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Neighbourhood diversity increases tree growth in experimental forests more in wetter climates but not in wetter years

Liting Zheng[1,2,3*], Inés Ibáñez[1], Laura J. Williams[4], Kai Zhu[1], Hernán Serrano-León[5,6], Joel Jensen[7], Nico Eisenhauer[2,3], Kris Verheyen[8], Michael Scherer-Lorenzen[6], Florian Schnabel[2,5,9], Holger Kreft[10,11], Nathaly R. Guerrero-Ramírez[10,11,12], Dirk Hölscher[11,13], Gustavo B. Paterno[10], Bambang Irawan[14,15], Quentin Ponette[16], Christian Messier[17,18], Alain Paquette[17], Artur Stefanski[19,20], Simone Mereu[21,22], Jürgen Bauhus[5], Peter Hajek[6], Charles A. Nock[6, 23], Jeannine Cavender-Bares[24], William C. Parker[25], Julius Quosh[2,3], Olga Ferlian[2,3], Harald Auge[3,26], Catherine Potvin[27], Enrong Yan[28], Baiyu Yang[28], Li Zhang[28], Zhao Zhao[28], Katherine Sinacore[29,30], Jefferson S. Hall[31], Joannès Guillemot[32,33,34], Agnès Robin[32, 33], Pedro H. S. Brancalion[34], Leti Sundawati[35], Peter B. Reich[1, 4, 20*]

Affiliations:

[1] Institute for Global Change Biology and School for Environment and Sustainability, University of Michigan, Ann Arbor, USA

[2] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3] Institute of Biology, Leipzig University, Leipzig, Germany

[4] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, Australia

[5] Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

[6] Geobotany, Faculty of Biology, University of Freiburg, Freiburg, Germany

[7] Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

[8] Forest and Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Melle-Gontrode, Belgium

[9] Systematic Botany and Functional Biodiversity, Leipzig University, Leipzig, Germany

[10] Biodiversity, Macroecology and Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

[11] Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany

[12] Silviculture and Forest Ecology of Temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, Germany

[13] Tropical Silviculture and Forest Ecology, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

[14] Forestry Department, Agriculture Faculty, University of Jambi Jln Raya Jambi, Jambi, Indonesia

[15] Land Use Transformation Systems Center of Excellence, University of Jambi, Jambi, Indonesia
[16] Earth and Life Institute, Université Catholique de Louvain, Louvain-la-Neuve, Belgium
[17] Département des sciences biologiques, Centre for Forest Research, Université du Québec à Montréal, Montréal, Canada
[18] Département des sciences naturelles, ISFORT, Université du Québec en Outaouais, Ripon, Canada
[19] College of Natural Resources, University of Wisconsin Stevens Point, Wisconsin, USA
[20] Department of Forest Resources, University of Minnesota, St. Paul, MN, USA
[21] Institute of BioEconomy, National Research Council of Italy, Traversa La Crucca 3, Sassari, Italy
[22] National Biodiversity Future Center (NBFC), Piazza Marina 61 (c/o palazzo Steri), Palermo, Italy
[23] Department of Renewable Resources, Faculty of Agriculture, Life and Environmental Sciences, University of Alberta, Edmonton, Canada
[24] Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA
[25] Ontario Ministry of Natural Resources and Forestry, Sault Ste. Marie, Canada
[26] Department of Community Ecology, Helmholtz-Centre for Environmental Research - UFZ, Halle (Saale), Germany
[27] Department of Biology, McGill University, Montréal, Quebec, Canada
[28] Zhejiang Zhoushan Island Observation and Research Station and Zhejiang Tiantong National Forest Ecosystem Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China
[29] Agua Salud Project, Smithsonian Tropical Research Institute, Balboa, 401 Ancón, Panamá, Panama
[30] USDA Forest Service, Rocky Mountain Research Station, 240 W Prospect Rd, Fort Collins, USA
[31] ForestGEO, Smithsonian Tropical Research Institute, Ancón, 0843-03092 Panama, Panam
[32] CIRAD, UMR Eco&Sols, Montpellier, France
[33] Eco&Sols, University Montpellier, CIRAD, INRAe, Institut Agro, IRD, Montpellier, France
[34] Department of Forest Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil
[35] Department of Forest Management, Faculty of Forestry and Environment, Institut Pertanian Bogor University, Bogor, Indonesia

*** Corresponding authors' email: litingz@umich.edu; preich@umich.edu**

Abstract

Tree diversity often increases stand-level growth, but whether neighbourhood diversity effects on individual tree growth change with climatic conditions remains unclear. Here, using 852,170 records of 113,701 individuals from 129 species in 15 tree-diversity experiments across four biomes, we address this knowledge gap with a synthesis of tree growth data spanning a broad climate gradient. We examine how neighbourhood-scale (defined as a focal tree and the adjacent trees) taxonomic and functional diversity effects on tree growth vary with climate spatially (across sites) and temporally (within sites). Increasing species richness and trait dissimilarity from monospecific to high-diversity neighbourhoods enhanced individual tree growth by 7 - 13% on average. The positive diversity effect increased from dry to wet climates, contrasting with most prior studies, but was unaffected by inter-annual climatic variation within sites. Given that tree-tree interactions are ubiquitous and likely to interact with climate in both young and old forests, our findings suggest incorporating neighbourhood diversity as a management tool to enhance forest productivity, while considering underlying mechanisms and interactions with climate, thereby facilitating targeted and site-specific climate and biodiversity benefits.

Introduction

Increasing the diversity of tree species in planted or naturally regenerated forests has been proposed as a nature-based solution to ameliorate the climate crisis and maintain ecosystem functioning under changing environmental conditions[1–4]. Greater tree diversity has been shown to promote individual tree and stand growth[5,6], tree survival[7], and forest resilience and stability under a variety of environmental conditions[4,8,9]. Tree diversity at the neighbourhood scale plays an important role in modulating the contribution of tree diversity to local forest productivity, as most mechanisms of diversity effects play out via tree-tree interactions at this scale[10–12]. Furthermore, the magnitude of effects of neighbourhood interactions may depend on climatic factors such as precipitation. Water availability can mediate the strength of facilitation (e.g., stress buffering under dry conditions) and of competition (e.g., for light and nutrients under moist conditions)[13–15]. However, it remains unclear how tree species interactions at various diversity levels influence tree growth across broad climatic conditions that vary both spatially (i.e., variation across sites) and temporally (i.e., interannual variation within sites). This knowledge is critical for understanding future forest growth, and especially relevant to reforestation and management practices aimed at maintaining or increasing forest productivity across environmental conditions, particularly under a changing climate with greater interannual variation[3].

Observational studies of naturally regenerated stands using large-scale forest inventory datasets have shown that tree diversity is often more beneficial for tree growth in drier sites[16–20] (see Supplementary Tables 1 and 2), which is potentially due to increased facilitation interactions under greater abiotic stress, as the stress-gradient hypothesis suggests[21,22]. By contrast, two global-scale meta-analyses of mixed-species plantations revealed higher diversity effects on tree growth in wetter or warmer climates, due to increased differentiation in nutrient and light use[5,23]. Why observational studies on natural stands differ from plantations in this respect is unknown. Moreover, until present, there have been no similar assessments based on the increasing pool of tree diversity experiments controlling for confounding effects, which was one of our main goals here.

Additionally, some experimental studies (often limited to individual sites) have explored the effects of tree diversity on tree growth in response to interannual climatic variation, and the evidence remains mixed (Supplementary Tables 1 and 2). Some studies show that tree diversity effects are more beneficial in dry years[13,24]. The enhanced diversity effects under drought can be related to improving water access for tree individuals through hydraulic lift[25,26], reducing competition for water among species as they differ in accessing water[27], mitigating negative drought impacts on tree growth[13], reducing individual mortality risk[7], favoring drought-tolerant trees due to weakened performance of less drought-tolerant neighbors[2,28,29], and enhancing nutrient and water uptake through diverse root traits as well as mycorrhizal associations[26]. However, some other studies have shown that diversity effects remain unchanged[30], decreased[31], or are negative[32] in drier years.

These inconsistent empirical findings might be partly caused by differences in diversity measures considered, such as the species richness versus phylogenetic and functional differences among neighboring tree species that relate to different species interactions (i.e., complementarity and competition)[26,33]. Additionally, those findings may vary contingent on spatial contexts and scales (most across-site studies are region-specific[34,35]), and/or temporal scale (most single-site studies cover only two or several contrasting climatic years[30,31]). To date, relatively few studies have simultaneously examined how different facets of diversity drive tree growth across various climate conditions spatially and temporally.

To our knowledge, two observational studies have evaluated the impacts of both temporal and spatial climate variation on tree diversity effects on forest productivity[16,36], and found greater effects of tree species richness and functional diversity in drier sites, with species richness effects unaffected by inter-annual variation, and increased functional diversity effects in drier years. However, these studies focused on the community rather than the neighbourhood scale at which species interactions take place, examined one facet of biodiversity (either tree species richness or functional diversity), and were limited to specific biomes (i.e. temperate and boreal forests)[16] or forest types (dryland forests)[36]. Here, we examine how tree diversity effects vary with climate spatially and temporally using individual tree growth and neighbourhood data from 15 tree diversity experiments across a broad range of climates and four biomes. Although data from young experimental forest sites have certain limitations and may not always be applicable to more mature, natural forests, our study advances our insight into the climate dependency of tree diversity effects. By covering a broader bioclimatic gradient than prior studies and using an explicit neighbourhood rather than community-scale approach, we examine how species richness and functional trait diversity drive neighbourhood influences on tree growth.

A number of metrics can be employed to quantify effects of tree diversity at the neighbourhood scale, including neighbourhood species richness, trait dissimilarity and trait hierarchy. Neighbourhood species richness has been considered a powerful metric to capture tree diversity effects on tree growth[11,37]. Richness effects on growth of an individual tree can differ in direction and magnitude[11,12], which may depend on the functional characteristics of the focal tree and the functional diversity of the neighbourhood[13,30,38]. Traits approaches can potentially lead to a more mechanistic understanding of species interactions. Functional traits that represent plant resource acquisition strategies[39,40] mediate outcomes of complementary (i.e., resource partitioning or facilitation) or competitive interactions among neighboring species[41–43]. Neighbourhood interactions expressed through trait differences among species may be non-directional (i.e., dissimilarity) or directional (i.e., hierarchy)[41,44,45]. Trait dissimilarity, a proxy for niche differences, may result in greater resource partitioning, and/or higher facilitation and lower competition[44], and is closely related to complementary interactions[43,46]. Trait hierarchy, a proxy for fitness differences, is closely related to competitive interactions[46]; tree growth responses to neighbourhood diversity may depend on the competitive advantage associated with particular trait values (i.e, whether the focal tree has higher or lower trait values compared to its neighbors)[43–45]. Therefore, we hypothesize that neighbourhood species richness, trait dissimilarity, and traits characterizing high competitive ability promote individual tree growth (H1; Fig. 1A).

We further hypothesize that neighbourhood diversity effects are stronger under drier conditions in terms of both spatial (across sites) and temporal (within sites) variability (H2a; Fig. 1B), based on the predictions of the stress-gradient hypothesis[21,22]. However, two other outcomes are also hypothetically possible. Neighbourhood diversity effects may vary with spatial climate variations rather than temporal variation (H2b), due to canopy structure and carbon reserves that buffer the influence of interannual climate variation[16,47,48]. Alternatively, neighbourhood diversity effects may be more strongly mediated by climate variation within than across sites (H2c), as the outcomes of plant interactions might be weakly related to spatial climate variation[41,49]. Identifying which of these hypotheses are fully or partly true is crucial to assess how neighbourhood diversity effects vary with climate variability in space and time.

In the present study we analyze 852,170 growth records of 113,701 tree individuals from 129 tree species, covering multiple years (4-14 inventories per site, 84 site × year combinations; Supplementary Figs. 1 and 2). Records were collated from 15 experiments, primarily within the TreeDivNet network (https://www.treedivnet.ugent.be), across a broad range of climates and four biomes (Fig. 2), which manipulated community tree species richness (in the early stages of stand development; from monocultures to 24-species mixtures), creating a gradient from monospecific to diverse tree neighbourhoods (1 to 12 species; Supplementary Table 3). To test H1, across all sites and years, we assessed the overall mean effects of neighbourhood species richness and trait differences associated with three key functional traits (Supplementary Fig. 3): specific leaf area, leaf nitrogen content, and wood density. These traits are linked to resource (e.g., light and carbon) acquisition and hydraulic efficiency[39,40]. To test H2 and its alternatives, we examined how neighbourhood diversity effects on tree growth relate to climatic water availability across and within sites.

Results

Positive neighbourhood diversity effect on tree growth

Focal tree growth, measured as annual basal area increment (BAI), ~~which reflects structural development over a short term and emphasizes physical growth and expansion,~~ was analyzed as a function of its size in the preceding year, the effects of neighbourhood competition intensity, and neighbourhood tree diversity (either neighbourhood species richness ~~(NSR)~~, trait dissimilarity or trait hierarchy). After accounting for the influence of the focal tree size and neighbourhood competition intensity (i.e., basal area of neighboring trees; Supplementary Fig. 4), we found a positive effect of neighbourhood species richness on tree growth (Fig. 3A; Supplementary Table 4). Individual tree growth was on average 8.7% (95% CI 1.1 to 17.4) higher in neighbourhoods with high species diversity (six different species, the highest richness common to most sites) compared to growth with monospecific neighbourhoods (Fig. 3B).

Neighbourhood trait dissimilarity also had a positive effect on focal tree growth: individual tree growth increased by 6.6% (95% CI 0.5 to 12.6), 7.9% (2.4 to 15.1), and 13.3% (2.9 to 24.8) with high dissimilarity (set at 90th percentile of dissimilarity indices across all sites; Supplementary Fig. 5A) of specific leaf area, leaf nitrogen content, and wood density, respectively. However, neighbourhood trait hierarchies — indicative of competitive ranks — did not show any significant associations with tree growth (Fig. 3A; all 95% CIs included zero). Overall, increasing neighbourhood species richness and trait dissimilarity from monospecific to high-diversity neighbourhoods enhanced individual tree growth by 7-13% on average. Additionally, the median-level (50th percentile) increases in neighbourhood species richness and trait dissimilarity also promoted focal tree growth by an average of 1%-3% (Fig. 3B).

Neighbourhood diversity effects vary with climatic conditions

We further examined whether neighbourhood diversity effects on focal tree basal area growth changed with climate spatially (across sites) and temporally (across years within sites). The positive effects of neighbourhood species richness on focal tree growth increased as water availability (precipitation / potential evapotranspiration; P/PET) increased across sites and years (Fig. 4; Supplementary Table 5), and this increase was almost exclusively caused by the differences between sites with different average water availability (Supplementary Table 6). Specifically, the neighbourhood species richness effect on tree growth was weak to negligible in ecosystems with low water availability, but stronger and more positive at sites with higher water availability. However, within sites, the strength of the neighbourhood species richness effect was generally not influenced by changes in water availability year to year (Fig. 4; slopes of the individual sites). When considering climate anomalies (standardized precipitation-evapotranspiration index, SPEI), the effects of neighbourhood species richness on tree growth did not change with the intensity of climate events (Supplementary Fig. 6).

The influence of neighbourhood trait dissimilarity for the three traits (specific leaf area, leaf nitrogen content, and wood density) on growth did not change along the water availability gradients both across and within sites (Fig. 5A-C and Supplementary Table 6), and the influences were generally positive at most sites (13 out of 15 sites). There were also weak associations between water availability and the effects of neighbourhood trait hierarchy across and within sites (Fig. 5D-F). When considering climate anomalies within sites (i.e., temporal variability), the effects of neighbourhood trait dissimilarity and hierarchy on tree growth did not change with variation in the intensity of climate events (in relation to SPEI; Supplementary Fig. 7).

Further results indicated that forest age was not a confounding factor affecting the observed relationships between neighbourhood diversity effects and climatic water availability. First, there was no significant correlation between model residuals and forest age (Supplementary Fig. 8). Second, when forest age was included as a covariate, it did not affect neighbourhood diversity effects (Supplementary Table 5). Additionally, the greater effects of neighbourhood species richness on tree growth in wetter sites were not attributable to longer experimental durations. Neighbourhood species richness still generally increased tree growth more with high water availability (Supplementary Fig. 9) when data was restricted in the earlier years (from 3 to 6 years; a common period to most sites). As tree size in the preceding year (usually highly correlated with age) was included as a covariate, our models controlled for stand age, allowing us to isolate the neighbourhood diversity effects on tree growth along the gradient of climatic gradient from temporal dynamics.

Discussion

We found that the positive neighbourhood diversity effect increased from dry to wet climates but was unaffected by inter-annual variation within sites. These results were inconsistent with our hypothesized scenarios regarding the climate dependency of tree diversity effects, and contrary to most previous studies which found amplified diversity effects in drier sites[13,16,17,24]. Still, our findings corroborate previous studies showing that plant diversity can enhance productivity and carbon storage, providing an effective nature-based solution at local scales[1–4]. We thus confirmed our hypothesis that neighbourhood tree diversity positively impacts tree growth across various climatic conditions. Overall, these findings highlight the crucial role of neighbourhood-scale tree diversity in enhancing growth, and reveal that its influence varies according to spatial climatic conditions.

Our study confirms the positive effects of neighbourhood species richness on tree growth, and also underscores the importance of functional trait dissimilarity and, to a lesser extent, trait hierarchy, both of which relate to two important components determining net diversity effects: complementarity and competitive interactions. The positive effects of neighbourhood trait dissimilarity indicate that dissimilarity in light and carbon capture (i.e., through specific leaf area and leaf nitrogen content) and hydraulic efficiency (i.e., through wood density) between focal and neighboring trees can enhance tree growth. Generally, mechanisms behind the positive effect are complementary strategies in light absorption[50], water uptake[26] and use[30,51], mineral nitrogen use[52], increases in tree water use efficiency[51], facilitation via hydraulic lift[53], and/or more stable microclimatic conditions[47,48]. We did not find consistent effects of neighbourhood trait hierarchies on tree growth. Competitive advantages can arise from high or low resource acquisition capacity or hydraulic efficiency across different climatic conditions. For example, species with high resource acquisition capacity and hydraulic efficiency (e.g., higher specific leaf area and leaf nitrogen content, and lower wood density) usually have great competitive advantages when the water availability is high, whereas species exhibiting drought-adapted trait values (e.g., higher wood density) have great competitive advantages in dry conditions[54].

We found that the intensity of neighbourhood species diversity effects on tree growth was stronger at sites with higher water availability. This may be due to enhanced light-use complementarity effects in wetter sites (where water is not the limiting resource but light is), leading to greater canopy niche partitioning and more efficient light utilization[34,38,55,56], thereby strengthening the positive impact of biodiversity on tree growth[57]. Additionally, stronger intra-specific competition and higher negative density dependent effects from natural enemies and pathogens could also contribute to the higher intensity of neighbourhood diversity effects in wetter sites[58]. For example, increased water availability tends to boost phytophagous insect activity[59] and pathogenic fungi infection rates on healthy hosts[60]. However, these multitrophic mechanisms might be weakly captured by leaf and wood trait differences (i.e., the absence of increased effects of trait dissimilarity and hierarchy of leaf economic traits and wood density at sites with higher water availability in this study). A more comprehensive understanding of climate-dependency of trait-based neighbourhood effects could be gained by integrating other combinations of traits (e.g., leaf metabolic and belowground traits[61,62]) from a multitrophic perspective[63], but currently we lack the trait data to capture such effects.

Our results differ from most previous studies that found stronger tree diversity effects in harsh environments (e.g., drier, colder, or poor site conditions)[13,16,17,24]. These stronger effects are typically attributed to decreased competition but increased complementarity or facilitation[16,17,20]. We found positive effects of neighbourhood trait dissimilarity, indicative of complementary interactions, at sites with low water availability. However, the focal tree's low competitive ability might diminish these complementary benefits, resulting in an overall weak effect of neighbourhood species diversity. Limited hydrological niche space and nutrient availability in dry sites may also constrain complementary interactions related to water and nutrient acquisition[64]. Furthermore, a modeling study indicated that biodiversity effects can be negative at both ends of the stress gradient, depending on how stress affects complementary and competitive species interactions[65]. Quantifying the strengths and importance of complementarity and competition in future studies may help gain better mechanistic insights into the influences of biodiversity on ecosystem functioning along climatic gradients.

The generally positive effects of neighbourhood species diversity and trait dissimilarity on tree growth did not vary with environmental variability within sites (i.e., dry/wet years). Still, the process by which diversity effects operate may differ between wet and dry years. In dry years, positive neighbourhood diversity effects on tree growth may arise through increased complementarity for water resources (e.g., functionally distinct neighbors partition water resources through contrasting uptake strategies[26], water stress release through hydraulic lift[53], or microclimatic buffering effects[48]). In wet years, neighbourhood diversity effects may take place via complementarity for light through enhanced light interception and use efficiency[34,56]. However, several previous studies have shown that increased tree species richness does not uniformly enhance their capacity to withstand drought[26,34,66]. While tree diversity might have positive or neutral effects under mild drought, it can become negative during severe or extreme drought due to intensified competition for limited soil water[29,32,34,65]. Furthermore, our results showed that the trait hierarchy of leaf nitrogen content (a focal tree has higher leaf nitrogen content than its neighbors) shifted from negative during severely dry conditions to positive during wet conditions, suggesting that competition for light and nutrient resources drive neighbourhood interactions in wet conditions[16]. Further studies are needed to quantify the strength of niche partitioning, facilitation, and interspecific competition under different resources to better explore mechanisms of neighbourhood diversity effect under varying drought intensities.

Due to data availability, we examined neighbourhood diversity effects on focal tree basal area increment rather than other growth metrics such as height, stem volume, or biomass. A previous study found similar diversity effects on tree height and basal area increment, with larger proportional influence on biomass due to allometry[5]. Thus, we expect neighbourhood diversity to have a proportionally larger effect on total tree carbon storage, as this increases with stem volume and biomass. Although the biodiversity-productivity relationship has been found to be non-linear along a broad climate gradient[19], we did not capture non-linear relationships between neighbourhood diversity effects and climatic water availability (Supplementary Table 7), possibly due to limited data from extreme climatic conditions. Climate change is expected to intensify drought and aridity, which will affect ecosystem functioning[67]. It remains unknown whether neighbourhood diversity effects on tree growth will follow linear trends under extreme climate conditions. Additionally, our study focused on young experimental plantations, which are usually more susceptible to climate variation than mature forests[68]. Furthermore, our results reveal considerable variation in effects of neighbourhood species richness on tree growth across and within forest biomes (Fig. 4). For instance, these effects increased from a water-limited Mediterranean site to water-abundant tropical sites, and also tended to increase with water availability within biomes (e.g., temperate forests). Further studies are needed to investigate the differences among and within biomes and to link them to local ecological contexts (e.g., light availability and soil characteristics) of forests.

The overall positive neighbourhood diversity effect on tree growth we found in young experimental forest communities aligns with previous studies showing that diversity effects are generally positive in natural forests and forest plantations, driven by complementary use of aboveground space[5,6,16,69,70]. However, the experimental pattern of tree neighbourhood diversity effects across diverse, spatial and temporal, climatic conditions, likely does not closely mirror those in natural forest ecosystems. Tree density in natural forests varies considerably across climatic gradients and over time (as opposed to being largely experimentally fixed), which may change the dynamics of complementarity and competition interactions, and therefore the tree diversity effects on growth[18,20]. The variation in tree density across different biomes/climates deserves further investigation to understand how tree diversity effects on productivity along climate gradients differ between experimental and natural systems. In addition, the influence of heterogeneous abiotic environments (e.g., soil characteristics and microclimate) may modulate diversity effects on tree growth[19,71]. Further studies with the combination of data from long-term forest diversity experiments and from natural forests are needed to further elucidate the spatial and temporal climatic dependence of tree diversity effects.

While neighbourhood diversity positively influences tree growth and regulates tree diversity–productivity relationships in forests[10,24,72], our results suggest its potential role in mitigating climate change impacts varies according to the local climate. Still, the average positive effects of neighbourhood tree diversity on tree growth across various climatic conditions suggest benefits for establishing multi-species stands with diverse neighbourhood as nature-based reforestation practices. Establishing and maintaining high-levels of neighbourhood diversity through appropriate approaches in young plantations can enhance tree growth, thereby improving the efficacy of nature-based climate solutions. Moreover, forest management approaches that incorporate tree neighbourhood diversity should consider the climate dependency of biodiversity effects (e.g., more benefits in wetter sites) to achieve more targeted and effective site-specific natural climate solutions.

Methods

Data collection

We assembled a dataset combining data from 15 forest biodiversity experiments, in which 14 of the experiments are within the global network TreeDivNet[73,74] (www.treedivnet.ugent.be). The studied experiments cover broad conditions ranging from tropical and subtropical to mediterranean and temperate biomes (Fig. 1, Supplementary Fig. 1). All tree diversity experiments were designed with a gradient of species richness at community level ranging from monocultures to 24-species mixtures (see the details of the experiments included in this study in Supplementary Table 3). At the neighbourhood scale, species richness ranged from 1 (focal trees grow in neighbourhoods with no heterospecific neighbors) to 12 (focal trees grow alongside heterospecific neighbors with 11 other species). Experiments included in this study met the following criteria: 1) experiments with measurements for at least three census intervals (i.e., four different years); 2) individual-level basal diameter (BD) (including monocultures and mixtures) measured at least every three years; 3) the x–y coordinates of individual trees within each plot were available for the calculation of local neighbourhood. Data from the initial two years after planting were excluded from each experiment because interactions among neighboring trees were not evident during this period. The dataset across the 15 sites included 852,170 growth records of 113,701 trees from 129 tree species, measured over 4-14 inventory years per site (Supplementary Fig. 1).

Climate data

We extracted annual mean temperature and precipitation, and mean annual evapotranspiration for each year at each experimental site from ERA5-Land[75], with a spatial resolution of 9 km. To estimate the annual water availability for each year at each site, we calculated the ratio of annual climate precipitation (P) to potential evapotranspiration (PET)[76]. Higher values of water availability (P/PET) indicate wetter conditions. For example, the drier sites usually have lower P/PET values (<0.65) whereas the wetter sites have higher P/PET values (>1) (Supplementary Fig. 2). We focused on climate-driven water availability, without accounting for the possible impacts of the soil water reserve.

We also obtained the Standardized Precipitation–Evapotranspiration Index (SPEI; from the global SPEIbase[77]; with a 0.5-degree spatial resolution) to determine annual water balances for each year at each site. SPEI is a site-specific indicator of the deviations of climatic balance (precipitation minus potential evapotranspiration) over a selected window from the historical long-term average (between 1901 and 2023), which can identify dry/wet years with “abnormal” climatic water balance for a given experimental site[77,78]. In this study, we considered annual water balances (calculated for a 12-month timescale) as previous studies have shown that annual growth rates respond to approximately annual water balances in both arid and humid biomes[78]. For example, both dry and wet sites can experience extremely dry ($\text{SPEI} \leq -1.5$) and wet years ($\text{SPEI} \geq 1.5$) based on each site’s historical average.

Calculation of individual tree growth

In our dataset, measured basal diameter at 5-10 cm above ground was available from 15 experiments, whereas only tree ring records were available from one experiment (BEF-China[30]). Although there were differences in the methods for tree growth measurements, combining them to test diversity effects on tree growth has been shown feasible[69]. We estimated individual tree growth as annual basal area increment (bai, cm^2 $year^{-1}$) based on the basal diameter (BD) measurements from the growth inventories or tree ring records. Annual basal area increment for each individual tree i, was calculated as the difference in the basal area in the current inventory year (t) and the previous inventory year (t_{t-1}) and divided by the time difference, in years, between measurements:

$$bai_{i,t} = \frac{\frac{\pi \cdot {BD_{i,t}}^2}{4} - \frac{\pi \cdot {BD_{i,t-1}}^2}{4}}{t_t - t_{t-1}} \qquad (1)$$

Species functional traits

We focused on species-specific leaf area (SLA; mm^2 mg^{-1}), leaf nitrogen content (LNC; mg g^{-1}), and wood density (WD; g cm^{-3}), as these traits are important for explaining plant resource acquisition strategies[38-39], and are available for a large number of species. Trait values were obtained from TRY[79], the Botanical Information and Ecology Network[80], and the global wood density database[40,81], or from site-specific measurements when available. We used species mean trait values to define plant resource-use strategies without accounting for intraspecific trait variation due to the lack of individual-level trait measurements across and within experiments. Trait values can vary depending on individual tree and stand conditions[82,83] and variability in specific functional traits within species can influence stand productivity and functioning[84,85]. However, interspecific trait variation is usually greater than intraspecific variation, and species-level trait means primarily reflect plants' acquisition strategies as an evolutionary outcome, and are effective in mediating outcomes of interactions among neighbors[41].

Data for SLA, LNC and WD were available for 92%, 92%, 98% of 129 species. Most species had measurements for three traits (n=113; Supplementary Fig. 3C). Missing trait values were gap-filled using the phylogenetic imputation procedure in the missForest R package[86]. The phylogeny was obtained using the R package V.Phylomaker[87], with the GBOTB phylogeny as the backbone[88]. The phylogeny in this analysis was fully resolved without polytomies (129 tips, 128 internal nodes). We compared the correlations between functional traits across species with complete measured traits (n=113) and across species with the imputed trait values, and found that they had similar patterns (Supplementary Fig. 3A,B), ranging from "conservative" (lower SLA, LNC and higher WD) to "acquisitive" strategies (higher SLA, LNC and lower WD). The density distributions of each trait for measured and imputed data were also similar (Supplementary Fig. 3C,D). We used the imputed trait dataset in the subsequent analyses of the effect of neighbourhood functional diversity on tree growth, which ensured a consistent dataset across all species richness-based and trait-based neighbourhood analyses.

Neighbourhood-scale competition index, species richness, trait dissimilarity and hierarchy

The distance of immediate neighbor trees surrounding a focal tree varies across different experiments due to the different planting distances (ranging from 0.4 to 3m, Supplementary Table 3). The neighbourhood radius was determined by calculating the diagonal distance in a grid-planted design using the maximum planting distance (3 m) across all experiments, calculated as 4.24 m ($\sqrt{3^2+3^2}$). This radius ensured a feasible distance to include all immediate neighbors around each focal tree, including individuals at grid diagonals, allowing for a standardized comparison across studies. Alternatively, we also used a varying neighbourhood radius (0.4-3m) for different experiments, which detected all the immediate individuals surrounding a focal tree within each site. Previous studies have shown that the detectable neighbourhood effects can extend beyond a focal tree's nearest neighbors[89]. The models using a varying neighbourhood radius produced similar results as those from the model with a fixed distance (Supplementary Fig. 10). For simplicity we opted for the latter, hence, the main results presented in this study were based on the fixed radius neighbourhood radius.

We calculated multiple indexes to capture the neighbourhood conditions of a focal tree, including neighbourhood competition index (NCI), neighbourhood species richness (NSR), trait dissimilarity (ND) and hierarchical trait difference (NHD) between a focal tree and its neighbors. NCI was estimated as the distance-dependent index based on the size and distance of its neighbors[45,90], in which the competitive effect of a neighbor k on the focal tree i varies as a direct function of the basal area of the neighbor k ($BA_{i,k}$) and an inverse function of the distance to the neighbor ($Distance_{i,k}$). NCI of all neighbors on the focal tree was summed over all neighbors n within the radius around the focal individual i (equation (2)). For focal tree i and its n neighbors k:

$$NCI_{i,t} = \sum_{k=1}^{n} BA_{k,t-1} \times \frac{1}{Distance_{i,k}} \qquad (2)$$

NSR was estimated as the number of heterospecific (different species identity as the focal tree) tree species within the radius around the focal individual. Neighbourhood trait dissimilarity (ND) and hierarchical difference (NHD) were estimated for each trait as the dissimilarity (i.e., absolute difference) and hierarchical difference (i.e., directional difference) in trait values between the focal tree and its neighbors, respectively[41,45]. ND is a proxy for the magnitude (but not direction) of niche differentiation among neighboring species, and greater trait dissimilarity may result in greater resource partitioning, and/or higher facilitation and lower competition. NHD is a proxy for differences in traits, which may reflect fitness differences, and is closely related to hierarchical competition. The overall ND or NHD of a focal tree was calculated as the mean of pairwise trait dissimilarity or hierarchical trait differences weighted by the distance and size of neighbors (equations (3) and (4)).

$$ND_{i,t} = \frac{\sum_{k=1}^{n} abs(T_i - T_k) \times \frac{BA_{k,t-1}}{Distance_{i,k}}}{\sum_{j=k}^{n} \frac{BA_{k,t-1}}{Distance_{i,k}}} \tag{3}$$

$$NHD_{i,t} = \frac{\sum_{k=1}^{n} (T_i - T_k) \times \frac{BA_{k,t-1}}{Distance_{i,k}}}{\sum_{k=1}^{n} \frac{BA_{k,t-1}}{Distance_{i,k}}} \tag{4}$$

ND ranged from zero to positive (see Supplementary Fig. 11), with a value of zero indicating that a focal tree only grows surrounded by monospecific neighbors, and an increasing value indicating that a focal tree grows with an increasing number of heterospecific neighbors that have dissimilar functional traits with the focal tree. NHD_{trait} ranged from negative to positive (see Supplementary Fig. 11). A positive value of NHD indicates that a focal tree has higher trait values (e.g., in this case, higher specific leaf area and leaf nitrogen content, or higher wood density) compared with its neighbors, and a negative NHD_{trait} indicates that a focal tree has lower trait values compared with its neighbors. There were large variances of neighbourhood hierarchical trait difference and trait dissimilarity related to different combinations of neighboring tree species within the same level of neighbourhood species richness (Supplementary Fig. 5B). In addition, NCI was very weakly correlated with each ND or NHD index (Supplementary Fig. 11).

Statistical analysis

We used two-level hierarchical Bayesian models to assess neighbourhood effects on tree growth. The hierarchical Bayesian model can effectively accommodate our data's hierarchical structures, incorporating dependencies and variations across different levels (including sites, years, species, and individuals) and providing coherent inference and reliable estimates[91].

At the first level, we modeled the growth of a focal individual tree (i) from species (j) in experimental site (s) in a specific year (t) as a function of the tree size in the preceding year, neighbourhood competition and tree diversity indices (either NSR, ND or NHD). We constructed separate models to test the effect on individual tree growth from NSR (equation 5.1), ND (equation 5.2) or NHD (equation 5.3).

Likelihood:

$$log(bai_{i,j,s,t}) \sim Normal\ (G_{i,j,s,t},\ \sigma_{j,s,t}{}^{2})$$

Process models:

$$G_{i,j,s,t} = \beta 0_{j,s,t} + \beta 1_{j,s,t}\ log(BA_{i,j,s,,t-1}) +\ \beta 2_{j,s,t}\ log(NCI_{i,j,s,t}) +\ \beta 3_{j,s,t}\ \boldsymbol{NSR}_{i,j,s,t} \quad (5.1)$$

or

$$G_{i,j,s,t} = \beta 0_{j,s,t} + \beta 1_{j,s,t}\ log(BA_{i,j,s,t-1}) +\ \beta 2_{j,s,t}\ log(NCI_{i,j,s,t}) +\ \beta 3_{j,s,t}\ \boldsymbol{ND}_{i,j,s,t} \quad (5.2)$$

or

$$G_{i,j,s,t} = \beta 0_{j,s,t} + \beta 1_{j,s,t}\ log(BA_{i,j,s,t-1}) +\ \beta 2_{j,s,t}\ log(NCI_{i,j,s,t}) +\ \beta 3_{j,s,t}\boldsymbol{NHD}_{i,j,s,t} \quad (5.3)$$

where log($bai_{i,j,s,t}$), log($BA_{i,j,s,t-1}$), and log($NCI_{i,j,s,t}$) represent the log-transformed annual growth, tree size in the preceding year, neighbourhood competition of focal tree i of species j in experimental site s in a specific year t; $\beta 0\text{-}3_{j,s,t}$ are the intercept and coefficients associated with log($bai_{i,j,s,t}$), log($BA_{i,j,s,t-1}$), log($NCI_{i,j,s,t}$), and $NSR_{i,j,s,t}$, or $ND_{i,j,s,t}$ or $NHD_{i,j,s,t}$. NCI captures the trait-independent competition for the focal tree, while ND and NHD reflect trait-dependent interaction processes[41]. The plot identity within each site was not included as a random factor in the model because: 1) there was insufficient replication within each species-site-year combination to reliably estimate plot-level variance, and 2) the plot effect was not identifiably different from the residual 'noise' term (Supplementary Fig. 12).

The effect of NCI on focal tree growth is represented by the β_2 coefficient, which can be negative or positive, indicating evidence of competition or facilitation, respectively. The effect of neighbourhood tree diversity indices (either NSR, ND or NHD) is determined by the β_3 coefficient. A positive coefficient of NSR (or trait dissimilarity, ND) indicates that neighbors with higher species richness (or greater trait differences with focal tree) is positively associated with the growth of the focal tree, via the amelioration of crowding effects or facilitation; a negative coefficient indicates that higher species richness (or greater trait differences) may diminish focal tree growth, likely due to intensified competition for resources. A positive coefficient of NHD indicates that tree growth is higher when the focal tree has a relatively higher trait value compared with its neighbors as it has a higher competitive advantage than the neighbors, and a negative coefficient of NHD indicates that tree growth is higher when the focal tree has a relatively lower trait value compared with its neighbors. We modeled one trait at a time to test the effects of trait dissimilarity or trait hierarchy on tree growth to manage model complexity and differences among traits.

To assess the overall effects of tree diversity (testing hypothesis 1), we modeled the coefficients from the first level (i.e., $\beta0\text{-}3_{j,s,t}$ from equations 5) as the overall average effect across all sites and years (B_{overall}), and the random effects for species j (ε_j, normally distributed around 0 with variance $\boldsymbol{\sigma}_j^2$) and experimental site s (ε_s, normally distributed around 0 with variance $\boldsymbol{\sigma}_s^2$) at the second level:

$$\beta_{j,s,t} \sim Normal\ (B_{j,s}, \sigma^2)$$

$$B_{j,s} = B_{overall} + \varepsilon_j + \varepsilon_s \qquad (6)$$

Based on the $B_{overall}$, we then predicted the percent change in focal tree growth from growing with monospecific neighbors at median (50th percentile of index across all sites) and high (90th percentile) level of neighbourhood diversity (Fig. 3; Supplementary Fig. 5A). The detailed interpretation of the predicted percent change (P, %) in individual tree growth with changing neighbourhood diversity can be found in the Supplementary Methods.

To assess the strengths of neighbourhood interactions along the climatic gradient (testing hypothesis 2), we constructed additional hierarchical Bayesian models. We modeled the coefficients for each species-level (i.e., $\beta 0\text{-}3_{j,s,t}$ from equations 5) as a linear function of the annual climatic variables at site *s* (equations 7). We estimated the overall relationship between the strengths of neighbourhood diversity and the climatic water availability across sites and years, also including random effects for experimental site *s* (ε_s) and species *j* (ε_j):

$$\beta_{j,s,t} \sim Normal\ (B_{j,s,t}, \sigma^2)$$

$$B_{j,s,t} = \gamma 0 + \gamma 1 \times Climate_{s,t} + \varepsilon_j + \varepsilon_s \qquad (7)$$

where

$$\varepsilon_j \sim Normal\ \left(0, \sigma_j{}^2\right), \varepsilon_s \sim\ Normal\ (0, \sigma_s{}^2)$$

The $\gamma 0$ here represents the overall neighbourhood diversity effects estimated in equations 6 after accounting for climatic effects.

To distinguish within- versus between-sites climate effects[92], we included both site mean climate and deviations from the site mean, we also included random intercepts and slopes for experimental site *s*, and the random intercepts for species *j* (ε_j) (equation 8):

$$B_{j,s,t} = G0\ +\ \gamma 0[s] + G1 \times \overline{Climate_s} +\ \gamma 1[s] \times (Climate_{s,t} -\ \overline{Climate_s}) + \varepsilon_j \qquad (8)$$

where $\text{Climate}_{s,t}$ refers to the climatic water availability of a specific year t at experimental site s, and $\overline{Climate_s}$ refers to the mean value of climatic water availability in the experimental site.

As tree diversity effects have been shown to be nonlinear along broad climatic gradients[19], we also constructed nonlinear models to examine whether there were any nonlinear relationships between neighbourhood diversity effects on tree growth and climatic water availability across sites and years. However, the model comparison indicated that the linear model had a better fit than the nonlinear model, i.e., Deviance Information Criterion[93] (DIC) of linear model was generally lower than the nonlinear model (Supplementary Table 7). Therefore, we reported the relationship between neighbourhood diversity effects and climatic water availability as a linear relationship. In addition, to evaluate whether forest age could confound the relationship between neighbourhood diversity effects and climatic water availability, we examined model residuals as a function of forest age. There was no significant correlation between the residuals of our current model and forest age (Supplementary Fig. 8), indicating that forest age was not a potentially confounding factor of the relationship between neighbourhood diversity effects and climatic water availability in this study.

We used non-informative prior distributions for all parameters (see Supplement for JAGS code), and estimated the parameters using Markov chain Monte Carlo (MCMC) sampling techniques in JAGS 4.3.2 and R 4.4.0[94] using the *rjags* package[95]. We ran three parallel chains (50,000 iterations following a 50,000-iteration burn-in period, followed by a thinning of 50, retaining 1000 posteriors per chain) with different initial values and checked parameter convergence by using Gelman and Rubin's convergence diagnostics (with a threshold value <1.1) and visual inspection of traceplots. To estimate standardized coefficients as the standardized effect size, explanatory variables were standardized (divided by their standard deviations) before analysis. Model selection for tree growth models was done based on comparisons of the DIC (Supplementary Table 8) and on goodness of fit (R^2, predicted vs. observed). Our neighbourhood-scale model had a Goodness-of-fit (R^2) ranging from 0.18 to 0.87 across species (Supplementary Fig. 13).

To test whether wetter sites with higher tree growth might have led to earlier aboveground interactions than drier sites, we compared the initial planting density and basal area accumulation over forest age across different experiments. In our dataset, the experiments in drier sites tended to have a higher planting density than those in wetter sites (Supplementary Fig. 14A). According to the comparison of neighbourhood-scale basal area (calculated as the sum of basal area for all individuals within the neighbourhood radius 4.24 m) in monocultures over time for different experiments, there was no evidence that the experiments in wetter sites (e.g., Sardinilla, a tropical experiment) began interacting sooner than those high-density experiments in drier sites (e.g., IDENT-Cloquet, a temperate experiment) (Supplementary Fig. 14B). Furthermore, we did not find that the experiments in wetter sites accumulated higher mean basal area than those high-density experiments in drier sites (Supplementary Fig. 14C). The high-density planting promoted neighboring trees to interact with each other earlier, allowing us to detect tree diversity effects and their mechanisms at an early stage. Therefore, we can somewhat rule out the possibility that the higher neighbourhood tree diversity effects detected in wetter sites were because trees began interacting sooner aboveground compared with drier sites. Meanwhile, the sites with greater neighbourhood species richness effects on tree growth did not correspond to those sites with higher initial planting density, indicating that the higher neighbourhood tree diversity effects were not caused by high initial planting density.

To further test whether greater neighbourhood diversity effects were driven by longer-running experiments that have had more time to accumulate diversity effects, we did a further sensitivity analysis by analyzing the neighbourhood tree species richness effects on tree growth along climatic gradients by limiting our data in the earlier years (from 3 to 6 years; a common period to most sites). We still found that neighbourhood species richness increased tree growth more with higher water availability (Supplementary Fig. 9). These results further indicate that climate, rather than forest age drove the pattern that we observed.

Data availability

The data including source data, information for each experiment, annual climate data, and species-level trait data used in this study are archived in Figshare (https://doi.org/10.6084/m9.figshare.29274887). Raw tree growth data from sites that have been published are publicly available, and non-public raw tree growth data are available upon reasonable request and with permission of the principal investigators of the TreeDivNet network coordinators (https://treedivnet.ugent.be).

Code availability

The R code for hierarchical Bayesian models used in this study is available at https://doi.org/10.6084/m9.figshare.29274887.

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Author contributions Statement

L. Zheng and P.B.R. conceived the project. L. Zheng, P.B.R., I.I., L.J.W. and K.Z. contributed to conceptual development. L. Zheng, H.S.-L., and J.J. assembled the data. L. Zheng performed the analyses with contributions from I.I. and P.B.R. The initial manuscript was prepared by the core group: L. Zheng, P.B.R., I.I., L.W., K.Z., H.S.-L., and J.J. All the following authors including N.E., K.V., H.K., N.R.G.-R., G.B.P., C.M., A.P., A.S., M.S.-L., F.S., D.H., B.I., Q.P., S.M., J.B., P.H., C.A.N., J.C.-B., W.C.P., O.F., H.A., C.P., E.Y., B.Y., L. Zhang, Z.Z., K.S., J.S.H., J.G., A.R., L.S., P.H.S.B. contributed to editing and improving several manuscript versions and/or data collection.

Competing interests Statement

The authors declare no competing interests.

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Figure Legends

Figure 1. Hypothesized effects of neighbourhood diversity on tree growth. a, An example illustrating the hypothesis that neighbourhood species richness, trait dissimilarity between a focal tree (t_f) and its neighbours (t_n), and higher competitive trait hierarchy all promote individual tree growth across broad climatic conditions (H1). A positive diversity effect can arise from complementary (related to trait dissimilarity) and competitive interactions (related to trait hierarchy). Trait dissimilarity: focal tree growth is greater when its trait values (Tt_f) are more dissimilar to those of its neighbors (Tt_n). Trait hierarchy: focal tree growth is greater when the focal tree has higher trait values of competitive ability than its neighbors. **b,** We further expect that the positive neighbourhood diversity effects vary with spatial (i.e., climate variation across sites) and/or temporal (i.e., interannual climatic variation within sites) climate variability (H2). Three possibilities: (H2.a) Neighbourhood diversity effects varying with climate should be observed both across and within sites, i.e., effects would be greater in both drier sites along the gradient of water availability and drier years within a site. Based on the stress gradient hypothesis[21,22], we posit that this is the most likely outcome. (H2.b) Neighbourhood diversity would have stronger effects at sites with less water availability, but nearly stable across wet and drought years within sites. (H2.c) Neighbourhood diversity may have stronger effects in dry or wet years within sites, but consistent across sites.

Figure 2. Locations of the experimental sites and annual climate during the study periods. a, Locations of experimental sites across different biomes. **B,** Distribution of annual climate during the experimental periods in this study**.** In panel B, Annual temperature and precipitation for each year (represented by a point) at each site (represented by an ellipse).

Point color represents climatic water availability (P/PET; precipitation / potential evapotranspiration), and ellipse color represents biomes (see A). The background represents the climate space of the major biomes according to the Whittaker diagram.

Figure 3. Individual tree basal area growth as a function of different metrics of neighbourhood diversity. a, Standardized growth coefficients of neighbourhood species richness (top orange), neighbourhood trait dissimilarity (middle green) and trait hierarchy (i.e., hierarchical trait difference; bottom blue) of specific leaf area (SLA), leaf nitrogen content (LNC) and wood density (WD). Dots represent species level coefficient means in different years at different sites (*n* = 675 species-year-site combinations) from 15 experimental sites, and large circles show the overall means (estimated $B_{overall}$ in Equation (6)) and 95% credible intervals (* indicates statistical significance, 95% credible intervals excluded zero). **b,** Predicted percent change (%, mean and 95%CI) in focal tree growth from growing with monospecific neighbors to median level (50th percentile of neighbourhood diversity indices across all 15 sites; lighter colours) and high level (90th; darker colours) neighbourhood species richness (top, orange), trait dissimilarity (middle, green), and trait hierarchy (bottom, blue). The prediction is based on the overall coefficient mean ($B_{overall}$, see Supplementary Methods).

Figure 4. Effects of neighbourhood species richness on individual focal tree basal area growth along a gradient of water availability across and within sites. The line shows species-level standardized coefficients of neighbourhood species richness (NSR) on focal tree basal area growth (n = 675 species-year-site combinations) in relation to P/PET, fitted by the hierarchical Bayesian model. The black line and bands indicate the relationship across sites and years (the 95% credible interval [CI] of the slope parameter excluded zero and shown as

solid line), and colored lines indicate relationships across years within each site (n = 15). The inset panel shows the site-level slopes and mean P/PET.

Figure 5. Effects of neighbourhood functional trait dissimilarity (a-c) and trait hierarchy (d-f) on individual focal tree basal area growth along a gradient of water availability across and within sites. The fitted line shows species-level standardized coefficients of trait dissimilarity and hierarchy (n = 675 species-year-site combinations) in relation to P/PET (potential precipitation/evapotranspiration). Black lines and bands indicate relationship averaged across sites and years (the 95% credible interval [CI] of the slope parameter overlapped zero and is shown as dashed lines), and colored lines indicate relationships across years within each site (n = 15). The inset panel shows the site-level slopes and mean P/PET.

Figure 1

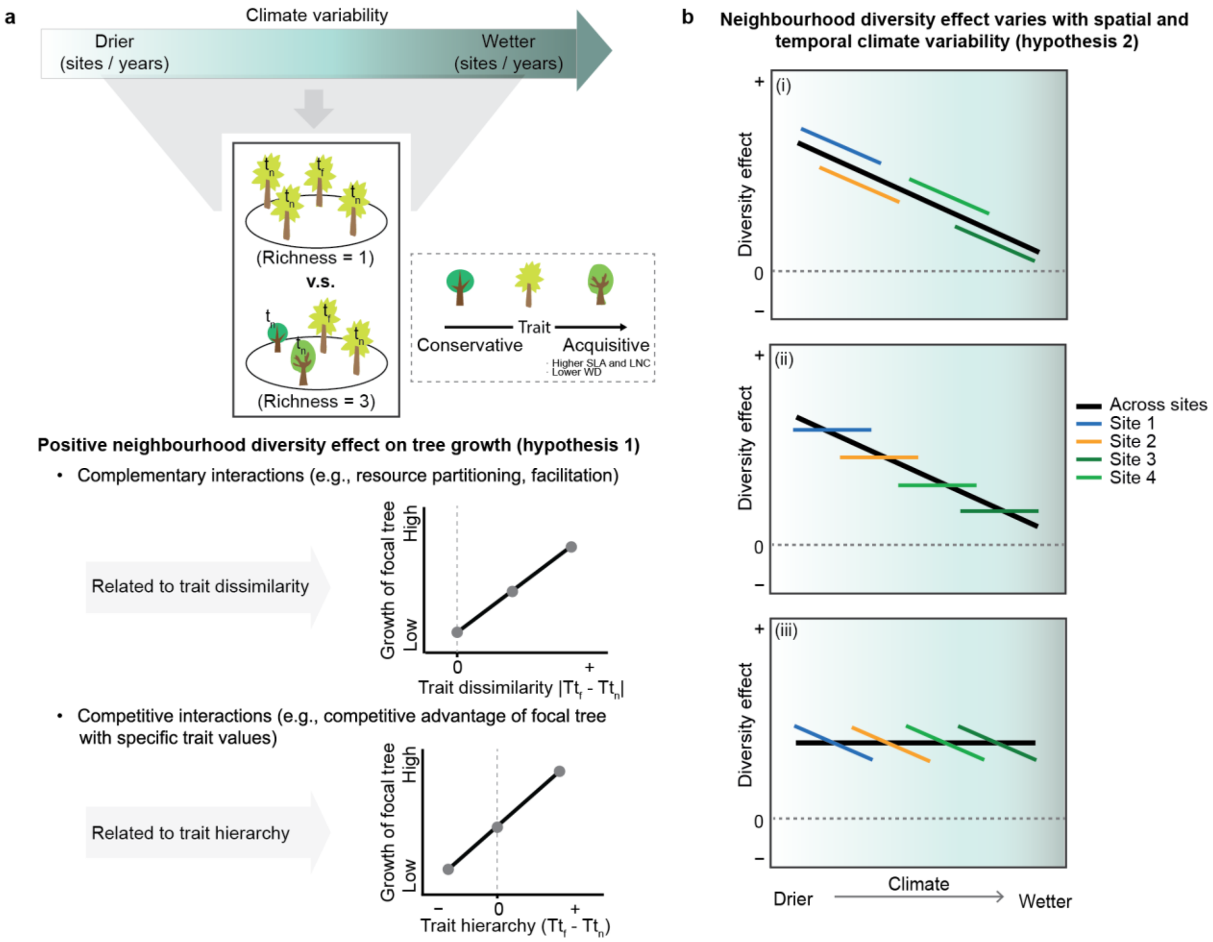
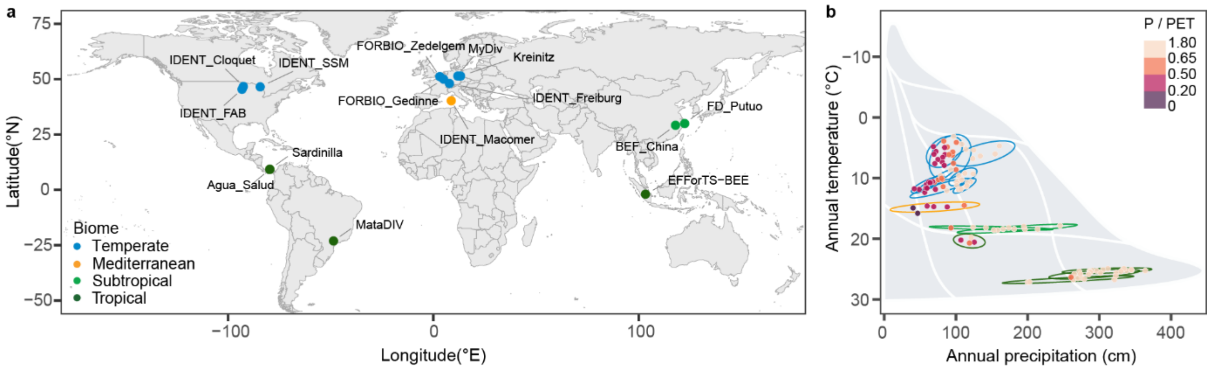
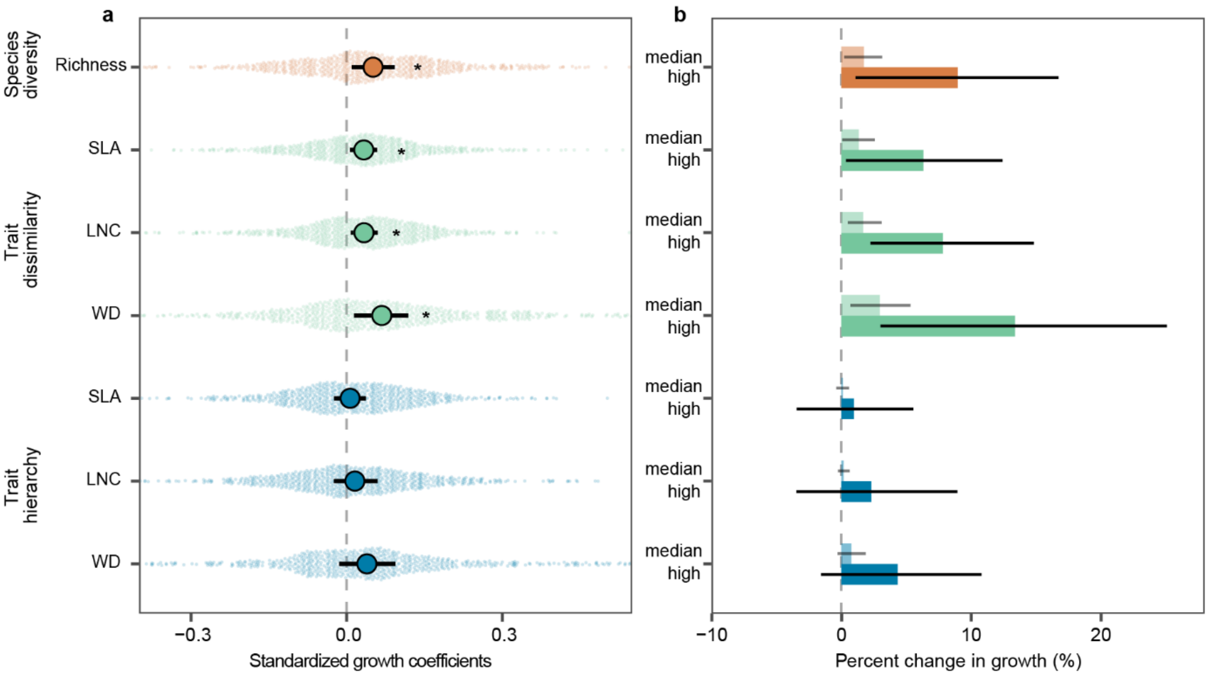

a
Climate variability
Drier
(sites / years)
Wetter
(sites / years)
t
n
t
f
(Richness = 1)
v.s.
(Richness = 3)
Trait
Conservative
Acquisitive
Higher SLA and LNC
Lower WD
Positive neighbourhood diversity effect on tree growth (hypothesis 1)
• Complementary interactions (e.g., resource partitioning, facilitation)
Related to trait dissimilarity
Growth of focal tree
Low
High
0
+
Trait dissimilarity |Tt_f - Tt_n|
• Competitive interactions (e.g., competitive advantage of focal tree with specific trait values)
Related to trait hierarchy
Growth of focal tree
Low
High
–
0
+
Trait hierarchy (Tt_f - Tt_n)
b
Neighbourhood diversity effect varies with spatial and temporal climate variability (hypothesis 2)
(i)
(ii)
(iii)
Diversity effect
+
0
–
Across sites
Site 1
Site 2
Site 3
Site 4
Drier
Climate
Wetter

Figure 2


a
75
50
25
0
−25
−50
Latitude(°N)
−100
0
100
Longitude(°E)
IDENT_Cloquet
IDENT_SSM
IDENT_FAB
FORBIO_Zedelgem
MyDiv
Kreinitz
FORBIO_Gedinne
IDENT_Freiburg
IDENT_Macomer
FD_Putuo
BEF_China
EFForTS−BEE
Sardinilla
Agua_Salud
MataDIV
Biome
Temperate
Mediterranean
Subtropical
Tropical
b
P / PET
1.80
0.65
0.50
0.20
0
−10
0
10
20
30
Annual temperature (°C)
0
100
200
300
400
Annual precipitation (cm)

959 Figure 3



960

Figure 4

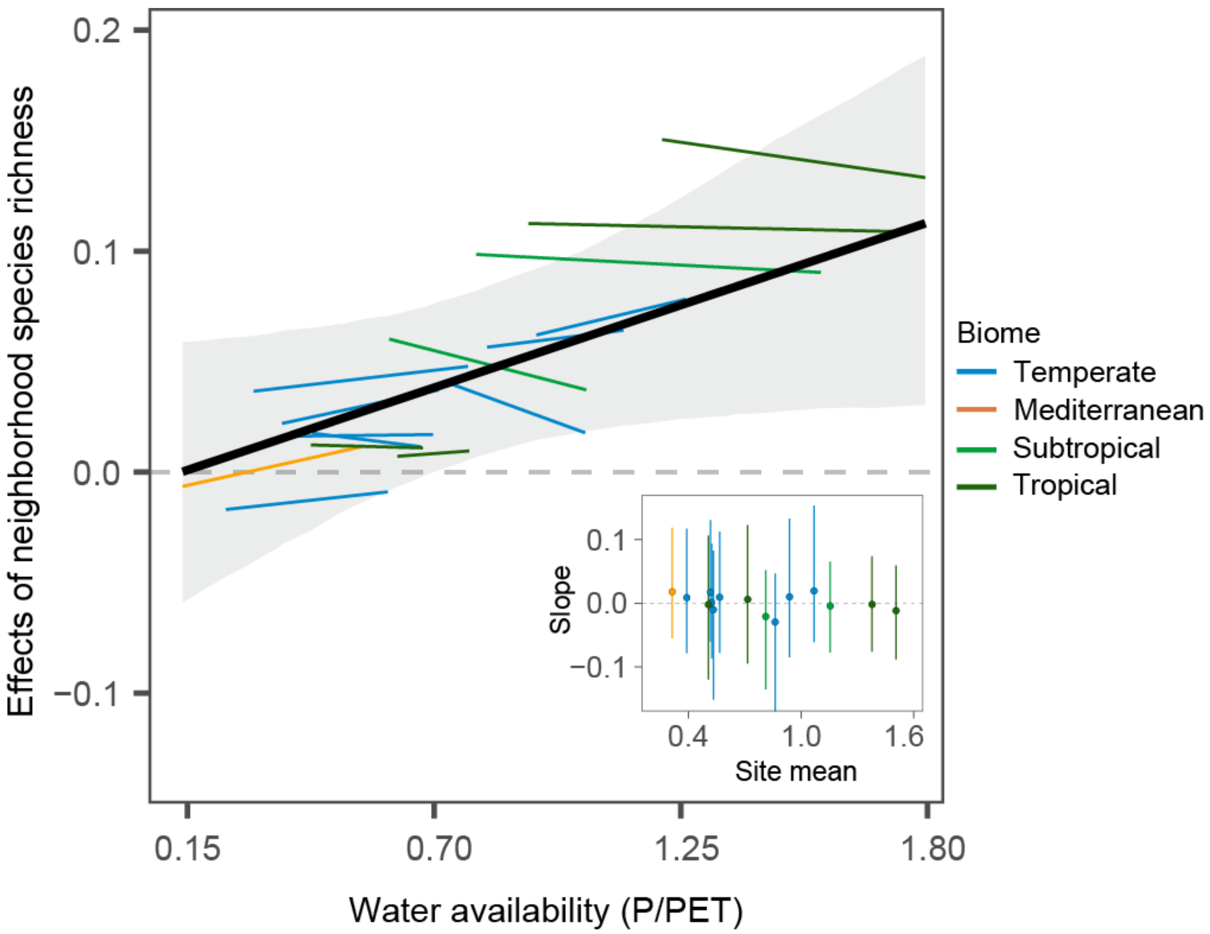
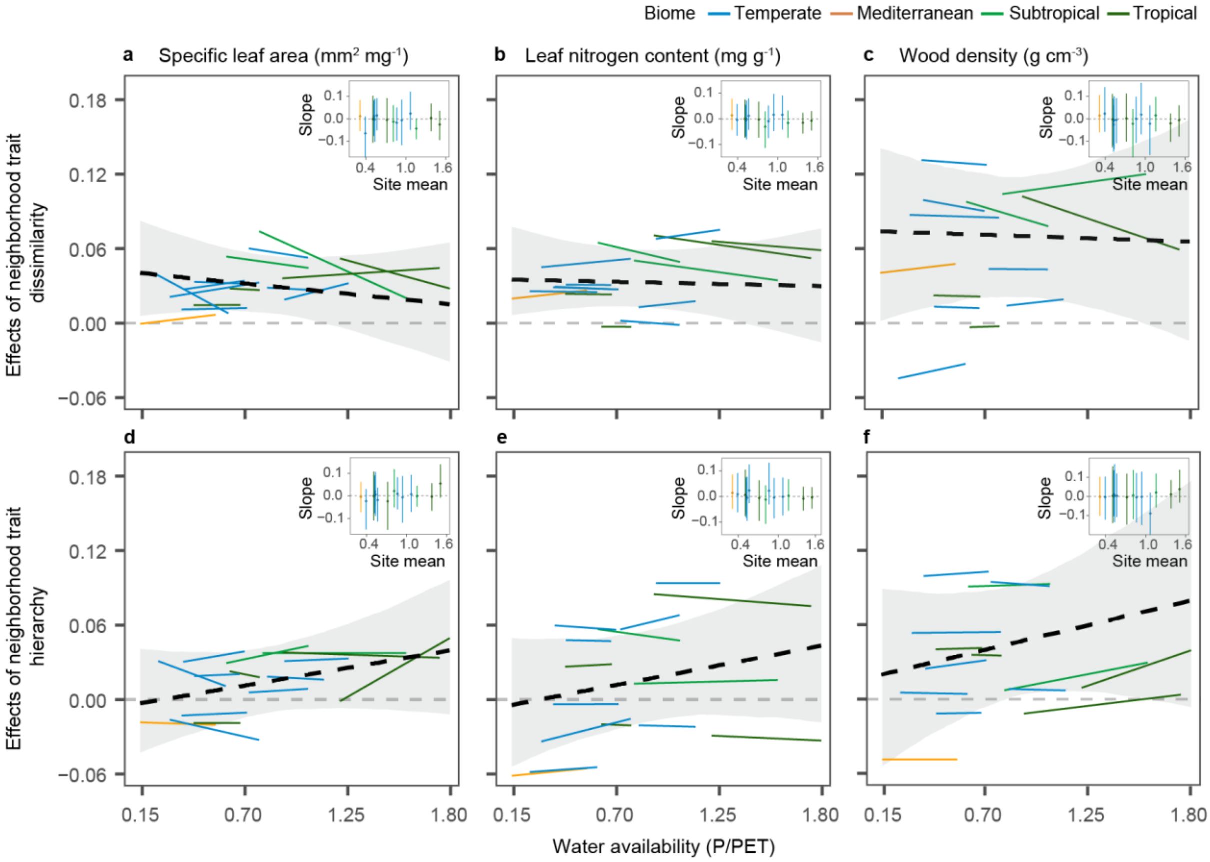

Effects of neighborhood species richness
0.2
0.1
0.0
−0.1
0.15
0.70
1.25
1.80
Water availability (P/PET)
Biome
Temperate
Mediterranean
Subtropical
Tropical
Slope
0.1
0.0
−0.1
0.4
1.0
1.6
Site mean

Figure 5


Biome — Temperate — Mediterranean — Subtropical — Tropical
a Specific leaf area (mm² mg⁻¹)
b Leaf nitrogen content (mg g⁻¹)
c Wood density (g cm⁻³)
d
e
f
Effects of neighborhood trait dissimilarity
Effects of neighborhood trait hierarchy
0.18
0.12
0.06
0.00
−0.06
Slope
0.1
0.0
−0.1
0.4
1.0
1.6
Site mean
0.15
0.70
1.25
1.80
Water availability (P/PET)