bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Neighbourhood species richness and drought-tolerance traits modulate tree growth and $\delta^{13}C$ responses to drought

Florian Schnabel[1,2*], *Kathryn E. Barry*[1,2,3], *Susanne Eckhardt*[2], *Joannès Guillemot*[4,5,6], *Heike Geilmann*[7], *Anja Kahl*[2], *Heiko Moossen*[7], *Jürgen Bauhus*[8], *Christian Wirth*[1,2,7]

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

[2]Systematic Botany and Functional Biodiversity, University of Leipzig, Leipzig, Germany

[3]Ecology and Biodiversity, Institute of Environmental Biology, Department of Biology, Utrecht University, Utrecht, Netherlands

[4]CIRAD, UMR Eco&Sols, Piracicaba, SP, Brazil

[5]Eco&Sols, Univ Montpellier, CIRAD, INRAE, Institut Agro, IRD, Montpellier, France

[6]Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, São Paulo, Brazil

[7]Max Planck Institute for Biogeochemistry, Jena, Germany

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

[*]Corresponding author: Florian Schnabel, Systematic Botany and Functional Biodiversity University of Leipzig, Johannisalle 21, 04103 Leipzig, Germany, florian.schnabel@idiv.de

Keywords: biodiversity-ecosystem functioning, climate change, functional traits, plant–plant interactions, tree rings, carbon isotopes, mixed-species forest, global change ecology

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Abstract

1. Mixed-species forests are promoted as a forest management strategy for climate change mitigation and adaptation because they are more productive and can be more resistant and resilient than monospecific forests under drought stress. However, the trait-based mechanisms driving these properties remain elusive, making it difficult to predict which functional identities of species best improve tree growth and decrease tree physiological water stress under drought.

2. We investigated tree growth and physiological stress responses (i.e. increase in wood carbon isotopic ratio; $\delta^{13}C$) to changes in climate-induced water availability (wet-to-dry years) along gradients in neighbourhood tree species richness and drought-tolerance traits. Using tree cores from a large-scale biodiversity experiment, we tested the overarching hypothesis that neighbourhood species richness increases growth and decreases $\delta^{13}C$. We further hypothesized that the abiotic (i.e. climatic conditions) and the biotic context modulate these biodiversity-ecosystem functioning relationships. We characterized the biotic context using drought-tolerance traits of focal trees and their neighbours. These traits are related to cavitation resistance vs. resource acquisition and stomatal control.

3. We found that tree growth increased with neighbourhood species richness. However, we did not observe a universal relief of water stress in species-rich neighbourhoods, nor an increase in the strength of the relationship between richness and growth and between richness and $\delta^{13}C$ from wet-to-dry years. Instead, these relationships depended on both the traits of the focal trees and their neighbours. At either end of each drought-tolerance gradient, species responded in opposing directions during drought and non-drought years.

4. Synthesis. We report that the biotic context can determine the strength and nature of biodiversity-ecosystem functioning relationships in experimental tree communities. We derive two key conclusions: (1) drought-tolerance traits of focal trees and their neighbours can explain divergent tree responses to drought and diversity, and (2) contrasting, trait-driven responses of tree species to wet *vs* dry climatic conditions can promote forest community stability. Mixing

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

tree species with a range of drought-tolerance traits may therefore increase forest productivity and stability.

Introduction

Forests are experiencing widespread mortality events due to climate extremes such as droughts across all biomes (Hammond et al., 2022; Hartmann et al., 2022). Droughts are predicted to increase in frequency and intensity with climate change (IPCC, 2014), threatening many ecosystem services that forests provide, including their capacity to mitigate climate change through carbon sequestration and storage (Anderegg et al., 2020). Large-scale forest restoration initiatives such as the Bonn Challenge, which aims to restore 350 Mha of forests by 2030 to mitigate climate change (Brancalion et al., 2019), need to optimize productivity and thus carbon storage while at the same time increasing these restored forests' stability against climate extremes. One key management strategy suggested to achieve this desired synergy between productivity and stability is to establish and maintain tree species mixtures instead of monocultures (Messier et al., 2021; Schnabel et al., 2019).

There is now accumulating evidence that species-rich forests provide higher levels and higher stability of various ecosystem functions than species-poor or monospecific forests (del Río et al., 2022; Messier et al., 2021; Schnabel et al., 2021; van der Plas, 2019). These positive species richness effects, for instance on tree growth, may be more pronounced under stress (Bertness & Callaway, 1994; Forrester & Bauhus, 2016) and have been shown to increase in dry compared to wet years (Fichtner et al., 2020; Schnabel et al., 2019). However, studies on net tree mixture responses to drought have produced divergent results, including positive, neutral and negative diversity effects under drought (reviewed by Grossiord (2020)) and we thus do not yet know when diversity is beneficial for forest functioning under drought.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Understanding the mechanisms driving this variation in biodiversity-ecosystem functioning (BEF) relationships may be best achieved through examining tree responses to drought and how they are modulated by tree species richness at the relevant scale at which tree-tree interactions take place, the local neighbourhood (Trogisch et al., 2021). This is because neighbourhood analyses allow studying diversity effects in concert with other factors such as tree size and competition, which may also influence growth, and to (partly) disentangle their respective contributions to growth (Forrester & Pretzsch, 2015; Stoll & Newbery, 2005). For instance, neighbourhood analyses showed that mean tree growth across species increases with tree neighbourhood species richness (hereafter called 'NSR') despite positive and negative NSR effects on the growth of individual species (Fichtner et al., 2018; Schnabel et al., 2019).

The recent history of these neighbourhood interactions can be analysed in the tree ring record of a focal tree, which captures its response to neighbours and climatic variation (Schweingruber, 1996; Vitali, Forrester, & Bauhus, 2018). The width of annual growth rings is an indicator of a tree's reaction to climate, with reduced growth in dry compared to wet years indicating increased drought stress (Schwarz et al., 2020). In addition to growth, the isotopic ratio of $^{13}C/^{12}C$ in wood (hereafter '$\delta^{13}C$') is a principal indicator of a tree's physiological reaction to water limitation and drought stress (Grossiord et al., 2014; Jucker et al., 2017). An increase in $\delta^{13}C$ indicates drought stress, as trees increasingly use the heavier ^{13}C when stomata close to avoid water loss from transpiration (Farquhar, Ehleringer, & Hubick, 1989; Grossiord et al., 2014). We expect that the mixed results on tree species richness effects on growth and $\delta^{13}C$ under drought reported in former studies (see above; Grossiord (2020)) may be explained by species-specific water-use strategies. We expect this because water-use strategies, which can be studied using functional traits, impact how species respond to their surrounding abiotic (i.e. climatic conditions) and biotic environment (i.e. their tree neighbours) (Forrester, 2017).

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Among other relevant traits, two key traits proposed to influence tree responses to drought are cavitation resistance and the stringency of stomatal control (McDowell et al., 2008), which we collectively refer to as 'drought-tolerance traits' (Schnabel et al., 2021). Xylem resistance to cavitation reduces embolism risk in vessels, which impair water transport and, at advanced stages, induce desiccation and, ultimately, tree death (Choat et al., 2012). Cavitation resistance is often quantified as the water potential where 50% of conductivity is lost due to cavitation (Ψ_{50}; Choat et al., 2012). Moreover, cavitation resistance has been shown to be associated with classic traits of the leaf economics spectrum in tropical tree species (Guillemot et al., 2022) and thus with resource use strategies. Accordingly, cavitation-sensitive species have traits indicative of acquisitive resource use (Fichtner et al., 2020; Schnabel et al., 2021). In addition to cavitation resistance, stomatal control differs among species (see McDowell et al., 2008): some species close their stomata early during water shortages to avoid transpirational water loss, whereas others keep their stomata open despite increasingly negative water potentials and increasing cavitation risks. In line with current perspectives (Martínez-Vilalta & Garcia-Forner, 2017), we use physiological traits such as stomatal conductance and its control under increasing vapour pressure deficits (VPD) to quantify stomatal control as a gradient from water savers, which close their stomata early as water stress develops, to water spenders, which keep their stomata open despite increasing VPD (Kröber & Bruelheide, 2014; Kröber, Zhang, Ehmig, & Bruelheide, 2014). Diversity in these traits, hereafter referred to as 'resistance-acquisition' and 'stomatal control' traits, has been recently shown to be positively related to the stability of forest community productivity under highly variable climatic conditions (Schnabel et al., 2021). However, these traits have not been used in a comprehensive framework to characterize the functional identity of focal trees (i.e. their traits) and their neighbours (i.e. the neighbourhood mean values of traits) to understand how these functional identities influence growth and wood

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

$\delta^{13}C$ responses to the interactive effects of NSR and contrasting climatic conditions (such as particularly dry and wet years).

A focal trees' functional (trait) identity, hereafter 'focal tree traits', may be crucial to understand responses of tree growth and $\delta^{13}C$ to the interactive effects of drought and NSR. Consistent with this expectation, Fichtner et al. (2020) showed that positive NSR effects on aboveground wood production were strongest for cavitation-sensitive species during drought. Moreover, another study, even though conducted in a wet year, found that increasing acquisitiveness and NSR caused decreased $\delta^{13}C$ values in tree twig tissues, indicating enhanced water availability in diverse neighbourhoods (Jansen, Oheimb, Bruelheide, Härdtle, & Fichtner, 2021). We expect growth to be more strongly related to resistance-acquisition traits and thus the leaf economics spectrum (Reich, 2014). Alternatively, we expect wood $\delta^{13}C$ to be primarily controlled by stomata aperture (Farquhar et al., 1989) and thereby stomatal control traits.

The trait identity of a focal trees' neighbours, hereafter 'neighbour traits', may also influence the growth and $\delta^{13}C$ of focal trees through interactions (Fortunel, Valencia, Wright, Garwood, & Kraft, 2016; Trogisch et al., 2021). In this view, neighbour traits may alter water use and with this local water availability. For example, during drought, growth reductions in water spenders may be lower and $\delta^{13}C$ increases smaller when growing with more water-saving neighbours because the reduced stomatal conductance of the latter may decrease overall water consumption and thus drought stress in focal trees (Forrester, 2017). Conversely, being surrounded by water spending neighbours during drought may amplify focal tree growth reductions and $\delta^{13}C$ increases. In summary, we expect that the abiotic context (i.e. climatic conditions) and the biotic context jointly modulate growth and $\delta^{13}C$ responses to NSR. We characterized this biotic context, which has received little attention compared to the many studies that examined the abiotic context dependency of BEF relationships (e.g. Forrester

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

& Bauhus, 2016; Grossiord, 2020; Jucker et al., 2016; Paquette & Messier, 2011), as traits of focal trees and as traits of their neighbours.

Here, we aim to understand how drought-tolerance traits influence the relationship between NSR and growth, and NSR and $\delta^{13}C$ under variable climatic conditions. We use trait-based neighbourhood models that account for NSR as well as focal tree and neighbour traits and examine how they jointly influence focal tree growth and $\delta^{13}C$ in a climatically dry, normal and wet year (Fig. 1) in a large-scale sub-tropical tree biodiversity-ecosystem functioning experiment (BEF-China experiment; Bruelheide et al., 2014; Huang et al., 2018). Specifically, we tested the following hypothesis:

H1: NSR increases growth and decreases $\delta^{13}C$ of focal trees, and the strength of this diversity effect increases from wet to dry years.

H2: Drought-tolerance traits of focal trees determine the relationship between NSR and growth, and NSR and $\delta^{13}C$ under variable climatic conditions. Specifically, during drought, NSR increases growth and decreases $\delta^{13}C$ for acquisitive and water-spending species, while the reverse pattern is found for cavitation-resistant and water-saving species.

H3: Drought-tolerance traits of neighbours influence the effect of climate on focal tree growth. Specifically, during drought, acquisitive and water-spending neighbours amplify drought stress.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

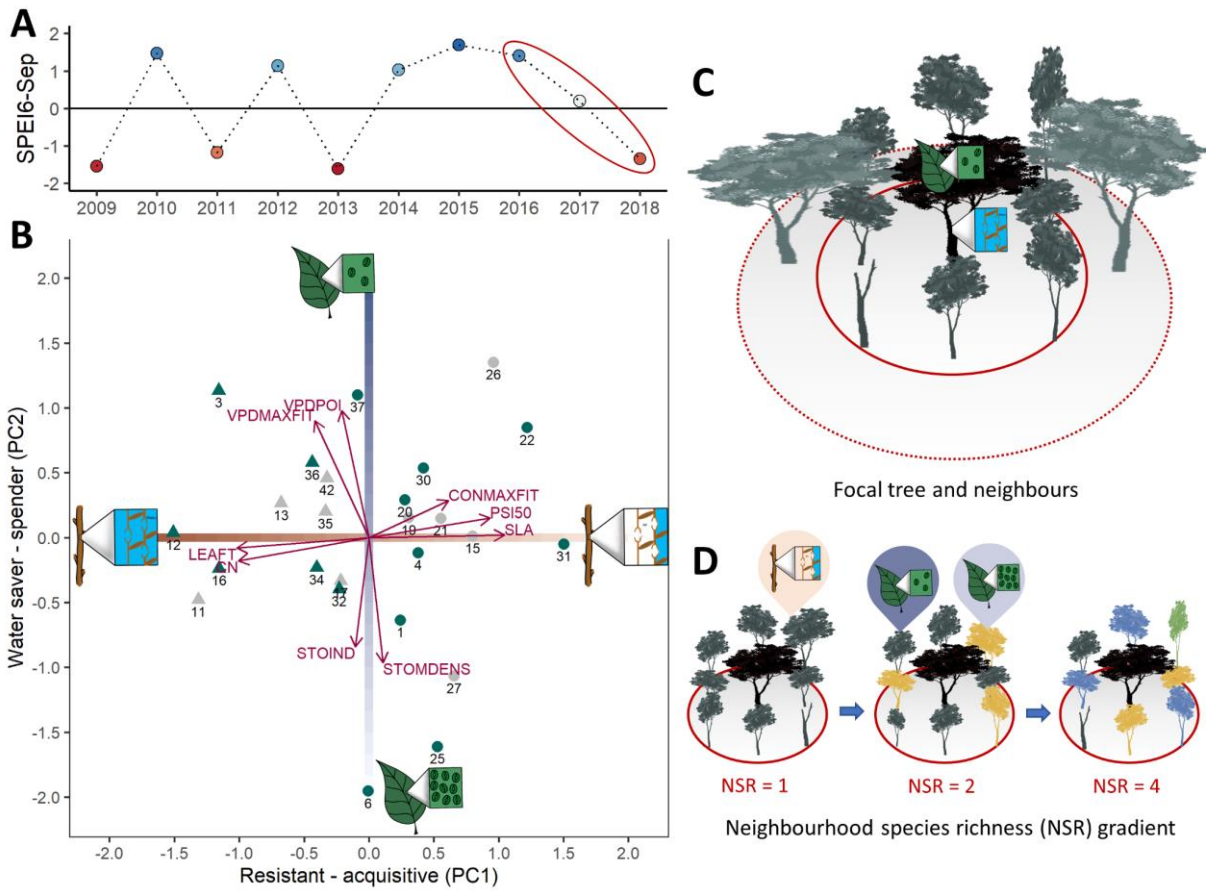

Fig. 1 Study design. **(A)** Climatic characterisation of the study years 2016 (wet), 2017 (intermediate) and 2018 (dry) based on the Standardised Precipitation-Evapotranspiration Index (SPEI) for the principal vegetation period (April-September) since the establishment of the BEF-China experiment (2009). The wet-to-dry study years under investigation are highlighted with a red oval. Blue points indicate wetter and red points drier conditions compared to the long-term mean (1901-2019); values below -1 and above 1 can be considered exceptional. **(B)** Species selection via their drought-tolerance traits based on principal component analysis (PCA) adapted from Schnabel et al. (2021). PC1 reflects a resistance-acquisition gradient running from cavitation-resistant (low Ψ_{50}, tough leaves (LEAFT), high C/N ratio) to acquisitive species (high Ψ_{50}, high specific leaf area (SLA), high maximum stomatal conductance (CONMAXFIT)). PC2 reflects a stomatal control gradient running from water spenders with late stomata closure under decreasing vapour pressure deficits (VPDs) (high VPD at the point of inflection of modelled stomatal conductance (VPDPOI), high VPD at CONMAXFIT (VPDMAXFIT)) to water savers with fast stomata closure (high stomatal density (STODENS), high stomatal index (STOIND)). The sketches illustrate the trait gradients: (PC1) high *vs* low cavitation resistance, (PC2)

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

water-spending *vs* water-saving stomatal control (few versus abundant stomata). We selected 15 species to cover the trait space (highlighted in green). See Table S1 for a list of tree species represented here by codes and Table S2 for details on the traits. **(C)** Tree neighbourhood design. We extracted increment cores from focal trees (black tree) of the 15 species and inventoried their 1st and 2nd order neighbours (grey trees). **(D)** Neighbourhood species richness (NSR) gradient. We sampled focal trees and their neighbours to create a realised NSR gradient of 1-, 2- and 4-neighbour species. The sketches in C and D illustrate that we examined the influence of focal tree and neighbour traits on the relationships between NSR, climate and growth as well as $\delta^{13}C$ for both trait gradients (resistance-acquisition and stomatal control). For additional details on the study design, see methods.

Materials and Methods

Study site and experimental design

We sampled trees in a large-scale tree biodiversity-ecosystem functioning experiment located in Xingangshan, Dexing, Jiangxi province, China (29°08′N to 29°11′N, 117°90′E to 117°93′E), the BEF-China experiment (Bruelheide et al., 2014; Huang et al., 2018). The experiment has two sites: A and B, each approximately 20 ha in size. The sites are characterised by a subtropical, monsoon climate with a mean annual temperature of 16.7 °C and a yearly precipitation sum of 1821 mm (Yang et al., 2013), with distinct differences between seasons. Summers are humid, with most annual precipitation falling from April to July, while winters are drier and cold (Gheyret et al., 2021). Deciduous and evergreen broadleaved tree species dominate the hyperdiverse native forests of the study region, sometimes interspersed with conifers (Bruelheide et al., 2014). The high diversity can be attributed, at least partially, to the location of the region in the transition zone of tropical and temperate climates with their respective flora (Shi, Michalski, Welk, Chen, & Durka, 2014; Wang, Kent, & Fang, 2007). This resulted also in a high diversity of water-use strategies among tree species, which makes these forests ideal for studying species response strategies to variable climatic conditions (Kröber et

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

al., 2014; Kröber & Bruelheide, 2014; Schnabel et al., 2021). Based on a pool of 40 native evergreen and deciduous broadleaf tree species, experimental tree species richness gradients were created with 1, 2, 4, 8, 16 and 24 tree-species mixtures. Species were assigned to different extinction scenarios following a broken-stick design, ensuring that all species were represented at each species richness level (Bruelheide et al., 2014; Huang et al., 2018). In 2009 (site A) and 2010 (site B), overall, 226,400 individual trees were planted at a distance of 1.29 meters (Fig. 1) on plots with a size of 25.8 × 25.8 m^2, with 400 trees being planted per plot. Species compositions and tree positions within plots were randomly assigned to each plot.

Climate-based selection of study years

We selected three study years with contrasting climatic conditions, a comparably wet (2016), an intermediate (2017) and a particularly dry year (2018). We selected consecutive years to minimise other factors than climate that may influence growth and $\delta^{13}C$, such as changes in stand structure. We used the standardised precipitation evapotranspiration index (SPEI) (Vicente-Serrano, Beguería, & López-Moreno, 2010) calculated from a high-resolution time-series of interpolated climate station data (CRU TS v4.04; Harris, Osborn, Jones, & Lister, 2020) to characterise climatic conditions. The SPEI represents a standardised climatic water balance of precipitation minus potential evapotranspiration (PET). We selected study years based on climatic conditions alone without taking tree growth reductions into account (see suggestions by Schwarz et al. (2020)) by comparing the SPEI series calculated for the three months of the peak vegetation period (SPEI3, April-July) for the six months of the entire vegetation period (SPEI6, April-September) and the twelve months of a whole year since the end of the vegetation period of the preceding year (SPEI12, October-September), with a climate reference period from 1901-2019 (Fig. 1A, Fig. S1). The subtropical vegetation period ranges from April-September with peak growth at the end of April (Gheyret et al., 2021), which corresponds well with the selected lengths of periods for which SPEI was calculated. All

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

periods (SPEI3, SPEI6, SPEI12) showed the same pattern of decreasing SPEI values from 2016-2017-2018 (Fig. S1), with drought severity in the dry year being comparable to drought conditions in the last 40 years (Fig. S2). In addition, we also examined intra-annual and non-standardized climatic water balances (Fig. S3).

Species selection via drought-tolerance traits

We used this experimental set-up to select tree species along two principal trait gradients related to resistance-acquisition and stomatal control traits (Fig. 1B) which allowed us to study their relative contributions to tree growth and $\delta^{13}C$. For this purpose, we relied on species-specific trait data related to cavitation resistance, resource acquisitiveness and stomatal control measured in the experiment (Table S2; Kröber et al., 2014; Kröber & Bruelheide, 2014). Trait data were analysed with principal component analysis (PCA), which partitioned the variation in drought-tolerance traits into two orthogonal trait gradients, a resistance-acquisition (PC1) and stomatal control (PC2) trait gradient (see Schnabel et al. (2021) for details). In brief, we quantified cavitation resistance as the water potential (Ψ_{50}) at which 50% of xylem conductivity is lost due to cavitation, which is a key physiological trait to characterise a species drought tolerance (Choat et al., 2012). In our study system, Ψ_{50} is related to classic traits of the leaf economics spectrum (Reich, 2014) in that cavitation-resistant species (low Ψ_{50} values) are also characterised by traits indicative of conservative resource use (tough leaves and high C/N ratio), while cavitation-sensitive species (less negative Ψ_{50} values) have traits indicative of acquisitive resource use such as high specific leaf area (SLA) and high maximum stomatal conductance (g_{smax}) (Fig. 1B). Including this gradient provided a balanced selection of deciduous and evergreen species. Second, we quantified stomatal control using modelled curves of stomatal conductance (g_s) under increasing vapour pressure deficits (VPD) and morphological traits (stomatal density and stomatal index, the product of stomatal density and size) (Fig. 1B). Water savers are characterised by a high stomatal density, high stomatal index values, and a fast down-

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

regulation of their conductance under increasing VPD. In contrast, water spenders down-regulate their stomatal conductance only at high VPD (high VPDMAXFIT and VPDPOI).

In 2019, we selected 15 tree species to cover the trait space as well as possible by choosing species at the extremes of both gradients (2 species at each end) and at intermediate values of trait expression (Fig. 1B). We used the species PCA scores on the resistance-acquisition and stomatal control trait gradient as focal tree traits, hereafter referred to as 'focal tree resistance-acquisition traits' and 'focal tree stomatal control traits'. We restricted this selection to 25 tree species (of 40 in total), which featured mid- to fast growth rates in our experiment (Li, Kröber, Bruelheide, Härdtle, & Oheimb, 2017), showed distinct radial growth rings (Böhnke, Kreißig, Kröber, Fang, & Bruelheide, 2012), and had comparably good survival rates to ensure sufficient tree and sample size for coring. As species pools in the BEF-China experiment overlap only partly between sites A and B (Bruelheide et al., 2014), we sampled seven species at site A, seven at site B and one species (*Schima superba*) at both sites to test for potential differences between sites (i.e. eight total species at each site).

Focal trees and their neighbourhood

We used focal trees and their neighbours to create a realised neighbourhood species richness (NSR) gradient of 1-, 2- and 4-neighbour species (Fig. 1C,D). In the field, we randomly selected 10 focal trees (7 trees for final analysis and 3 trees as backup) per species (N=15) and NSR level (N=3), which resulted in 485 trees in total (one species was sampled at both sites). Focal trees were selected outside the plot's inventoried core area to avoid interference with other projects and not near plot borders unless the adjacent plot contained species for which complete trait information existed. We defined NSR as the realised neighbourhood species richness at sampling (2019). In a few cases (*Idesia polycarpa*, *Triadica cochinchinensis*), we used the original plot-level richness at the time of planting due to the high mortality of focal and

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

neighbour species. For NSR=1 and NSR=2, we selected trees only from plots with the respective plot-level design richness (monocultures and 2-species mixtures). The random planting design of BEF-China substantially reduced the likelihood of finding high-diversity neighbourhoods. At NSR=4, we thus also selected plots with a higher plot-level design richness, i.e. 8- and 16-species mixtures in this order of preference. Sampling neighbourhoods with four species only in 4-species mixtures was impossible due to the high mortality of neighbour species. We sampled focal trees in as many different plots and species compositions as possible to increase the generality of our results (N=122 plots) and avoided overlapping neighbourhoods to minimise spatial-autocorrelation. We used a focal tree threshold diameter at breast height (dbh, at 1.3m) of > 8cm (in a few cases ~6cm) to avoid damaging the trees when extracting cores for analysis (see below). For each focal tree, we recorded its position, species' identity and dbh. When trees had multiple stems, the stem diameters of the two largest stems were recorded to calculate the sum of the basal areas of both stems.

We defined a focal tree's neighbourhood as all alive direct neighbours (occupying the immediately adjacent original planting space; maximum eight trees) and second-order neighbours (occupying the original planting spaces one further out from the direct neighbours) if their crown and the focal tree's crown interacted (Fig. 1C). For each neighbour, we recorded its position, species' identity, and dbh and visually estimated the height difference of neighbours compared to focal trees as a measure of shading by neighbours. We used these data to characterise the competitive environment of focal trees using eight different diameter-, height-, and distance-based neighbourhood competition indices frequently used in other studies (Table S3). Tree basal area (cm^2, based on dbh), and in the case of multi-stemmed trees, the sum of basal areas of individual stems was used in these analyses. We calculated neighbour traits, i.e. the functional identity of a focal trees' neighbourhood, as the neighbourhood-weighted mean (NWM) trait value of each neighbourhood for both gradients, hereafter called

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

'NWM of resistance-acquisition' and 'NWM of stomatal control', similarly to the calculation of community-weighted mean traits often used in BEF studies (see, e.g. Craven et al., 2018) as:

$$NWM = \sum_{i=1}^{n} a_{ba\,i}\, t_i \quad (1)$$

Where a_{ba} is the abundance of species i measured as its basal area relative to the basal area of the other neighbour species and t_i is the score of species i on the respective trait gradient (PCA axes reflecting resistance-acquisition or stomatal control; Fig. 1).

Tree growth and stable carbon isotopes

We used tree growth and carbon isotopic ratios as indicators of focal tree responses to the interactive effects of climate, NSR and drought-tolerance traits. We extracted one increment core at dbh from each focal tree perpendicular to the slope (avoiding tension wood) using a 3-threaded Haglöf increment borer with 3.5 mm core diameter. We extracted cores from the largest stem and recorded tree diameter at the coring position if coring at dbh was not possible. Cores were tightly wrapped in paper to avoid bending and dried for 72 hours at 70 °C. Core surfaces were prepared with a core-microtome (Gärtner & Nievergelt, 2010) to visualise tree-ring boundaries. Annual tree-ring width (mm) was measured using a LINTAB™ 6 system and the TSAPWin Professional 4.64 program © 2002–2009 Frank Rinn / RINNTECH with a measurement accuracy of 1/1000 mm. We measured each core twice and cross-compared series within species to ensure the correct dating of rings. No master chronology per species could be constructed owing to the short length of individual series (mostly 5-7 years). Tree-ring series of 474 trees from 15 species could be dated (see Fig. S4 for an overview of wood anatomy). Basal area increment (cm^2) is less influenced by biological age trends than tree-ring width (see Fig. S5 for a comparison). It is thus a more reliable indicator of temporal trends in tree growth, particularly in young, open-grown trees like the ones examined here (Biondi & Qeadan, 2008).

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Therefore, in the following, we present and discuss results based on basal area increment (also referred to as growth). We present results for tree-ring width, which yielded similar results, in the appendix. Basal area increment was calculated using tree-ring width, bark thickness and the tree diameter at coring-position with the bai.out() function in the dplR package in R (Bunn et al., 2020).

The carbon isotopic ratio in the wood of focal trees ($\delta^{13}C$) was quantified for the years 2016-2018 on the same cores. The rings of the years were separated, their wood homogenised and 0.8 mg woody material was weighed and placed in tin capsules. We determined $\delta^{13}C$ in bulk wood rather than extracted cellulose fraction, because both materials produce highly correlated signals (Loader, Robertson, & McCarroll, 2003; Schulze et al., 2004). Carbon isotope analyses were conducted on an elemental analyser (NA1110, CE Instruments, Milan, Italy) coupled to a Delta+XL isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) via a ConFlow III at the stable isotope laboratory (BGC-IsoLab) of the Max Planck Institute for Biogeochemistry in Jena, Germany. We present carbon isotope ratio results as $\delta^{13}C$ values on the VPDB-LSVEC scale (Coplen et al., 2006). The $\delta^{13}C$ values are reported in per mil (‰) by multiplying the delta value by the factor 1000 (Coplen, 2011).

$$\delta^{13}C = \left(\frac{\delta^{13}C\ (sample)}{\delta^{13}C(standard)} - 1\right) \quad (2)$$

Samples were scaled against the in-house standard (acetanilide) with a $\delta^{13}C$ value of -30.06 ± 0.1 ‰. Caffeine (caf-j3; $\delta^{13}C$: -40.46 ± 0.1 ‰) was analysed several times in each sequence as quality control. Linearity, blank and drift corrections were done for each sequence according to Werner and Brand (2001). We randomly remeasured a subset of samples to estimate measurement precision. The mean standard-deviation of samples from the same year and tree

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

lay with 0.05 ± 0.03 ‰ well in the range of the in-house standard precision. We used the mean of these repeated measurements in the further analyses.

Wood $\delta^{13}C$ is influenced both by stomatal aperture and CO_2 assimilation (Farquhar et al., 1989; Grams, Kozovits, Häberle, Matyssek, & Dawson, 2007), with the latter being largely influenced by shading from neighbouring trees and the former by water availability. One common approach to separate the effects of water availability from shading on $\delta^{13}C$ is to analyse isotopic signals in tree rings from (co-)dominant trees who experience no or only slight shading from neighbours (Grossiord et al., 2014; Jucker et al., 2017). In contrast to a former study which did not control for tree size and canopy position during sampling and consequently found strong shading effects on $\delta^{13}C$ (Jansen et al., 2021), we aimed at maximizing the climate-induced water availability signal in $\delta^{13}C$. We did this in two ways. First, our selection of species with mid- to fast growth rates and the use of a minimum dbh of 8 cm (see above) resulted in a sample of (co-)dominant individuals. Second, to further reduce shading effects on focal trees and to simultaneously ensure the same sample size across species and NSR levels, we carried out an *a priori* selection of those focal trees that experienced least shading by their neighbourhood. For that purpose, those focal trees with the highest sum of relative heights of neighbours (height of focal tree minus height of neighbour) (see above) to select 7 trees per species, NSR-level and site for statistical analysis. We constrained this selection to keep a minimum of two trees per plot. The final, completely balanced dataset per species, NSR-level and year comprised 336 trees from 114 plots with at least two trees per plot (see Fig. S6 for an overview of basal area increment and $\delta^{13}C$ values per species and NSR-level).

Statistical analysis

We used linear mixed-effects models (LMMs) to model growth (basal area increment and tree-ring width) and wood $\delta^{13}C$ responses to the interactive effects of climate, NSR and drought-

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

tolerance traits. Our modelling framework consisted of three main steps. First, we built trait-independent neighbourhood models that accounted for the size of focal trees, its competition with neighbours, climate and NSR, and the interaction between climate × NSR as fixed effects. We accounted for our experimental design through a nested random effect structure of focal tree identity (to account for repeated measurements) nested within plot and site. We included focal tree size as the log-transformed initial dbh (at the end of 2015) before our analysis period (2016-2018), which we estimated using tree-ring width and the trees' dbh recorded in 2019. We then tested eight neighbourhood competition indices (Table S3) and selected the best-performing one via the Akaike Information Criterion (AIC). We accounted for differences in average annual climatic conditions using year (2016-wet, 2017-intermediate and 2018-dry, Fig. 1A) as a fixed effect, coded as an integer variable as we expected linear trends. We also checked for non-linear behaviour through alternative models with year as a categorical fixed effect. We used years rather than SPEI-values as we only examined three years with a clear gradient in climate-induced water availability. Reported relationships would be the same if using SPEI values (checked via alternative LMMs with SPEI-values as a fixed effect). We selected the most parsimonious random effect structure using the step function in lmerTest (α=0.2, a conservative choice), which retained tree identity and plot but not site as nested random effects for models to explain growth and $\delta^{13}C$. We kept this random effect structure in all further analyses. A separate analysis of *Schima superba*, the species sampled at both sites, confirmed that growth and $\delta^{13}C$ responses did not differ between sites (supplementary analysis 1). Finally, we selected the most parsimonious trait-independent neighbourhood model through backward elimination of fixed effects (α=0.05). In a second step, we examined how focal tree traits modulate growth and $\delta^{13}C$ responses by including the 3-way interaction between NSR, climate and either resistance-acquisition or stomatal control traits of focal trees and all potential 2-way interactions as fixed effects in the trait-independent models of step 1. We selected the most parsimonious focal tree trait model through backward elimination of fixed effects. Third, to

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

understand how neighbour traits modulate growth and $\delta^{13}C$, we included the 2-way interaction of climate with either the resistance-acquisition or stomatal control traits of neighbours as fixed effects in the trait-independent models (step 1) and again selected the most parsimonious model structure via backward elimination of fixed effects. Hence, in contrast to former studies (Fichtner et al., 2020; Jansen et al., 2021), we explicitly accounted for interactions between focal trees and their neighbourhood on growth and $\delta^{13}C$ through modelling the effect of neighbourhood species composition not as a random effect but as a fixed effect expressed through the NWM of species' drought-tolerance traits. We used separate models for understanding the effects of focal tree and neighbour traits (steps 2 and 3). The validity of this choice was confirmed, as joint focal tree and neighbour trait models consistently dropped one term (mostly neighbour traits), which was highly significant if examined alone. Across the examined 15 species, we observed large species-specific differences in growth and particularly in $\delta^{13}C$ (Fig. S6). As we were interested in relative species responses to the interactive effects of NSR, climate and drought-tolerance traits and not in absolute species differences, we standardised basal area increment and tree-ring width values by dividing each value by its species' mean and $\delta^{13}C$ values by subtracting its species' mean in all analyses to reduce total variance in the data, referred to as bai_{std}, trw_{std} and $\Delta\delta^{13}C$, respectively. Alternative models with species identity as a random effect yielded similar results (results not shown). LMMs were fit in R version 4.1.2 with the packages lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). Model assumptions (normality and heteroscedasticity) were visually checked via quantile-quantile plots and through examining model residuals. We used a log transformation for basal area increment and a square-root transformation for tree-ring width to normalise residuals, centred and scaled all predictors (via subtracting μ and dividing by σ) except year and NSR before analysis and used an α of 0.05 for reporting significant effects.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Results

Using trait-independent models, we found that focal tree growth (expressed as basal area increment) increased with the logarithm of tree size ($t = 5.01$, $P < 0.001$), decreased with competition by neighbours ($t = -5.91$, $P < 0.001$), and increased with NSR by 11.4% from 1-species to 4-species neighbourhoods ($t = 2.29$, $P = 0.024$) (Fig. 2, Table S4). The Hegyi index, which accounts for neighbour distance and basal area relative to the focal tree, was the best-performing competition index (Table S5). NSR effects on growth did not change with annual climatic conditions, nor did we observe absolute differences in growth across years (2016-wet, 2017-intermediate, 2018-dry). The trait-independent models for $\delta^{13}C$ in the wood of focal trees showed a linear decrease in $\delta^{13}C$ from the wet-to-dry year ($t = -9.06$, $P < 0.001$; Fig. S7, Table S6). Neither tree size, competition, NSR, nor the interaction between NSR and year significantly affected $\delta^{13}C$ (Tables S6,7).

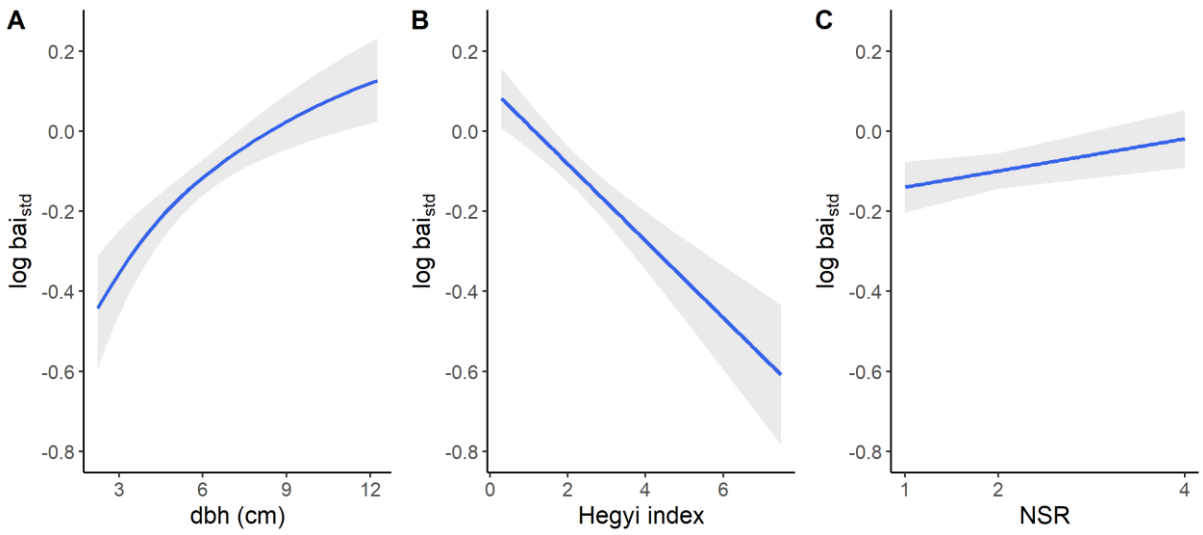

Fig. 2 Effects of tree size (dbh), neighbourhood competition (Hegyi index) and neighbourhood species richness (NSR) on the logarithm of focal tree basal area increment (bai_{std}). The blue lines are mixed-effects model fits and grey bands show a 95% confidence interval. See Table S4 for details on the fitted model.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

The effect of drought-tolerance traits on tree growth

Using trait-dependent models to explain focal tree growth, we found that the resistance-acquisition traits of focal trees significantly modulated the relationship between NSR and growth and between climate and growth (Fig. 3A,B, Table S8). With increasing NSR, acquisitive, cavitation-sensitive species grew 29.7 % more in 4-species compared to 1-species neighbourhoods, whereas growth of conservative, cavitation-resistant species decreased by 8.9% in 4-species compared to 1-species neighbourhoods (NSR × focal tree resistance-acquisition traits, $t = 2.45$, $P = 0.015$; Fig. 3A). Growth of resistant species increased from the wet-to-dry year, while it declined in acquisitive species (year × focal tree resistance-acquisition traits, $t = -6.84$, $P < 0.001$; Fig. 3B). We also found that the resistance-acquisition traits of focal trees tended to induce contrasting relationships between NSR, climate and growth. Still, this 3-way interaction was only marginally significant (NSR × year × focal tree resistance-acquisition traits, $t = -1.75$, $P = 0.080$; Fig. S8, Table S10): Effects of the resistance-acquisition traits of focal trees were strongly contrasting (acquisitive species grew better and resistant species grew less with increasing NSR) during the wet year, while effects in the dry year were weaker but predominately positive (acquisitive species still grew more with increasing NSR, while NSR did not affect the growth of resistant species). Notably, the resistance-acquisition traits of neighbours significantly influenced growth responses; that is, focal trees in a neighbourhood dominated by resistant species grew more from the wet-to-dry year, while focal trees in an acquisitive neighbourhood grew less (year × NWM of resistance-acquisition, $t = -4.17$, $P < 0.001$; Fig. 3C, Table S9).

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

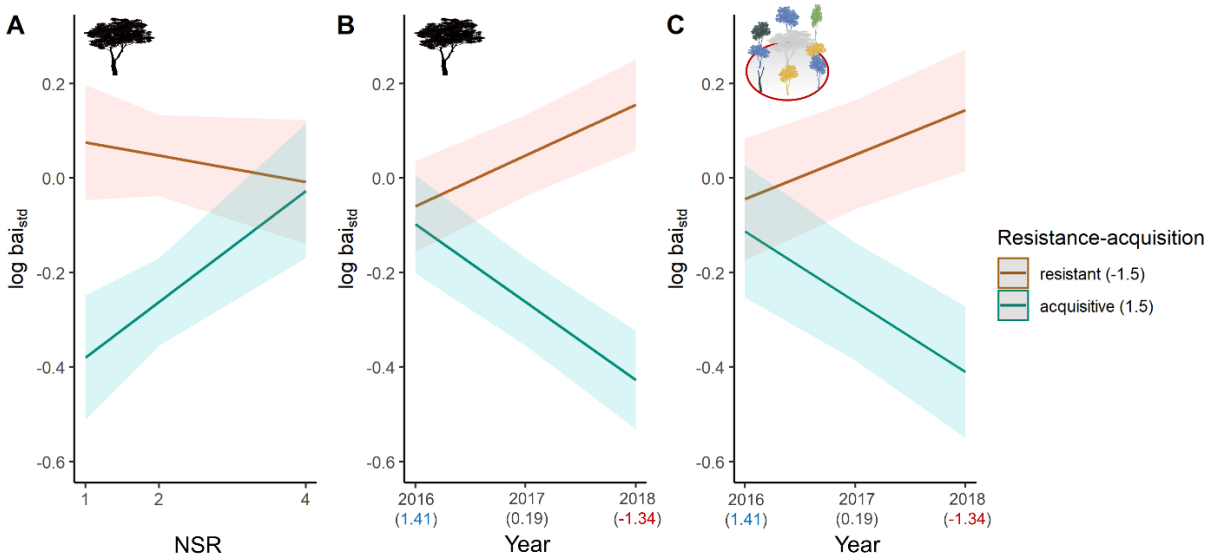

Fig. 3 Modulation of the relationship between neighbourhood species richness (NSR) and growth and between climate and growth by resistance-acquisition traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant effects of NSR and study year (2016-2018 with wet-to-dry climate, SPEI values in brackets) on the logarithm of basal area increment (bai_{std}) of focal trees predicted for cavitation resistant (PC1 value of -1.5) and acquisitive species (PC1 value of 1.5). The panels illustrate the influence of focal tree resistance-acquisition traits (black tree; A, B) and neighbour resistance-acquisition traits (C) on the relationships. See Fig. 1 for details on the study design and Tables S8,9 for details on the fitted models.

The stomatal control traits of focal trees significantly modulated relationships between climate and growth but not between NSR and growth nor between NSR, climate and growth (Fig. 4A, Table S11). Growth increased for water-saving species but decreased for water-spending species from the wet-to-dry year (year × focal tree stomatal control traits, $t = -5.10$, $P < 0.001$; Fig. 4A). The stomatal control traits of neighbours significantly influenced the relationship between climate and growth: Focal trees in a neighbourhood dominated by water-saving species grew better from the wet-to-dry year, while growth of focal trees in a water spending neighbourhood declined (year × NWM of stomatal control, $t = -3.04$, $P = 0.002$; Fig. 4B, Table S12). Growth responses for basal area increment described here were similar for tree-ring

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

width, except for a general decline in tree-ring width from 2016-2018 and with tree size, presumably due to an age trend (Figs. S9-11). The 3-way interaction of NSR, year and the resistance-acquisition traits of focal trees was significant for tree-ring width (t = -2.21, P = 0.027; Fig. S10).

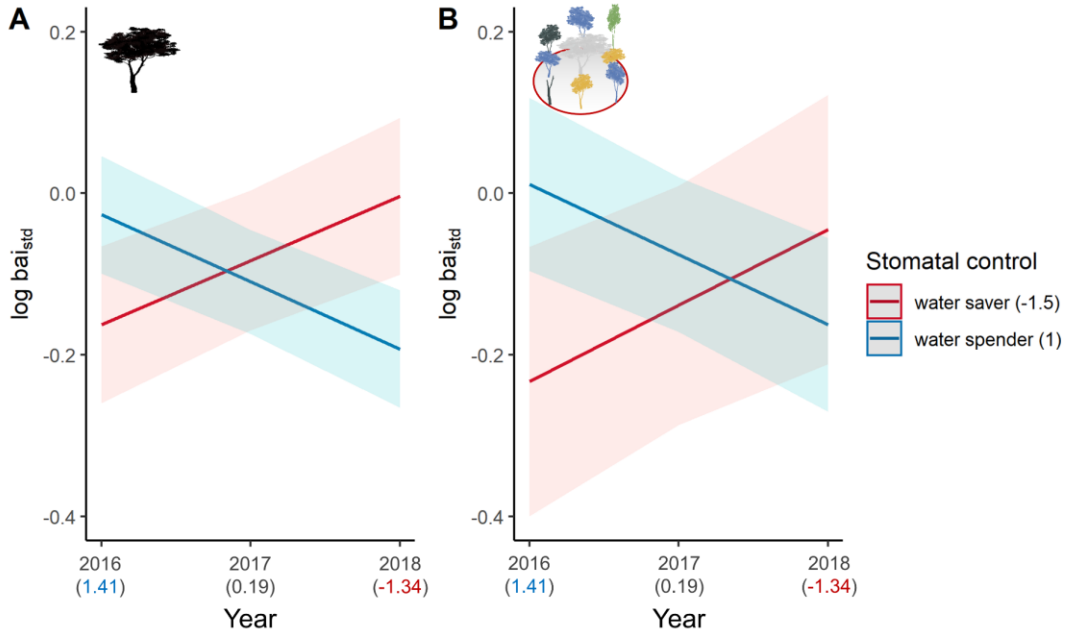

Fig. 4 Modulation of the relationship between climate and growth by stomatal control traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant effects of study year (2016-2018 with wet-to-dry climate, SPEI values in brackets) on the logarithm of basal area increment (bai_{std}) of focal trees predicted for water savers (PC2 value of -1.5) and water spenders (PC2 value of 1.0). The panels illustrate the influence of focal tree stomatal control traits (black tree; A) and neighbour stomatal control traits (tree neighbourhood; B) on the relationship. See Fig. 1 for details on the study design and Tables S11,12 for details on the fitted models.

The effect of drought-tolerance traits on $\delta^{13}C$

Using trait-dependent models to explain variations in $\delta^{13}C$ in the wood of focal trees, we found significant interactions of resistance-acquisition traits with climate, but the effect of neighbour

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

traits was stronger than that of focal tree traits (Fig. 5, Tables S13,14). In the intermediate- and dry-year, we observed higher $\delta^{13}C$ (higher water stress) in focal trees in an acquisitive neighbourhood than in a resistant one. However, lower $\delta^{13}C$ (lower water stress) occurred in focal trees in an acquisitive neighbourhood in the wet year (year × NWM of resistance-acquisition, year as a categorical fixed effect, $F = 9.45$, $P < 0.001$; Fig. 5B). The difference between focal trees in resistant *vs* acquisitive neighbourhoods was biggest in the year with intermediate water availability (2017; Fig. 5B).

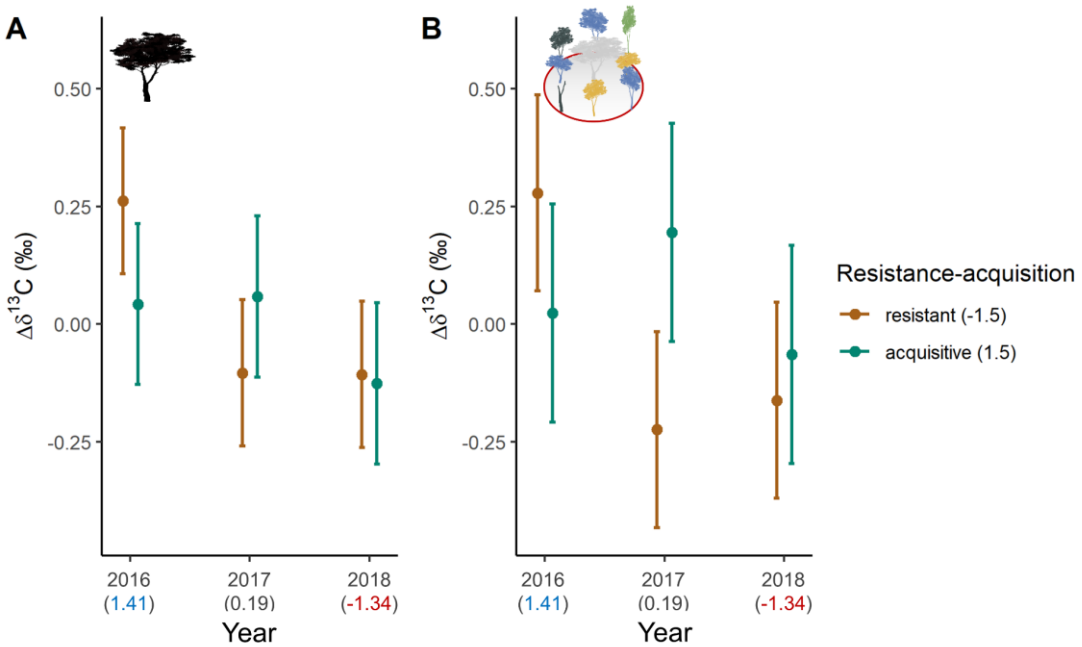

Fig. 5 Modulation of the relationship between climate and $\delta^{13}C$ by resistance-acquisition traits. Points represent linear mixed-effects model fits and error bars show a 95% confidence interval. The models depict significant effects of study year (2016-2018 with wet-to-dry climate, SPEI values in brackets) on $\delta^{13}C$ in the wood of focal trees predicted for cavitation resistant (PC1 value of -1.5) and acquisitive species (PC1 value of 1.5). The panels illustrate the influence of focal tree resistance-acquisition traits (black tree; A) and neighbour resistance-acquisition traits (tree neighbourhood; B) on the relationship. See Fig. 1 for details on the study design and Tables S13,14 for details on the fitted models.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

The stomatal control traits of focal trees significantly modulated the relationship between NSR, climate and $\delta^{13}C$ (NSR × year × focal tree stomatal control traits, t = -2.66, P = 0.008; Fig. 6, Table S15): We found contrasting NSR effects on $\delta^{13}C$ for water-saving and water-spending species, which weakened from wet-to-dry climatic conditions (Fig. 6). In the wet year, $\delta^{13}C$ decreased in water savers with increasing NSR. However, this positive diversity effect declined towards similar $\delta^{13}C$ across NSR levels in the dry year. In contrast, water spending species tended to show increasing $\delta^{13}C$ with increasing NSR in the wet year but decreasing $\delta^{13}C$ with increasing NSR in the dry year. Hence, water savers benefited from more species-rich neighbourhoods (NSR) via lower water stress during wet conditions. In contrast, water spenders benefited from higher NSR during dry climatic conditions, even though effect sizes were relatively small. Finally, stomatal control traits of neighbours influenced $\delta^{13}C$ in the wood of focal trees (year × NWM of stomatal control, t = 3.43, P = 0.001; Fig. S12, Table S16). Focal trees in a water-saving neighbourhood had lower $\delta^{13}C$ in the dry than in the wet year, but this effect was potentially enhanced by the overall decline in $\delta^{13}C$ from the wet-to-dry year (Fig. S7).

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

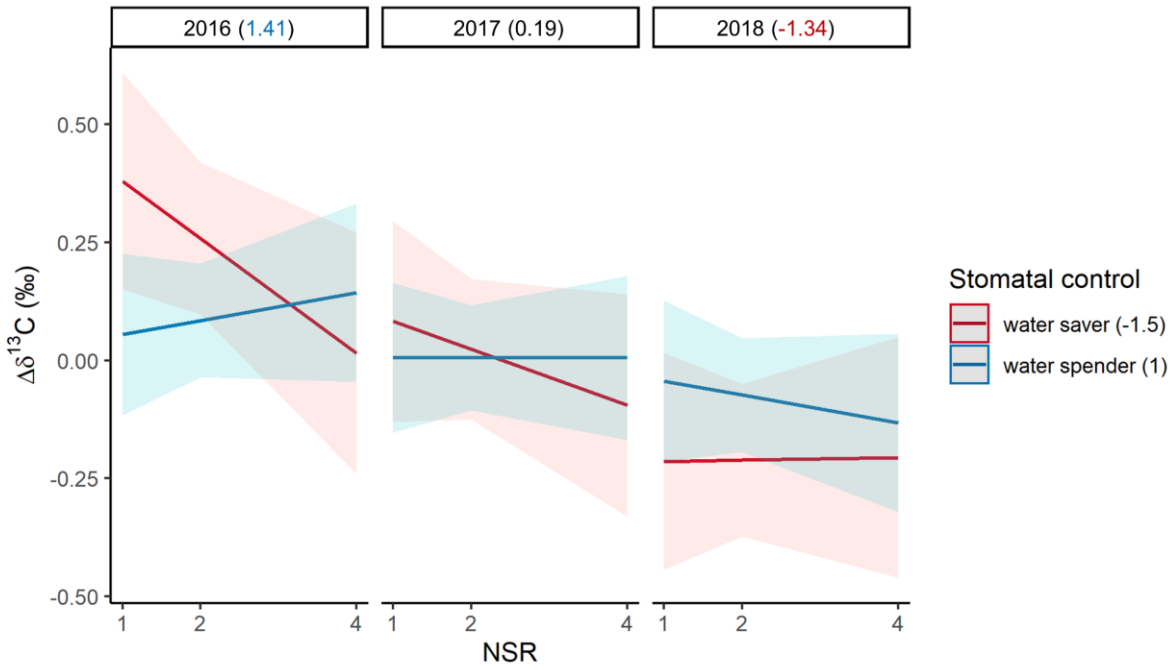

Fig. 6 Modulation of the relationship between neighbourhood species richness (NSR), climate and $\delta^{13}C$ by stomatal control traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant, interactive effects of NSR and study year (2016-2018 with wet-to-dry climate, SPEI values in brackets) on $\delta^{13}C$ in the wood of focal trees predicted for water savers (PC2 value of -1.5) and water spenders (PC2 value of 1.0). See Fig. 1 for details on the study design and Table S15 for details on the fitted model.

Discussion

The growth of focal trees increased with neighbourhood tree species richness (NSR) across the 15 species examined. However, we did not find an overall significant effect of NSR on carbon isotopic ratios in the wood of focal trees ($\delta^{13}C$), nor an increase in the strength of the relationship between NSR and growth and between NSR and $\delta^{13}C$ from wet-to-dry climatic conditions. Instead, relationships between NSR, climate and growth or $\delta^{13}C$ were modulated by drought-tolerance traits of focal trees regarding cavitation resistance vs. resource acquisition and stomatal control. Species with contrasting drought-tolerance traits showed opposite responses to NSR and climate. Using trait-dependent tree neighbourhood models, we could further show

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

that the drought-tolerance traits of tree neighbours consistently changed the nature of focal tree growth and $\delta^{13}C$ responses to climatic conditions. These changes by the traits of neighbours operated in the same direction as the changes induced by the traits of focal trees, thereby amplifying tree responses to climate. The biotic context, which we quantified in terms of drought-tolerance traits of focal trees and their neighbours, thus determined the strength and nature of BEF relationships in the examined tree communities.

Tree diversity increases growth but does not universally relieve drought stress

As postulated in H1, NSR increased growth, which is consistent with findings from other studies (Guillemot et al., 2020; Schnabel et al., 2019; Trogisch et al., 2021), including those from our experiment (Fichtner et al., 2018; Fichtner et al., 2020). Still, NSR effects on the growth of individual species can be both positive and negative and vary with climatic conditions (Fig. S6; e.g. Vitali et al., 2018). Tree growth is an integrated signal of many biotic and abiotic drivers (Grossiord, 2020). The positive effect of NSR on growth is thus likely the result of different and interacting mechanisms operating at the neighbourhood scale (Trogisch et al., 2021). The positive interactions potentially include resource partitioning (of light, water and nutrients), abiotic facilitation (such as microclimate amelioration) and biotic interactions (such as dilution of generalist pathogens) (Barry et al., 2019).

Water stress in focal trees causes changes in the carbon isotope composition of wood, and we thus consider $\delta^{13}C$ as a proxy for neighbourhood-scale water availability (Grossiord et al., 2014; Jucker et al., 2017). Contrary to our expectation and an earlier study on twig $\delta^{13}C$ in our experiment conducted during the particularly wet year 2015 (Fig. 1A; Jansen et al., 2021), we did not detect an overall decrease in $\delta^{13}C$ with NSR and thus no general enhancement of water availability in more diverse tree neighbourhoods. Similarly to our finding, other studies found mixed results and no universal decrease in $\delta^{13}C$ in mixtures compared to monocultures

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

(Grossiord, 2020; Haberstroh & Werner, 2022). Jansen et al. (2021) found the strongest relationship between NSR and $\delta^{13}C$ for trees with high a high degree of crown competition from neighbours and only marginal effects for trees with low crown competition. We thus expect that the net negative effect of NSR on $\delta^{13}C$ in their study resulted from increased shading at high NSR and not from enhanced water availability. This interpretation is supported by the finding that tree biomass and thus shading increased with species richness in BEF-China (Huang et al., 2018). In contrast, our $\delta^{13}C$ values should be primarily influenced by climate-induced water availability as we only studied (co-)dominant trees with slight shading, which is supported by the non-significant effect of all competition indices (Table S7) on $\delta^{13}C$.

Abiotic context dependency

The abiotic context, such as inter-annual changes in water availability, may determine the strength and nature of BEF relationships (e.g., Forrester & Bauhus, 2016). To analyse this abiotic context dependency, we selected the years for our analysis based on standardised climatic water balances which presented a gradient from wet-to-dry climatic conditions (SPEIs; Fig. S1). This analysis of wet-to-dry years prevented negative carry-over effects of drought, but positive carry-over effects from favourable years may have buffered drought impacts through the mobilisation of carbon reserves (McDowell et al., 2022). Moreover, drought stress may have been less severe than suggested by SPEIs. The dry year we examined had similar SPEIs as past drought years (Fig. S2), but non-standardised climatic water balances were rarely negative (Fig. S3). Together, these points may explain why we observed no overall decline in tree growth and decreasing $\delta^{13}C$ values from the wet to the dry year. Hence, even though all forest biomes, including the comparably humid subtropical forests examined here, are threatened by drought (Hartmann et al., 2022), responses may be more pronounced during extreme droughts (e.g. during hotter droughts; Schnabel et al., 2022).

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

We also expected that increasing NSR would benefit growth and relief water stress more with increasingly limited water availability. Yet, we did not find such an overall increase in diversity effects from wet-to-dry climatic conditions, suggesting that either water availability was not limited, or that the diversity signal on water availability is only expressed in growth and $\delta^{13}C$ when water stress reaches a certain threshold. Alternatively, other resources than water, such as light, may have been the more limiting factor in our study system (Forrester & Bauhus, 2016). Other experimental studies reported stronger diversity effects on growth during dry (Fichtner et al., 2020; Schnabel et al., 2019) and during wet years (Belluau, Vitali, Parker, Paquette, & Messier, 2021). Similarly, positive, neutral and negative effects of species richness on growth and $\delta^{13}C$ have been reported under drought (Forrester et al., 2016; Grossiord et al., 2014; Grossiord, 2020). One problem in this context is that it has been challenging to quantify the type and intensity of stress causing changes in the strength and nature of BEF relationships. Here, we attempted to address this by considering the biotic context dependency of BEF relationships under drought.

Biotic context dependency

Trait-based neighbourhood models have been used to understand community assembly (Kunstler et al., 2012; Uriarte et al., 2010) and in few cases to understand how focal tree traits modulate responses to NSR and climate (e.g. Fichtner et al., 2020). However, despite compelling arguments for why the traits of neighbouring trees may alter local water availability (Forrester, 2017), we account here for the first time for both focal tree and neighbour traits and thus the biotic context dependency of BEF relationships in experimental tree communities.

The omission of this biotic context, which reversed the direction of BEF relationships in our study, could be one reason for the mixed results of former studies on tree diversity's role during drought. Given the different drought-tolerance traits in the examined species, it is not surprising

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

that we detected a net zero or only a weak overall effect of NSR on focal tree responses in our study as we examined a balanced sample (in terms of species and number of individuals; N=336) along both drought-tolerance trait gradients (Fig. 1B). In contrast, a former study in BEF-China found a strengthening of positive NSR effects on growth under dry conditions, using census data of all inventoried trees (N=3397) without controlling for a balanced sample of traits (Fichtner et al., 2020). Differences in drought severity between the examined dry years (2011 in Fichtner et al. *vs* 2018 in our study) are unlikely to have caused these different results, as climatic conditions were comparable (Fig. 1A). Instead, the contrasting water-use strategies of focal trees and their neighbours may be one fundamental missing link for explaining divergent results of tree responses to drought in mixed-species forests.

The importance of focal tree traits

Consistent with H2, we found that during drought, NSR increased growth and decreased wood $\delta^{13}C$ of acquisitive (cavitation-sensitive) and water-spending focal tree species. Hence, high neighbourhood diversity supported the more vulnerable species in the forest community during drought (Fichtner et al., 2020). In contrast, cavitation-resistant and water-saving species did not respond to NSR, presumably because their strategies to cope with drought were not aided by species interactions. Moreover, acquisitive and water-spending species showed decreased growth from the wet to the dry year, whereas in cavitation-resistant and water-saving species growth increased.

In general, the likelihood of having heterospecific neighbours increases with increasing NSR. This presence of heterospecific neighbours with different traits than the focal tree may have influenced focal species responses by enhancing or reducing competition or promoting facilitation (Forrester, 2017; Forrester & Pretzsch, 2015). In our study system, enhanced growth of acquisitive focal species at high NSR is likely related to the higher ability of these species to

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

acquire and use resources such as light and water relative to their heterospecific (more conservative) neighbours under wet and dry climatic conditions, respectively (Fichtner et al., 2017; Fichtner et al., 2020). Our focus on (co-)dominant trees probably restricted our analysis to conditions of low neighbourhood competition where acquisitive species benefit from high NSR while conservative species do not (Fichtner et al., 2017). At high NSR, acquisitive (cavitation-sensitive) species were thus protected by diversity, which mitigated drought stress through lower inter- compared to intraspecific competition for water (Fichtner et al., 2020). Moreover, growth responses to declining water availability were likely related not only to resource acquisition but also to cavitation resistance, as cavitation-resistant species may have been able to grow better under drought due to lower degrees of embolism in their vessels (McDowell et al., 2008).

Similarly, water savers may have grown better during dry years as they faced lower cavitation risks (McDowell et al., 2008), while water spenders may have grown better during wet years as they were able to operate optimally without facing hydraulic damage. The lower physiological water stress (lower $\delta^{13}C$) we found in water-spending species during drought at high NSR indicates a novel drought mitigation effect of diversity in addition to the protection of acquisitive species reported formerly (Fichtner et al., 2020). NSR may have relieved water stress during drought as it increases the likelihood of having water-saving neighbours, which transpire less water, thereby increasing local soil water availability (Forrester, 2017). In contrast, during the wet year, where higher high soil moisture enables higher evapotranspiration potentials (Frenne et al., 2021), water-saving species may have profited from NSR because they benefitted from microclimate amelioration by water-spending neighbours (Forrester, 2017). This finding also indicates that the tight stomatal regulation of water savers induces $\delta^{13}C$ responses already during short dry periods (negative climatic water balances appeared each year; Fig. S3) (Jansen et al., 2021) and not only during prolonged drought periods.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

The importance of neighbour traits

Consistent with H3, focal trees grew less in neighbourhoods dominated by acquisitive and water-spending species during drought, while they grew more in resistant and water-saving neighbourhoods. We also observed higher $\delta^{13}C$ values in focal trees in acquisitive neighbourhoods during the intermediate- and dry-year. Both observations indicate reductions in local water availability and thus enhanced water stress (Forrester, 2017; Grossiord et al., 2014) in neighbourhoods dominated by acquisitive and water-spending species relative to neighbourhoods dominated by resistant and water-saving species. This finding may be explained by acquisitive and water-spending neighbours having a higher water consumption during drought. Acquisitive species tend to have a high maximum xylem hydraulic conductance (Bongers et al., 2021), while water spenders close their stomata only late during dry conditions and thus continue to transpire and consume water (McDowell et al., 2008).

Fichtner et al. (2020) already suggested that reduced competition for water between heterospecific neighbours benefits cavitation-sensitive species in diverse neighbourhoods. Still, they could not test this assumption as they did not quantify the influence of neighbour traits. Explicitly accounting for neighbour traits – instead of using neighbourhood species composition as a random effect (e.g. Fichtner et al., 2020; Jansen et al., 2021) – allowed us to quantify the influence of the functional identity of neighbourhoods and the influence of their diversity.

Coordination of drought-tolerance traits

Resistance-acquisition traits primarily modulated climate and NSR effects on growth, whereas stomatal control traits primarily influenced wood $\delta^{13}C$. As expected, growth was thus more strongly related to the leaf economics spectrum (Reich, 2014), while $\delta^{13}C$ was controlled by

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

stomatal aperture (Farquhar et al., 1989). The orthogonality of the resistance-acquisition and stomatal control gradient in our study system (Fig. 1B) allowed us to disentangle the respective contributions of both gradients through exploring the effects of stomatal control (or resistance-acquisition) traits at mean levels of the other gradient. The species responses in years with different water availability were consistent with the current understanding of trade-offs between high cavitation resistance (low Ψ_{50}) and acquisitive resource use (Guillemot et al., 2022; Reich, 2014) and between water-spending and water-saving stomatal control (Martínez-Vilalta & Garcia-Forner, 2017). However, despite the orthogonality in our study system, some association between resistance-acquisition and stomatal control traits may be expected in general (e.g. Klein, 2014) but may not manifest itself in local studies (e.g. Laughlin et al., 2020), as relationships between drought-tolerance traits likely depend on study extent and traits measured. We discuss these points in detail in Supplementary Discussion 1.

Finally, other traits related to drought tolerance may have influenced the observed responses despite our consideration of multiple traits. Such traits include the storage of non-structural carbohydrates, which trees use for maintaining turgor and for defending themselves against biotic agents (Hartmann et al., 2022; McDowell et al., 2022), and attributes of the root system (Weigelt et al., 2021). For instance, carbohydrate storage influences diversity effects on tree survival under drought (Hajek et al., 2022). Therefore, future studies should examine such traits and their relationships with the herein-examined ones to provide a more holistic picture of tree drought responses and their modulation by functional traits.

Conclusion

In a large-scale tree diversity experiment, we analysed tree growth and wood $\delta^{13}C$ responses to contrasting climatic conditions for trees sampled along gradients in neighbourhood species

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

richness (NSR) and drought-tolerance traits. We found enhanced growth but no universal relief of water stress in diverse tree neighbourhoods. Instead, drought tolerance traits related to cavitation resistance vs. resource acquisition and stomatal control of focal trees and their neighbours modulated the relationship between NSR and growth and between NSR and $\delta^{13}C$ under variable climatic conditions. We derived two key conclusions: (1) Considering the functional identity of focal trees and their neighbours resolved the biotic context dependency of BEF relationships; such a trait-based perspective may help to explain positive and negative mixing effects under drought. (2) Drought-tolerance traits of focal trees and interactions with their tree neighbours induced contrasting species responses to wet *vs* dry climatic conditions; this trait-driven species asynchrony is a key driver of positive diversity-stability relationships in forests (Schnabel et al., 2021). The biotic context we analysed using a trait-based approach, with traits tailored to the target ecosystem functions assessed, may help to generalize the context dependency of BEF relationships and is relevant for designing tree mixtures suitable to cope with a range of different drought conditions. It can give insight into the optimal configuration of tree neighbourhoods in terms of diversity and identity in drought-tolerance traits. This may help to optimise forest productivity and foster stability to climate extremes.

Acknowledgements

We thank local workers, in particular Mr. Wang and Mr. Shi, for invaluable help in the field, Luise Münsterberg, Paulina Tjandraputri and Lara Schmitt for supporting the sample preparation for the carbon isotope analyses and Wenzel Kröber and Helge Bruelheide for trait measurements. This research was supported by the International Research Training Group TreeDì funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 319936945/GRK2324 and the University of Chinese Academy of Sciences.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Conflict of interest

The authors declare no conflicts of interest.

Author contributions

Florian Schnabel, Kathryn E. Barry, Anja Kahl, Joannès Guillemot, Jürgen Bauhus and Christian Wirth conceived the ideas of the study and designed the methodology; Florian Schnabel, Susanne Eckhardt, Heike Geilmann, Anja Kahl and Heiko Moossen collected the data; Florian Schnabel and Susanne Eckhardt analysed the data and Kathryn E. Barry, Joannès Guillemot, Jürgen Bauhus and Christian Wirth joined the interpretation of the data and results; Florian Schnabel created the figures; Florian Schnabel wrote the manuscript; All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Tree growth and stable carbon isotope data are available from the BEF-China project database (https://data.botanik.uni-halle.de/bef-china; data will be made publicly available before publication). Climate and trait data are available from the Climatic Research Unit (CRU TS v4.04; Harris et al., 2020) and from Kröber et al. (2014), respectively.

References

Anderegg, W. R. L., Trugman, A. T., Badgley, G., Anderson, C. M., Bartuska, A., Ciais, P., . . . Randerson, J. T. (2020). Climate-driven risks to the climate mitigation potential of forests. *Science*, *368*(6497). https://doi.org/10.1126/science.aaz7005

Barry, K. E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A. J., Bai, Y., . . . Weigelt, A. (2019). The Future of Complementarity: Disentangling Causes from Consequences. *Trends in Ecology & Evolution*, *34*(2), 167–180.

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Belluau, M., Vitali, V., Parker, W., Paquette, A., & Messier, C. (2021). Overyielding in young tree communities does not support the stress-gradient hypothesis and is favoured by functional diversity and higher water availability. *Journal of Ecology*, *109*(4). https://doi.org/10.1111/1365-2745.13602

Bertness, M. D., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), 191–193. https://doi.org/10.1016/0169-5347(94)90088-4

Biondi, F., & Qeadan, F. (2008). A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. *Tree-Ring Research*, *64*(2), 81–96. https://doi.org/10.3959/2008-6.1

Böhnke, M., Kreißig, N., Kröber, W., Fang, T., & Bruelheide, H. (2012). Wood trait-environment relationships in a secondary forest succession in South-East China. *Trees*, *26*(2), 641–651.

Bongers, F. J., Schmid, B., Bruelheide, H., Bongers, F., Li, S., Oheimb, G. von, . . . Liu, X. (2021). Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nature Ecology & Evolution.* Advance online publication. https://doi.org/10.1038/s41559-021-01564-3

Brancalion, P. H. S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F. S. M., Almeyda Zambrano, A. M., . . . Chazdon, R. L. (2019). Global restoration opportunities in tropical rainforest landscapes. *Science Advances*, *5*(7), eaav3223. https://doi.org/10.1126/sciadv.aav3223

Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F., . . . Schmid, B. (2014). Designing forest biodiversity experiments: General considerations illustrated by a

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

new large experiment in subtropical China. *Methods in Ecology and Evolution*, *5*(1), 74–89. https://doi.org/10.1111/2041-210X.12126

Bunn, A. G., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., & Zang, C. (2020). *dplR: Dendrochronology Program Library in R*. Retrieved from https://CRAN.R-project.org/package=dplR

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., . . . Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*(7426), 752–755. https://doi.org/10.1038/nature11688

Coplen, T. B. (2011). Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid Communications in Mass Spectrometry: RCM*, *25*(17), 2538–2560. https://doi.org/10.1002/rcm.5129

Coplen, T. B., Brand, W. A., Gehre, M., Gröning, M., Meijer, H. A. J., Toman, B., & Verkouteren, R. M. (2006). New guidelines for delta13C measurements. *Analytical Chemistry*, *78*(7), 2439–2441. https://doi.org/10.1021/ac052027c

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., . . . Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*, *2*(10), 1579–1587. https://doi.org/10.1038/s41559-018-0647-7

Del Río, M., Pretzsch, H., Ruiz-Peinado, R., Jactel, H., Coll, L., Löf, M., . . . Bravo-Oviedo, A. (2022). Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect. *Journal of Applied Ecology*. Advance online publication. https://doi.org/10.1111/1365-2664.14267

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y. [Ying], & Oheimb, G. von (2018). Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications*, *9*(1), 1144. https://doi.org/10.1038/s41467-018-03529-w

Fichtner, A., Härdtle, W., Li, Y. [Ying], Bruelheide, H., Kunz, M., & Oheimb, G. von (2017). From competition to facilitation: How tree species respond to neighbourhood diversity. *Ecology Letters*, *20*(7), 892–900. https://doi.org/10.1111/ele.12786

Fichtner, A., Schnabel, F., Bruelheide, H., Kunz, M., Mausolf, K., Schuldt, A., . . . Oheimb, G. von (2020). Neighbourhood diversity mitigates drought impacts on tree growth. *Journal of Ecology*, *108*(3), 865–875. https://doi.org/10.1111/1365-2745.13353

Forrester, D. I. (2017). Ecological and Physiological Processes in Mixed Versus Monospecific Stands. In H. Pretzsch, D. I. Forrester, & J. Bauhus (Eds.), *Mixed-species forests: Ecology and management* (pp. 73–115). Berlin, Germany: Springer Nature.

Forrester, D. I., & Bauhus, J. (2016). A Review of Processes Behind Diversity—Productivity Relationships in Forests. *Current Forestry Reports*, *2*(1), 45–61. https://doi.org/10.1007/s40725-016-0031-2

Forrester, D. I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., & Grossiord, C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *Journal of Applied Ecology*, *53*(6), 1725–1734. https://doi.org/10.1111/1365-2664.12745

Forrester, D. I., & Pretzsch, H. (2015). Tamm Review: On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. *Forest Ecology and Management*, *356*, 41–53. https://doi.org/10.1016/j.foreco.2015.08.016

Fortunel, C., Valencia, R., Wright, S. J., Garwood, N. C., & Kraft, N. J. B. (2016). Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. *Ecology Letters*, *19*(9), 1062–1070. https://doi.org/10.1111/ele.12642

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Frenne, P. de, Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., . . . Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/gcb.15569

Gärtner, H., & Nievergelt, D. (2010). The core-microtome: A new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia*, *28*(2), 85–92. https://doi.org/10.1016/j.dendro.2009.09.002

Gheyret, G., Zhang, H.-T., Guo, Y., Liu, T.-Y., Bai, Y.-H., Li, S., . . . Tang, Z. (2021). Radial growth response of trees to seasonal soil humidity in a subtropical forest. *Basic and Applied Ecology*, *55*, 74–86. https://doi.org/10.1016/j.baae.2021.02.015

Grams, T. E. E., Kozovits, A. R., Häberle, K.-H., Matyssek, R., & Dawson, T. E. (2007). Combining delta 13 C and delta 18 O analyses to unravel competition, CO2 and O3 effects on the physiological performance of different-aged trees. *Plant, Cell and Environment*, *30*(8), 1023–1034. https://doi.org/10.1111/j.1365-3040.2007.01696.x

Grossiord, C. (2020). Having the right neighbors: How tree species diversity modulates drought impacts on forests. *New Phytologist*, *228*(1), 42–49. https://doi.org/10.1111/nph.15667

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Checko, E., . . . Gessler, A. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(41), 14812–14815. https://doi.org/10.1073/pnas.1411970111

Guillemot, J., Kunz, M., Schnabel, F., Fichtner, A., Madsen, C. P., Gebauer, T., . . . Potvin, C. (2020). Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. *New Phytologist*, *228*(4), 1256–1268. https://doi.org/10.1111/nph.16722

Guillemot, J., Martin-StPaul, N., Bulascoschi, L., Poorter, L., Morin, X., Pinho, B. X., . . . Brancalion, P. H. S. (2022). Small and slow is safe: On the drought tolerance of tropical tree

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

species. *Global Change Biology*. Advance online publication. https://doi.org/10.1111/gcb.16082

Haberstroh, S., & Werner, C. (2022). The role of species interactions for forest resilience to drought. *Plant Biology*. Advance online publication. https://doi.org/10.1111/plb.13415

Hajek, P., Link, R. M., Nock, C. A., Bauhus, J., Gebauer, T., Gessler, A., . . . Schuldt, B. (2022). Mutually inclusive mechanisms of drought-induced tree mortality. *Global Change Biology*, *28*(10), 3365–3378. https://doi.org/10.1111/gcb.16146

Hammond, W. M., Williams, A. P., Abatzoglou, J. T., Adams, H. D., Klein, T., López, R., . . . Allen, C. D. (2022). Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications*, *13*(1), 1761. https://doi.org/10.1038/s41467-022-29289-2

Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, *7*(1), 109. https://doi.org/10.1038/s41597-020-0453-3

Hartmann, H., Bastos, A., Das, A. J., Esquivel-Muelbert, A., Hammond, W. M., Martínez-Vilalta, J., . . . Allen, C. D. (2022). Climate Change Risks to Global Forest Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide. *Annual Review of Plant Biology*. Advance online publication. https://doi.org/10.1146/annurev-arplant-102820-012804

Huang, Y., Chen, Y., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., . . . Schmid, B. (2018). Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, *362*(6410), 80–83. https://doi.org/10.1126/science.aat6405

IPCC (2014). *Climate change 2014. Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of*

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

the Intergovernmental Panel on Climate Change. New York, NY: Cambridge University Press.

Jansen, K., Oheimb, G. von, Bruelheide, H., Härdtle, W., & Fichtner, A. (2021). Tree species richness modulates water supply in the local tree neighbourhood: Evidence from wood δ13C signatures in a large-scale forest experiment. *Proceedings. Biological Sciences*, *288*(1946), 20203100. https://doi.org/10.1098/rspb.2020.3100

Jucker, T., Avacaritei, D., Barnoaiea, I., Duduman, G., Bouriaud, O., & Coomes, D. A. (2016). Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, *104*(2), 388–398. https://doi.org/10.1111/1365-2745.12522

Jucker, T., Grossiord, C., Bonal, D., Bouriaud, O., Gessler, A., & Coomes, D. A. (2017). Detecting the fingerprint of drought across Europe's forests: do carbon isotope ratios and stem growth rates tell similar stories? *Forest Ecosystems*, *4*(1), 706. https://doi.org/10.1186/s40663-017-0111-1

Klein, T. (2014). The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Functional Ecology*, *28*(6), 1313–1320. https://doi.org/10.1111/1365-2435.12289

Kröber, W., & Bruelheide, H. (2014). Transpiration and stomatal control: a cross-species study of leaf traits in 39 evergreen and deciduous broadleaved subtropical tree species. *Trees*, *28*(3), 901–914. https://doi.org/10.1007/s00468-014-1004-3

Kröber, W., Zhang, S., Ehmig, M., & Bruelheide, H. (2014). Linking xylem hydraulic conductivity and vulnerability to the leaf economics spectrum--a cross-species study of 39 evergreen and deciduous broadleaved subtropical tree species. *PLoS ONE*, *9*(11), e109211. https://doi.org/10.1371/journal.pone.0109211

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., . . . Coomes, D. A. (2012). Competitive interactions between forest

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, *15*(8), 831–840. https://doi.org/10.1111/j.1461-0248.2012.01803.x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13). https://doi.org/10.18637/jss.v082.i13

Laughlin, D. C., Delzon, S., Clearwater, M. J., Bellingham, P. J., McGlone, M. S., & Richardson, S. J. (2020). Climatic limits of temperate rainforest tree species are explained by xylem embolism resistance among angiosperms but not among conifers. *New Phytologist*, *226*(3), 727–740. https://doi.org/10.1111/nph.16448

Li, Y. [Ying], Kröber, W., Bruelheide, H., Härdtle, W., & Oheimb, G. von (2017). Crown and leaf traits as predictors of subtropical tree sapling growth rates. *Journal of Plant Ecology*, *10*(1), 136–145. https://doi.org/10.1093/jpe/rtw041

Loader, N. J., Robertson, I., & McCarroll, D. (2003). Comparison of stable carbon isotope ratios in the whole wood, cellulose and lignin of oak tree-rings. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *196*(3-4), 395–407. https://doi.org/10.1016/S0031-0182(03)00466-8

Martínez-Vilalta, J., & Garcia-Forner, N. (2017). Water potential regulation, stomatal behaviour and hydraulic transport under drought: Deconstructing the iso/anisohydric concept. *Plant, Cell and Environment*, *40*(6), 962–976. https://doi.org/10.1111/pce.12846

McDowell, N. G., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., . . . Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

McDowell, N. G., Sapes, G., Pivovaroff, A., Adams, H. D., Allen, C. D., Anderegg, W. R. L., . . . Xu, C. (2022). Mechanisms of woody-plant mortality under rising drought, CO2 and vapour pressure deficit. *Nature Reviews Earth and Environment*, *3*, 294–308. https://doi.org/10.1038/s43017-022-00272-1

Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., . . . Zemp, D. C. (2021). For the sake of resilience and multifunctionality, let's diversify planted forests! *Conservation Letters*, *15*(1), e12829. https://doi.org/10.1111/conl.12829

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, *20*(1), 170–180. https://doi.org/10.1111/j.1466-8238.2010.00592.x

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Schnabel, F., Liu, X., Kunz, M., Barry, K. E., Bongers, F. J., Bruelheide, H., . . . Wirth, C. (2021). Species richness stabilizes productivity via asynchrony and drought-tolerance diversity in a large-scale tree biodiversity experiment. *Science Advances*, *7*(51). https://doi.org/10.1126/sciadv.abk1643

Schnabel, F., Purrucker, S., Schmitt, L., Engelmann, R. A., Kahl, A., Richter, R., . . . Wirth, C. (2022). Cumulative growth and stress responses to the 2018-2019 drought in a European floodplain forest. *Global Change Biology*, *28*(5), 1870–1883. https://doi.org/10.1111/gcb.16028

Schnabel, F., Schwarz, J. A., Dănescu, A., Fichtner, A., Nock, C. A., Bauhus, J., & Potvin, C. (2019). Drivers of productivity and its temporal stability in a tropical tree diversity experiment. *Global Change Biology*, *25*(12), 4257-4272. https://doi.org/10.1111/gcb.14792

Schulze, B., Wirth, C., Linke, P., Brand, W. A., Kuhlmann, I., Horna, V., & Schulze, E.-D. (2004). Laser ablation-combustion-GC-IRMS--a new method for online analysis of intra-

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

annual variation of delta13C in tree rings. *Tree Physiology*, *24*(11), 1193–1201. https://doi.org/10.1093/treephys/24.11.1193

Schwarz, J. A., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., & Bauhus, J. (2020). Quantifying Growth Responses of Trees to Drought—a Critique of Commonly Used Resilience Indices and Recommendations for Future Studies. *Current Forestry Reports*, *6*, 185–200. https://doi.org/10.1007/s40725-020-00119-2

Schweingruber, F. H. (1996). *Tree rings and environment: dendroecology*. Berne, Switzerland: Paul Haupt AG Bern.

Shi, M.-M., Michalski, S. G., Welk, E., Chen, X.-Y., & Durka, W. (2014). Phylogeography of a widespread Asian subtropical tree: genetic east-west differentiation and climate envelope modelling suggest multiple glacial refugia. *Journal of Biogeography*, *41*(9), 1710–1720. https://doi.org/10.1111/jbi.12322

Stoll, P., & Newbery, D. M. (2005). Evidence of species-specific neighborhood effects in the dipterocarpaceae of a Bornean rain forest. *Ecology*, *86*(11), 3048–3062. https://doi.org/10.1890/04-1540

Trogisch, S., Liu, X., Rutten, G., Xue, K., Bauhus, J., Brose, U., . . . Bruelheide, H. (2021). The significance of tree-tree interactions for forest ecosystem functioning. *Basic and Applied Ecology*, *55*, 33–52. https://doi.org/10.1016/j.baae.2021.02.003

Uriarte, M., Swenson, N. G., Chazdon, R. L., Comita, L. S., John Kress, W., Erickson, D., . . . Thompson, J. (2010). Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: Implications for community assembly. *Ecology Letters*, *13*(12), 1503–1514. https://doi.org/10.1111/j.1461-0248.2010.01541.x

Van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, *94*(4), 1220–1245. https://doi.org/10.1111/brv.12499

bioRxiv preprint doi: https://doi.org/10.1101/2022.11.22.517351; this version posted November 24, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate*, *23*(7), 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vitali, V., Forrester, D. I., & Bauhus, J. (2018). 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*(6), 1215–1229. https://doi.org/10.1007/s10021-017-0214-0

Wang, X.-H., Kent, M., & Fang, X.-F. (2007). Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration. *Forest Ecology and Management*, *245*(1-3), 76–87. https://doi.org/10.1016/j.foreco.2007.03.043

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., . . . McCormack, M. L. (2021). An integrated framework of plant form and function: The belowground perspective. *New Phytologist*, *232*(1), 42–59. https://doi.org/10.1111/nph.17590

Werner, R. A., & Brand, W. A. (2001). Referencing strategies and techniques in stable isotope ratio analysis. *Rapid Communications in Mass Spectrometry: RCM*, *15*(7), 501–519. https://doi.org/10.1002/rcm.258

Yang, X., Bauhus, J., Both, S., Fang, T., Härdtle, W., Kröber, W., . . . Bruelheide, H. (2013). Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *European Journal of Forest Research*, *132*(4), 593–606. https://doi.org/10.1007/s10342-013-0696-z