 18 predictor variables, including drought frequency and intensity, and 16 environmental variables of climate, soil properties, soil nutrients, topography, forest age and fraction of managed forests (Supplementary Table 1). The drought frequency was calculated as the ratio of number of drought months to the total number of months during a growing season, and drought intensity was calculated as the average SPEI for drought months. All the data points within each ecoregion were used to fit regression models. We have at least 20 parameters in the regression models, and a minimum sample size of 10 times the number of parameters (at least 200 data points) is needed for an accurate estimation of θ (ref. 39). Therefore, we removed ecoregions where the number of forest plots was less than 200. Note that most sampling plots of species richness are derived from temperate forests, while forest plots from boreal and tropical forests are insufficient in number and scattered across different ecoregions. We therefore merged 40 ecoregions in South America as an ecoregion of the tropical forest (246 forest plots) and 8 ecoregions in midwestern Canada as an ecoregion of the boreal forest (262 forest plots). We also kept the two ecoregions from the tropical forests that have less than 200 forest plots (163 plots for Puerto Rican moist forests and 154 plots for Serra do Mar coastal forests). Finally, we obtained data from 79 ecoregions for analysis, with 4 from tropical moist broadleaf forests, 5 from boreal forests and 70 from temperate biomes.

As the area of the sampling plot could have a large impact on the species richness, differences in the sizes of plots within an ecoregion could potentially affect our estimation of θ . The GFBI plots within an ecoregion generally fell within the same size level since the majority of plots are derived from the same NFI dataset (Supplementary Fig. 4). For some ecoregions where a small proportion of plots have the area size different from the majority, we discarded these plots and calculated the average number of species from plots within each 0.05° pixel to match the scale of drought resistance. One exception is the tropical forests from South America, where there are plots from the BIEN dataset with an area of 1,000 m² and plots from individual studies with an area of 10,000 m² (refs. 40,41). For the tropical ecoregions where plots are derived from multiple sources, we estimated the number of species at a target plot size (1,000 m², the size of the most abundant plots) from that at its original size, using a power function species–area relationship ($S = cA^z$) with $z=0.25$ (ref. 42).

We developed a multiple regression model to estimate the species diversity effect (θ) while controlling the potential confounded effect from environmental covariates:

$$R_{ti} = \theta \times \hat{S}_i + \sum_{j=1}^m \alpha_j \times X_{ij} + \varepsilon \quad (2)$$

where R_{ti} is resistance for pixel i , \hat{S}_i is relative species richness calculated as the ratio of percentages of species richness and the maximal species richness in the ecoregion, X_j is environmental variable j , α_j is the regression coefficient of environmental variable j and ε is the residual term. To ensure the linear model follows the normal distribution, we log transformed both R_t and \hat{S} . Note that the robust regression was conducted to avoid influences from outliers using the "robustbase" package in R.

To test the robustness of our calculation using the multiple regression technique, we also adopted other types of regression models (two types of sequential regression models and a structural equation model) that were suggested to well separate or remove the confounded effect from environmental covariates

on drought resistance⁴³. For the first type of sequential regression model, we regressed species richness against environmental variables to obtain the residuals of species richness after removing its covariation with environmental variables, which is denoted as residual(\hat{S}_i) in equation (4). The residuals of species richness, together with environmental variables, were then regressed against forest drought resistance to estimate θ , which is considered to be devoid of the influence from environmental covariates. This sequential regression model was expressed as:

$$\hat{S}_i = \sum_{j=1}^{j=m} \alpha_j \times X_{ij} + \varepsilon \quad (3)$$

$$Rt_i = \theta \times \text{residual}(\hat{S}_i) + \sum_{j=1}^{j=m} \alpha_j \times X_{ij} + \varepsilon \quad (4)$$

The estimated θ s are identical with that from the multiple regression model (Extended Data Fig. 2a). For the second type of sequential regression model, we regressed forest drought resistance against all the environmental variables, and the residuals of this regression represent the component of forest drought resistance that could not be explained by environmental variables, which is denoted as residual(Rt_i) in equation (6). We then regressed this residual against species richness to obtain an estimate of θ . The second type of sequential regression model is structured as follows:

$$Rt_i = \sum_{j=1}^{j=m} \alpha_j \times X_{ij} + \varepsilon \quad (5)$$

$$\text{residual}(Rt_i) = \theta \times \hat{S}_i + \varepsilon \quad (6)$$

The θ estimated from the second type of sequential regression model is also highly consistent with the estimation using a multiple regression model (slope = 0.78, $R^2 = 0.98$, $P < 0.01$; Extended Data Fig. 2b).

In addition, we used structural equation modeling (SEM) to estimate θ by including the direct and indirect effects of environmental variables on drought resistance. Specifically, we introduced a composite variable ENV to denote the combined effect from all the 18 environmental variables and developed the model structure as shown in Extended Data Fig. 3a. The coefficient θ denotes the species diversity effect, and the coefficient β_1 represents the direct impact of environmental variables on forest drought resistance. The product of coefficients θ and β_2 is the indirect effect of environmental variables on forest drought resistance through species richness, representing the potential confounding effect of environmental covariates on drought resistance (Extended Data Fig. 3b). Such confounded effect was rather small, with its value (0.003 ± 0.01) being orders of magnitude weaker than those from the direct environmental effect (0.48 ± 0.11) and the species diversity effect (0.03 ± 0.04). The estimate of θ from SEM is also comparable to that from the multiple regression model (slope = 1.13, $R^2 = 0.85$, $P < 0.01$, Extended Data Fig. 3c).

We then extrapolated these θ s to global forest ecoregions by developing a predictive model, which linked θ to environmental variables (Supplementary Table 1), including the categorical variable (for example, the biome type) across 79 ecoregions using a regularization approach. Specifically, θ was modelled as a function of all predictors, including the nonlinear effect of all predictors and the interaction effect among predictor variables. We fitted this predictive model using the least absolute shrinkage and selection operator approach for regularization based on “glmnet” package in R programme.

To have a qualitative understanding of the relative strength of θ in the predicted map, we classified θ values into three classes (weak, moderate and strong effect) using different thresholds. To determine these thresholds, we resorted to logistic regression that could specify the probability that a binary response variable (taking on values 0 or 1) is one class given the value of the explanatory variable. Specifically, we conducted a logistic regression using significance/non-significance of θ at the level of 0.05 as the response variable and θ from 79 ecoregions as the explanatory variable (Supplementary Fig. 5). Thus, θ with the estimated probability of significance less than 30%, corresponding to an absolute value smaller than 0.025, indicates a weak effect; θ with probability of significance between 30% and 70%, corresponding to absolute value between 0.025 and 0.049, indicates a moderate effect; and θ with probability of significance above 70%, corresponding to the absolute value greater than 0.049, indicates a strong effect.

The comparison of predicted θ with field-based estimation. We amassed 20 studies that reported the tree species diversity effect on drought resistance over 24 sites (Supplementary Table 2). The studied ecosystems range from subtropical and tropical (three sites), temperate (17 sites) and Mediterranean (two sites) to boreal (two sites) forest. These field studies differ in terms of the measurements used to denote forest drought resistance and the scales at which the species diversity effect was explored (Supplementary Table 2). At three-quarters of these sites, forest drought resistance was measured using the changes in annual tree rings (as a proxy of vegetation growth) under drought. This metric is conceptually coherent with our

metric using changes in satellite-derived vegetation growth (for example, NDVI). At the remaining one-quarter of these sites, the increase in $\delta^{13}\text{C}$ of plant material (for example, late wood) from wet to dry years was used to approximate drought resistance, which reflects the balance between net CO_2 assimilation and stomatal conductance. Specifically, the increase in $\delta^{13}\text{C}$ is attributed more to the stomatal conductance reduction under drought conditions than to the decline in net CO_2 assimilation. It was widely used as an indicator of the intensity of drought exposure in trees¹³. The use of different metrics for drought resistance could lead to different results. For example, there is a larger increase in $\delta^{13}\text{C}$ in mixed forest ecosystems than pure forests under drought, suggesting more severe drought exposure, thus a lower drought resistance in mixed forests¹³. Such exacerbated drought exposure, however, did not translate into a larger decline in stand basal area increment in mixed forests, instead suggesting a neutral species diversity effect when using tree growth responses to measure drought resistance¹³. This is mainly because tree growth is a synthesized metric, which integrates all physiological processes related to resource acquisition and use (for example, stomatal response and carbon allocation). For the studies in which results using both vegetation growth and $\delta^{13}\text{C}$ were reported in one study, we selected only the results using vegetation growth responses for comparison.

Estimating the effect of increasing species diversity on resistance in global plantations. We quantified the benefit of enhancing species diversity in global plantations using the estimated global map of θ . The number of tree species varied widely from one to hundreds of species across regions, so the effect of increasing one species in plantations could differ greatly between species-poor and species-rich forests. Therefore, we first quantified the relative change of the species richness to its potential maxima (ecoregion maxima) on the basis of the data of species richness. For the ecoregions lacking species richness observations, we used the biome maxima as an alternative. Extremely high values of species richness for each biome were considered to be outliers and were removed using Tukey fences with $k = 1.5$ (refs. ⁴⁴). Increasing one species in monocultural plantations was then equivalent to a relative increase in species richness of 20.7–41.5% for Mediterranean forests and 0.2–0.5% for moist tropical broadleaf forests (Supplementary Fig. 6).

Increasing relative species richness in plantations from S_1 to S_2 can lead to relative changes in resistance:

$$\Delta Rt = \frac{Rt(S_2) - Rt(S_1)}{Rt(S_1)} \times 100\% \quad (7)$$

On the basis of equations (2) and (7), we calculated the relative change of resistance due to introducing four species, which is commonly found in temperate broadleaf forests, in monocultural plantations. We further combined changes in resistance with MODIS gross primary productivity data to calculate the corresponding changes in forest productivity.

Data availability

The GFBI species-richness data can be accessed at <https://www.gfbinitiative.org/metadata-gfb1>. The BIEN species-richness data is available from <https://doi.org/10.6084/m9.figshare.7436951.v1>. The SPEI dataset can be downloaded from <https://spei.csic.es/database.html>. The MOD13C2 collection 6 NDVI product can be accessed at https://e4ftl01.cr.usgs.gov/MODV6_Cmp_C/MOLT/MOD13C2.006/. The MOD17A2 dataset was derived from http://files.ntsg.unt.edu/data/NTSG_Products/MOD17/GeoTIFF/Monthly_MOD17A2/. The forest-change data are available at <https://earthenginepartners.appspot.com/science-2013-global-forest>. The distribution of global plantations is freely available at <https://www.environmentalgeography.nl/site/>. Other datasets supporting the findings of this manuscript are available in the main text or Supplementary Information. The estimated species diversity effect for global forests can be accessed at <https://zenodo.org/record/6948912#.YufCT3ZByUk>. Source data are provided with this paper.

Code availability

All computer codes used in this study can be provided by the corresponding author upon reasonable request.

References

- Liang, J. et al. Positive biodiversity–productivity relationship predominant in global forests. *Science* **354**, aaf8957 (2016).
- Wieczynski, D. J. et al. Climate shapes and shifts functional biodiversity in forests worldwide. *P. Natl Acad. Sci. USA* **116**, 587–592 (2019).
- Tomppo, E. et al. National Forest Inventories: Pathways for Common Reporting (Springer, 2010).
- Chirici, G. et al. National Forest Inventories: Contributions to Forest Biodiversity Assessments (Springer, 2011).
- Magnussen, S., Smith, B. & Uribe, S. National Forest inventories in North America for monitoring forest tree species diversity. *Plant Biosyst.* **141**, 113–122 (2007).
- Lesiv, M. et al. Global forest management data for 2015 at a 100 m resolution. *Sci. Data* **9**, 199 (2022).

33. Vicente-Serrano, S. M., Beguería, S. & López-Moreno, J. I. A. Multiscalar drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. *J. Clim.* **23**, 1696–1718 (2010).
34. Hansen, M. C. et al. High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850 (2013).
35. *Forest Resources Assessment 2015* (FAO, 2015).
36. Lyapustin, A. et al. Scientific impact of MODIS C5 calibration degradation and C6+ improvements. *Atmos. Meas. Tech.* **7**, 4353–4365 (2014).
37. Didan, K. & Brreto, A. NASA MEaSUREs Vegetation Index and Phenology (VIP) Phenology EVI2 Yearly Global 0.05Deg CMG, NASA EOSDIS Land Processes DAAC, https://doi.org/10.5067/MEaSUREs/VIP/VIPPHEN_EVI2.004 (2016).
38. Olson, D. M. et al. Terrestrial Ecoregions of the World: A New Map of Life on Earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51**, 933–938 (2001).
39. Kline, T. J. B. Sample issues, methodological implications, and best practices. *Can. J. Behav. Sci.* **49**, 71–77 (2017).
40. Gourlet-Fleury, S. et al. Tropical forest recovery from logging: a 24 year silvicultural experiment from Central Africa. *Phil. Trans. R. Soc. B* **368**, 20120302 (2013).
41. Obiang, N. L. E. et al. Spatial pattern of central African rainforests can be predicted from average tree size. *Oikos* **119**, 1643–1653 (2010).
42. Plotkin, J. B. et al. Predicting species diversity in tropical forests. *P. Natl Acad. Sci. USA* **97**, 10850–10854 (2000).
43. Graham, M. H. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809–2815 (2003).
44. Tukey, J. W. *Exploratory Data Analysis* (Addison-Wesley, 1977).

Acknowledgements

This study was supported by the National Natural Science Foundation of China (41922004 and 41871104) (T.W.), Second Tibetan Plateau Scientific Expedition and Research Programme (2019QZKK0606) and the NSFC project Basic Science Centre for Tibetan Plateau Earth System (41988101-04) (D.L., T.W. and S.P.).

Author contributions

T.W. designed the study. D.L. performed the analysis and prepared the figures. T.W. and D.L. drafted the manuscript. J.P. and S.P. contributed to the interpretations of the results and to the text.

Competing interests

The authors declare no competing interests.

Additional information

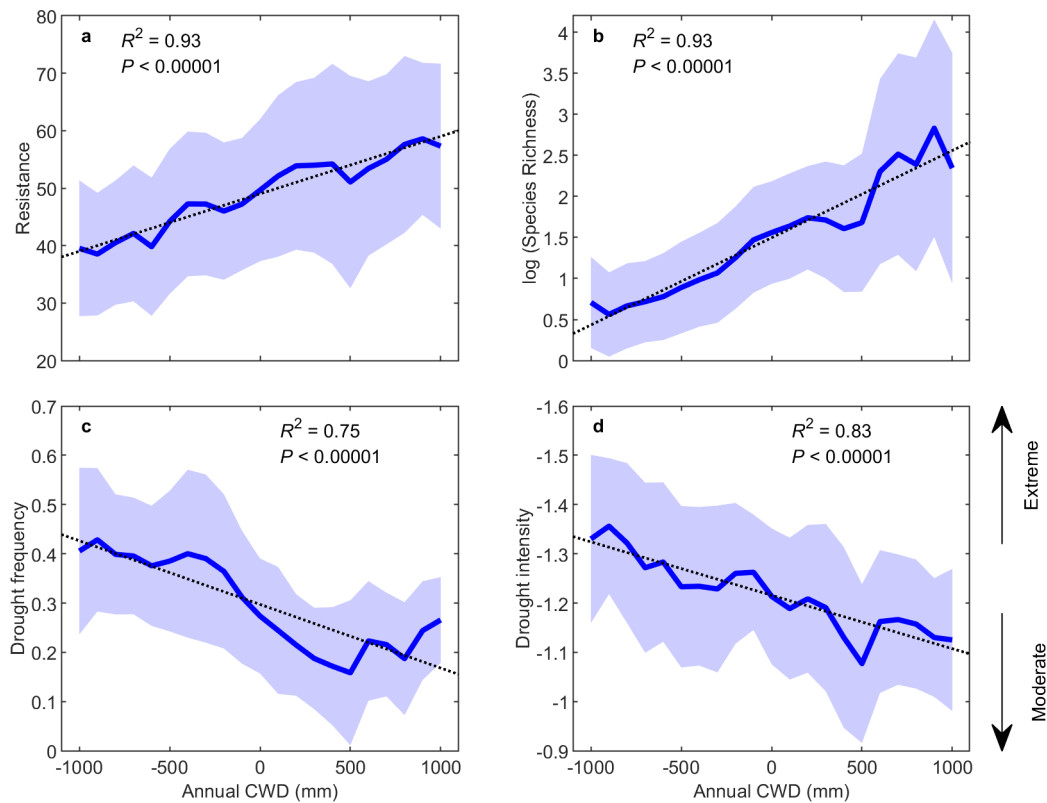
Extended data is available for this paper at <https://doi.org/10.1038/s41561-022-01026-w>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41561-022-01026-w>.

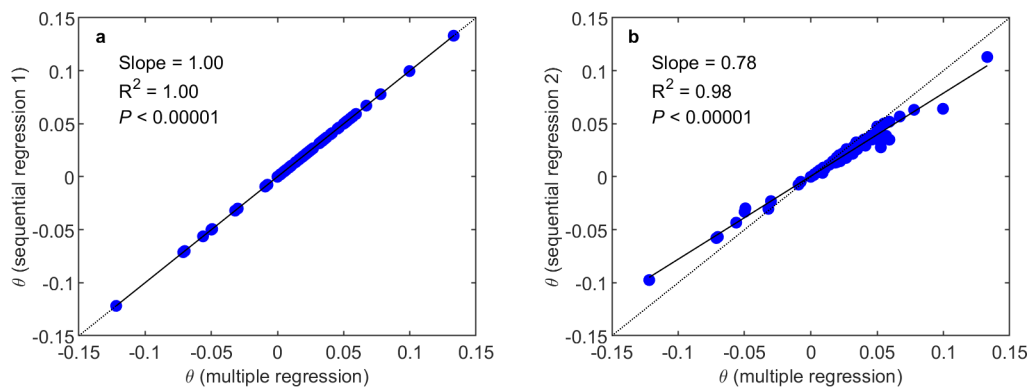
Correspondence and requests for materials should be addressed to Tao Wang.

Peer review information *Nature Geoscience* thanks Michael O'Brien, Carsten Dormann and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Primary Handling Editors: Simon Harold and Xujia Jiang, in collaboration with the *Nature Geoscience* team.

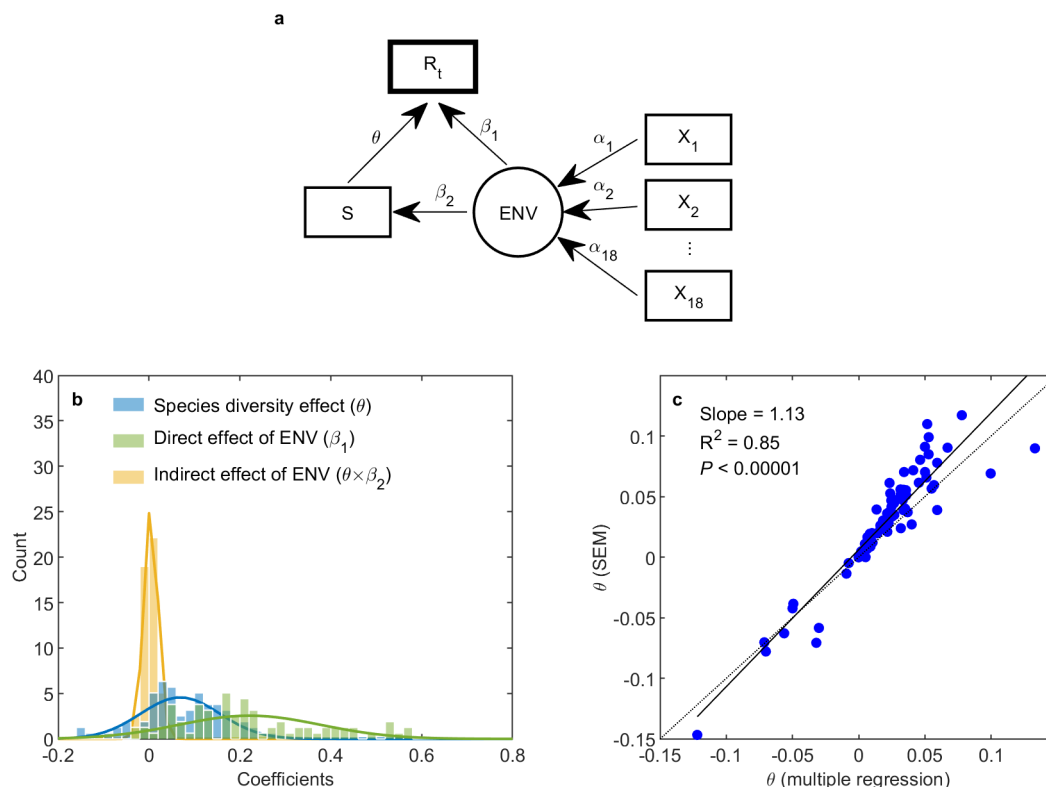
Reprints and permissions information is available at www.nature.com/reprints.



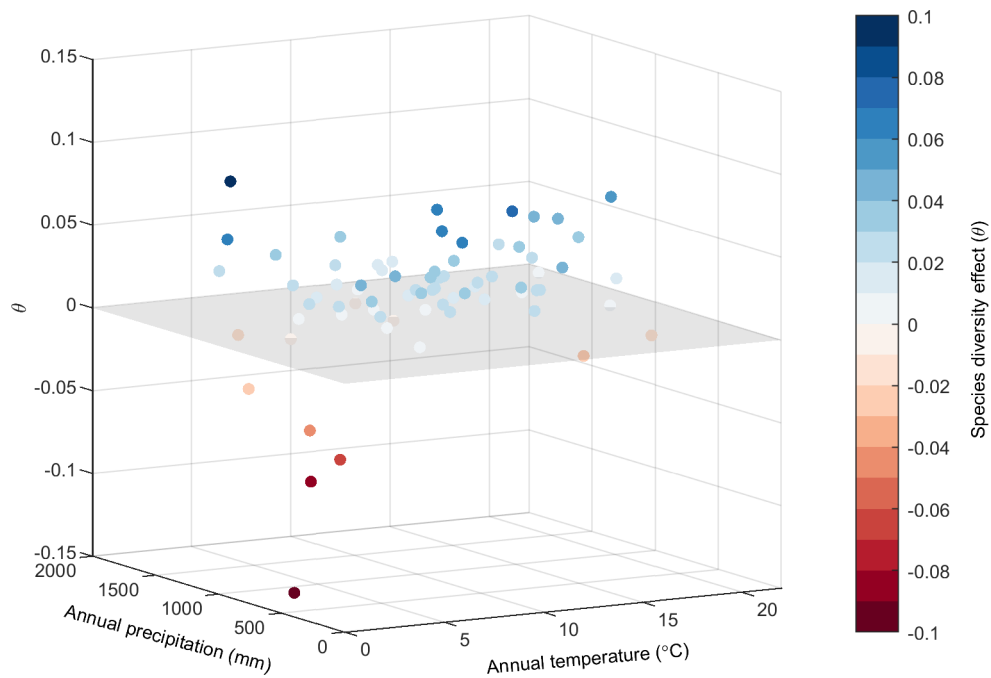
Extended Data Fig. 1 | Spatial pattern along gradient of water availability. Resistance (a), species richness (b), drought frequency (c) and intensity (d) along spatial gradient of water availability. The annual climatic water deficit (CWD), which considers both water supply and atmospheric water demand was used to describe water availability. The CWD was calculated as precipitation minus potential evapotranspiration, with positive values suggest wet climate and negative values dry climate. The line illustrates the mean value of the response variable for each 100-mm interval of CWD, and the range of the error band shows the associated standard deviation. The significance was based on the t-statistics using two-tailed test ($N = 21$).



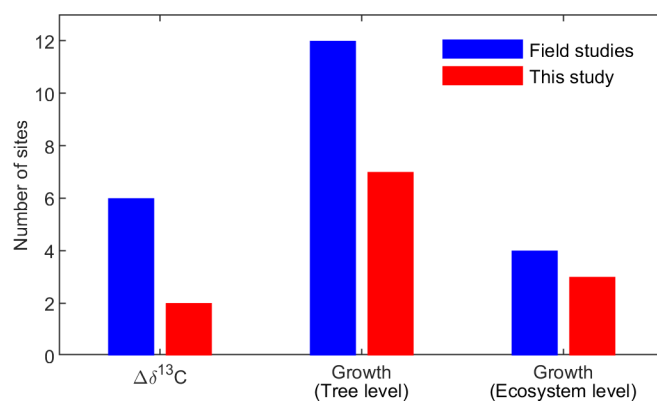
Extended Data Fig. 2 | Comparison between multiple regression model and sequential regression models. Comparison of θ estimated using the multiple regression model against that based on the sequential regression models. The multiple regression model was constructed as ' $R_t \sim \hat{S}_i + X_1 + X_2 + \dots + X_n$ '. The first type of sequential regression model was constructed as ' $\hat{S}_i \sim X_1 + X_2 + \dots + X_n$; $R_t \sim \text{residual}(\hat{S}_i) + X_1 + X_2 + \dots + X_n$ '. The second type of sequential regression model was constructed as ' $R_t \sim X_1 + X_2 + \dots + X_n$; $\text{residual}(R_t) \sim \hat{S}_i$ '. The significance was based on the t -statistics using two-tailed test with sample size of 79 ecoregions.



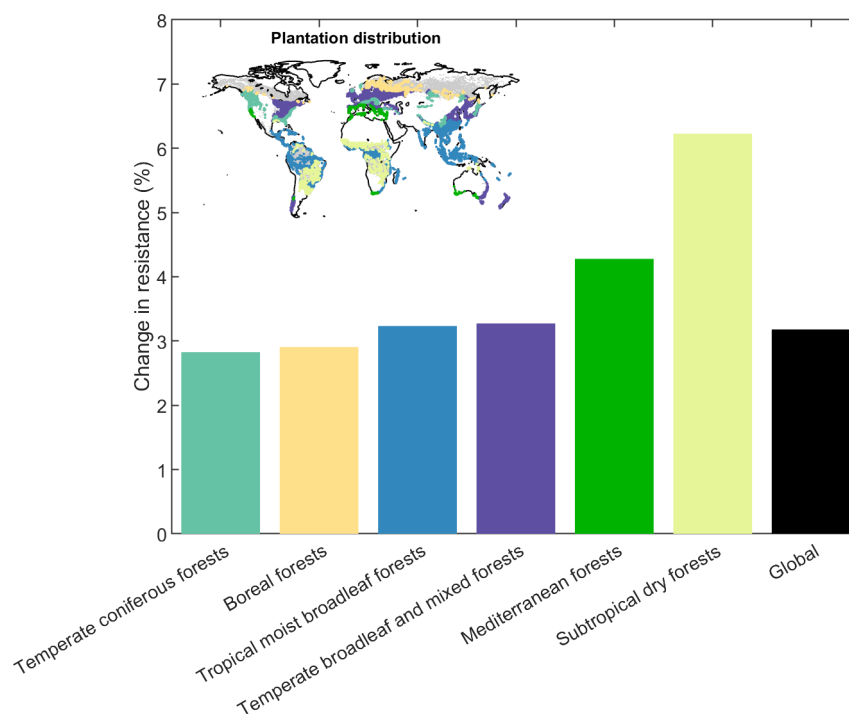
Extended Data Fig. 3 | Comparison between multiple regression model and structural equation model. A structural equation model representing the relationships among the 18 environmental variables (X_1 – X_{18}), species richness (S), a composite variable (ENV), and the response variable (R_t). (a) shows the structure of the model. Arrows depict the linkage among variables. (b) is the histogram of the estimated coefficients from all investigated ecoregions. All variables are standardized, and the coefficients are then comparable between each other. (c) shows the comparison between the estimated θ derived from multiple regression model and that from structural equation model. The significance was based on the t -statistics using two-tailed test with sample size of 79 ecoregions.



Extended Data Fig. 4 | Estimated species diversity effect at the ecoregion level. Estimated species diversity effect (θ) at the ecoregion level.



Extended Data Fig. 5 | Comparison between predicted θ with field-based studies. The blue bars show the number of sites using $\delta^{13}\text{C}$ change to measure drought resistance at both tree and ecosystem levels ($\Delta\delta^{13}\text{C}$), using changes in annual tree rings to measure drought resistance at the tree level (Growth, Tree level) and using changes in annual tree rings at the ecosystem scale (Growth, Ecosystem level). The red bars show the number of sites where the sign of predicted θ is consistent with that of documented species diversity effect from field studies. The data used in this plot are listed in Supplementary Table 2.



Extended Data Fig. 6 | Increase in drought resistance induced by converting monocultured plantations to forests with four species. The average change in resistance for each biome is marked with a distinct color, and the associated distribution of forest plantations for the biome is presented in the inset with the same color, and area in grey shows global forest distribution.