



HAL
open science

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

F Schnabel, K E Barry, S Eckhardt, Joannès Guillemot, H Geilmann, A Kahl, H Moossen, J Bauhus, C Wirth

► To cite this version:

F Schnabel, K E Barry, S Eckhardt, Joannès Guillemot, H Geilmann, et al.. Neighbourhood species richness and drought-tolerance traits modulate tree growth and $\delta^{13}\text{C}$ responses to drought. *Plant Biology*, 2024, 26, pp.330 - 345. 10.1111/plb.13611 . hal-04530276

HAL Id: hal-04530276

<https://hal.inrae.fr/hal-04530276>

Submitted on 3 Apr 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.









Distributed under a Creative Commons Attribution 4.0 International License



RESEARCH ARTICLE

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

F. Schnabel^{1,2,3} , K. E. Barry^{1,2,4} , S. Eckhardt², J. Guillemot^{5,6,7} , H. Geilmann⁸, A. Kahl² , H. Moossen⁸, J. Bauhus³  & C. Wirth^{1,2,8} 

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

2 Systematic Botany and Functional Biodiversity, Leipzig University, Leipzig, Germany

3 Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

4 Ecology and Biodiversity, Department of Biology, Institute of Environmental Biology, Utrecht University, Utrecht, Netherlands

5 CIRAD, UMR Eco&Sols, Piracicaba, Brazil

6 Eco&Sols, Univ Montpellier, CIRAD, INRAE, Institut Agro, IRD, Campus SupAgro, Montpellier, France

7 Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, Brazil

8 Max Planck Institute for Biogeochemistry, Jena, Germany

Keywords

biodiversity–ecosystem functioning; carbon isotopes; climate change; functional traits; mixed-species forest; plant–plant interactions; tree rings.

Correspondence

F. Schnabel, Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstr. 4, Freiburg 79106, Germany.
E-mail: florian.schnabel@waldbau.uni-freiburg.de

Editor

C. Werner

Received: 14 July 2023;

Accepted: 24 November 2023

doi:10.1111/plb.13611

ABSTRACT

- Mixed-species forests are promoted as a forest management strategy for climate change adaptation, but whether they are more resistant to drought than monospecific forests remains contested. In particular, the trait-based mechanisms driving the role of tree diversity under drought remain elusive.
- Using tree cores from a large-scale biodiversity experiment, we investigated tree growth and physiological stress responses (*i.e.* increase in wood carbon isotopic ratio; $\delta^{13}\text{C}$) to changes in climate-induced water availability (wet to dry years) along gradients in neighbourhood tree species richness and drought-tolerance traits. We hypothesized that neighbourhood species richness increases growth and decreases $\delta^{13}\text{C}$ and that these relationships are modulated by the abiotic (*i.e.* climatic conditions) and the biotic context. We characterised the biotic context using drought-tolerance traits of focal trees and their neighbours. These traits are related to cavitation resistance *versus* resource acquisition and stomatal control.
- Tree growth increased with neighbourhood species richness. However, we did not observe a universal relief of water stress in species-rich neighbourhoods. The effects of neighbourhood species richness and climate on growth and $\delta^{13}\text{C}$ were modulated by the traits of focal trees and the traits of their neighbours. At either end of each drought-tolerance gradient, species responded in opposing directions during dry and wet years.
- We show that species' drought-tolerance traits can explain the strength and nature of biodiversity–ecosystem functioning relationships in experimental tree communities experiencing drought. Mixing tree species can increase growth but may not universally relieve drought stress.

INTRODUCTION

The world's forests are experiencing widespread mortality events because of climate extremes like droughts (Hartmann *et al.* 2022). Such climate extremes are predicted to increase in frequency and intensity with climate change in many regions (IPCC 2022), threatening multiple 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 optimise productivity and thus carbon storage while at the same time increasing these restored forests' ecological stability against climate extremes (Bauhus *et al.* 2017). 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 (Jucker *et al.* 2014; Messier *et al.* 2021).

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 (van der Plas 2019; Messier *et al.* 2021; Schnabel *et al.* 2021). Such tree species richness effects can be best studied at the neighbourhood scale, where tree–tree interactions occur (Trogisch *et al.* 2021). This is because neighbourhood analyses allow studying neighbourhood species richness (hereafter called 'NSR') effects alongside factors such as tree size and competition, which can impact tree performance (Stoll & Newbery 2005; Forrester & Pretzsch 2015). Importantly, positive NSR 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 (Schnabel *et al.* 2019; Fichtner *et al.* 2020). 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. These mixed results may be driven by species-specific water-use strategies. This is 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 (*i.e.* their tree neighbours) environment (Forrester 2017). We characterised this biotic context, which has received little attention compared to the many studies that examined the abiotic context dependency of biodiversity–ecosystem functioning (BEF) relationships (*e.g.* Forrester & Bauhus 2016; Jucker *et al.* 2016; Grossiord 2020), as traits of focal trees and as traits of their neighbours.

The recent history of an abiotic and biotic control on BEF relationships can be analysed in the tree ring record of a focal tree, which captures its response to neighbours and climatic variations (Schweingruber 1996; Vitali *et al.* 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, and given that growth does not completely stop during drought, the isotopic ratio of $^{13}\text{C}/^{12}\text{C}$ in wood (hereafter ' $\delta^{13}\text{C}$ ') is a principal indicator of a tree's physiological reaction to water limitation and drought, with higher $\delta^{13}\text{C}$ values suggesting greater drought stress. $\delta^{13}\text{C}$ captures the ratio of CO_2 concentration inside the cells and in the atmosphere during the time of carbon fixation, thus reflecting the balance between net CO_2 assimilation and stomatal conductance of trees (Farquhar *et al.* 1989; Grams *et al.* 2007). Under drought stress, trees close their stomata to avoid water loss from transpiration, and as stomatal conductance is more affected than assimilation, $\delta^{13}\text{C}$ increases under drought (Farquhar *et al.* 1989; Grossiord *et al.* 2014). Therefore, $\delta^{13}\text{C}$ is widely recognised as an indicator of the severity of drought exposure in trees, and we consider it as a proxy for neighbourhood-scale water availability (Grossiord *et al.* 2014; Jucker *et al.* 2017).

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' (see Schnabel *et al.* 2021 for details). In brief, 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 often 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: some species close their stomata early during water shortages to avoid transpirational water loss (called 'water-saving' or 'isohydric' species), whereas others keep their stomata open despite increasingly negative water potentials and increasing cavitation risks (called

'water-spending' or 'anisohydric' species) (McDowell *et al.* 2008; Martínez-Vilalta & García-Fórner 2017). In line with current perspectives, we do not use the regulation of leaf water potential (Ψ_L) as measure for stomatal control, as it was shown to be a poor proxy (Martínez-Vilalta & García-Fórner 2017). Instead, 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 *et al.* 2014; Schnabel *et al.* 2021). 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 characterise 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 $\delta^{13}\text{C}$ responses to the interactive effects of NSR and contrasting climatic conditions (such as particularly dry and wet years).

A focal tree's functional (trait) identity, hereafter 'focal tree traits', may be crucial to understand responses of tree growth and $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values in tree twig tissues, indicating enhanced water availability in diverse neighbourhoods (Jansen *et al.* 2021). In this context, growth may be more strongly related to resistance–acquisition traits and thus the leaf economics spectrum (Reich 2014). Alternatively, wood $\delta^{13}\text{C}$ may be primarily controlled by stomata aperture (Farquhar *et al.* 1989) and thus stomatal control traits.

The trait identity of a focal tree's neighbours, hereafter 'neighbour traits', may also influence the growth and $\delta^{13}\text{C}$ of focal trees through their influence on biotic interactions (*e.g.* Fortunel *et al.* 2016; Trogisch *et al.* 2021; Yang *et al.* 2021). In this view, neighbour traits may alter water use and with this local soil water availability. For example, during drought, growth reductions in water spenders may be lower and $\delta^{13}\text{C}$ increases smaller when growing with more water-saving neighbours, because the lower stomatal conductance of the latter may decrease overall water consumption and thus lower edaphic drought stress in focal trees (Forrester 2017). Conversely, being surrounded by water-spending neighbours may reduce soil water availability during drought and hence amplify focal tree growth reductions and $\delta^{13}\text{C}$ increases.

Here, we aim to understand how drought-tolerance traits influence the relationship between NSR and growth, and NSR and $\delta^{13}\text{C}$ under variable climatic conditions to shed light on the abiotic and biotic context dependency of forest BEF relationships. 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 $\delta^{13}\text{C}$ in a climatically dry, normal and wet year in a large-scale subtropical 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ under variable climatic conditions. Specifically, during drought, NSR increases growth and decreases $\delta^{13}\text{C}$ 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.

MATERIAL 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 (Bruehlheide *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 (mean from 1971 to 2000; 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 broad-leaved trees dominate the diverse native forests in the study region, sometimes mixed with conifers (Bruehlheide *et al.* 2014). The region's location between tropical and temperate climates with their respective flora (Wang *et al.* 2007; Shi *et al.* 2014), makes it ideal for studying diverse water-use strategies and species responses to variable climatic conditions (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 monocultures 2-, 4-, 8-, 16- and 24-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 (Bruehlheide *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 m on plots with a size of 25.8 × 25.8 m², 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 (2018) year. The analysis of consecutive years allowed us to minimise other factors than climate that may

influence growth and $\delta^{13}\text{C}$, such as changes in stand structure. We used the standardised precipitation evapotranspiration index (SPEI) (Vicente-Serrano *et al.* 2010) calculated from a high-resolution time-series of interpolated climate station data (CRU TS v4.04; Harris *et al.* 2020) to characterise climatic conditions. The SPEI represents a standardised climatic water balance of precipitation minus potential evapotranspiration. We selected study years following suggestions by Schwarz *et al.* (2020) by comparing SPEI series for the peak vegetation period (SPEI3, April–July), the full vegetation period (SPEI6, April–September) and the entire year (SPEI12, October–September), using 1901–2019 as climate reference period (Fig. 1A, Figures S1 and S2). The subtropical vegetation period in the study region ranges from April–September with peak growth at the end of April (Gheyret *et al.* 2021), which corresponds well with the selected SPEI lengths. All periods (SPEI3, SPEI6, SPEI12) showed the same pattern of decreasing SPEI values from 2016 to 2017 to 2018 (Figure S1), with drought severity in the dry year being comparable to drought conditions in the last 40 years (Figure S2). In addition, we also examined intra-annual and non-standardised climatic water balances (Figure S3).

Species selection via drought-tolerance traits

We used this experimental set-up to select tree species (Table S1) along two orthogonal trait gradients related to resistance–acquisition and stomatal control traits (Fig. 1B) which allowed us to study their relative contributions to tree growth and $\delta^{13}\text{C}$. 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 & Bruehlheide 2014). Trait data were analysed with principal components 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), hereafter referred to as 'resistant species' (Fig. 1B). In contrast, 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}), hereafter referred to as 'acquisitive species'. 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-regulation of their conductance under increasing VPD. In contrast, water spenders down-regulate their stomatal conductance only at high VPD.

In 2019, *i.e.*, 9–10 years after planting, we selected 15 tree species to cover the trait space as well as possible by choosing

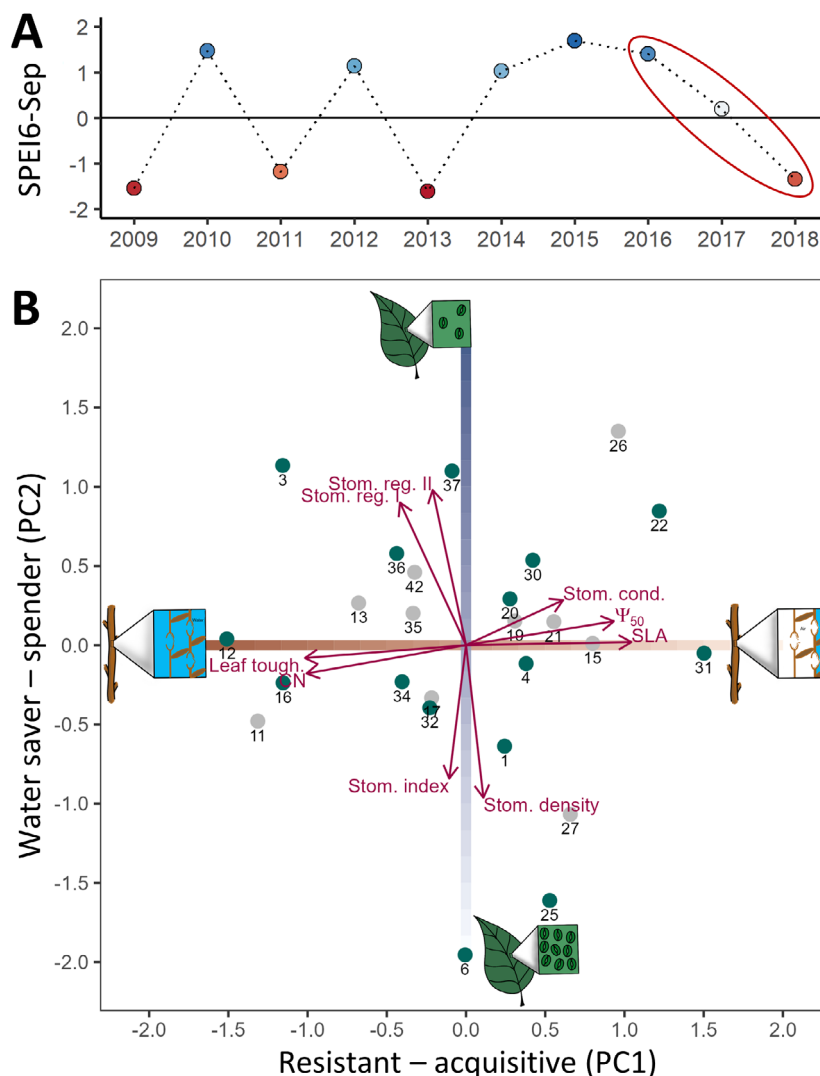


Fig. 1. Selection of study years and species. A: Climate-based selection of the study years 2016–2018 based on the standardised precipitation–evapotranspiration index of the vegetation period (SPEI6, April–September). Blue points indicate wetter and red points drier conditions compared to the long-term mean; values below -1 and above 1 can be considered exceptional. B: Species selection via their drought-tolerance traits based on principal components analysis (PCA) adapted from Schnabel *et al.* (2021); species represented by codes. PC1 reflects a resistance–acquisition gradient running from cavitation-resistant (low Ψ_{50} , high leaf toughness and C/N ratio) to acquisitive species (high Ψ_{50} , specific leaf area (SLA), maximum stomatal conductance). PC2 reflects a stomatal control gradient running from water spenders with late stomatal closure under decreasing vapour pressure deficits (stomatal regulation traits I and II) to water savers with fast stomatal closure (high stomatal density and stomatal index). The sketches illustrate the trait gradients: (PC1) high versus low cavitation resistance, (PC2) few versus abundant stomata. We selected focal trees from 15 species to cover the trait space (highlighted in green). See Table S1 for a list of tree species and Table S2 for details on the traits.

species at the extremes of both gradients (two 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’. As species pools in the BEF-China experiment overlap only partly between sites A and B (Bruehlheide *et al.* 2014), we sampled seven species at site A, seven at site B and one species (*Schima superba* Gardn. Et Champ.) at both sites (*i.e.* 15 species in total and eight species at each site) to test for potential differences between sites. We selected these species out of a pool of 25 potential tree species, which all featured mid- to fast growth rates in our experiment

(Li *et al.* 2017), showed distinct radial growth rings (Böhnke *et al.* 2012), and had comparably good survival rates to ensure sufficient tree and sample size for coring.

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-neighbourhood species (Fig. 2A, B). In the field, we randomly selected 10 focal trees (seven trees for final analysis and three 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). We sampled focal trees in as many different plots

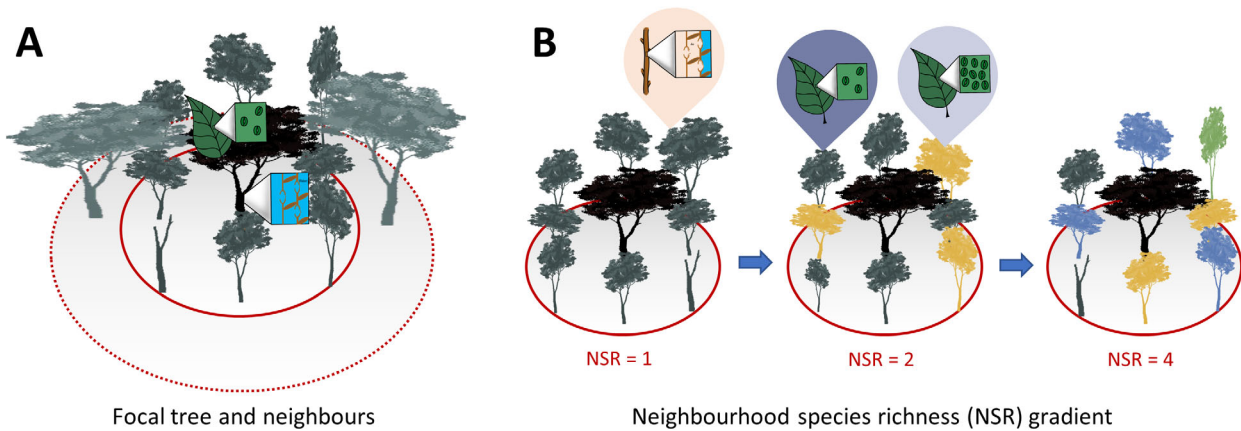


Fig. 2. Tree neighbourhood design. A: Focal trees (black tree) and their neighbours (grey trees). B: Neighbourhood species richness (NSR) gradient of 1-, 2- and 4-neighbour species. The sketches illustrate the influence of focal tree and neighbour traits on the relationships between NSR, climate and growth as well as $\delta^{13}\text{C}$.

and species compositions as possible to increase the generality of our results ($N = 122$ plots) and avoided overlapping neighbourhoods to minimise spatial autocorrelation (see Method S1 for details on the focal tree selection). For each focal tree, we recorded its position, species' identity and diameter at breast height (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 live 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. 2A). 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). We calculated neighbour traits, *i.e.* the functional identity of a focal tree's neighbourhood, as the neighbourhood-weighted mean (NWM) trait value of each neighbourhood for both gradients, hereafter called '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:

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

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. 1B).

Tree growth and carbon stable isotopes

We used tree growth and carbon isotope ratios as indicators of focal tree responses to the interactive effects of NSR, climate and drought-tolerance traits. We extracted one increment core

at dbh from each focal tree perpendicular to the slope (avoiding tension wood) using a three-threaded Hagl of 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 h at 70 °C. Core surfaces were prepared with a core-microtome (G rtner & Nievergelt 2010) to visualise tree-ring boundaries. Annual tree-ring width (mm) was measured using a LINTABTM 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 because of the short length of individual series (mostly 5 to 7 years). Tree-ring series of 474 trees from 15 species could be dated (see Figure S4 for an overview of wood anatomy). We used basal area increment (cm^2) as an indicator of temporal trends in tree growth as it is, particularly in young, open-grown trees (Biondi & Qeadan 2008), less influenced by biological age trends than tree-ring width (see Figure S5 for a comparison). In the Supplement, we present results for tree-ring width, which yielded similar results, to allow for a comparison of both proxies following suggestions of Schwarz *et al.* (2020). Basal area increment was calculated using tree-ring width, bark thickness and diameter with the `bai.out()` function in the `dplR` package in R (Bunn *et al.* 2020).

The carbon isotope ratio in the wood of focal trees ($\delta^{13}\text{C}$) 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 $\delta^{13}\text{C}$ in bulk wood rather than in extracted cellulose because both materials produce highly correlated signals and capture similar inter-annual variation in $\delta^{13}\text{C}$ (Schulze *et al.* 2004; Sohn *et al.* 2012; Gessler *et al.* 2014). 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 $\delta^{13}\text{C}$ values on the VPDB-LSVEC scale (Coplen *et al.* 2006). The $\delta^{13}\text{C}$ values are reported in per mil (‰) by multiplying the delta value by the factor 1000 (Coplen 2011).

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

Samples were scaled against the in-house standard (acetanilide) with a $\delta^{13}\text{C}$ value of $-30.06 \pm 0.1\text{‰}$. Caffeine (caf-j3; $\delta^{13}\text{C}$: $-40.46 \pm 0.1\text{‰}$) was analysed several times in each sequence as quality control. In order to verify their stability, in-house standards of the BGC-IsoLab are analysed twice per year against international stable isotope standards IAEA-603 ($+1.46 \pm 0.01\text{‰}$) and NBS22 ($-30.03 \pm 0.04\text{‰}$), see also suggestions of Dunn *et al.* (2021) for in-house reference materials. Linearity, blank and drift corrections were done for each sequence according to Werner & 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 lay within $0.05 \pm 0.03\text{‰}$, well within the range of the in-house standard precision. We used the mean of these repeated measurements in the further analyses.

In forests, the effects of water availability on $\delta^{13}\text{C}$ can be separated from those of CO_2 assimilation by analysing isotopic signals in tree rings from (co-)dominant trees that experience little shading from neighbours, which minimises shading effects on assimilation (Grossiord *et al.* 2014; Jucker *et al.* 2017). We selected (co-)dominant focal trees through the use of a minimum dbh of 8 cm and an *a priori* selection of those trees that experienced least shading by their neighbourhood. The final, completely balanced dataset with seven trees per species, NSR-level and year comprised 336 trees from 114 plots with at least two trees per plot.

Statistical analysis

We used linear mixed-effects models (LMMs) to model growth (basal area increment) and wood $\delta^{13}\text{C}$ responses to the interactive effects of NSR, climate and drought-tolerance traits. Our modelling framework consisted of two main steps. First, we built trait-independent neighbourhood models that accounted for the initial size of focal trees, their competition with neighbours, NSR and climate conditions, and the interaction between NSR \times climate as fixed effects. We compared eight neighbourhood competition indices (Table S3) and selected the Hegyi index, which considers the distance and basal area of neighbour trees relative to the focal tree, as the best-performing one *via* the Akaike Information Criterion (Table S4). We accounted for our experimental design and repeated measurements through a nested random effect structure of focal tree identity nested within plot and site. A separate analysis of *Schima superba*, the species sampled at both sites, showed that growth and $\delta^{13}\text{C}$ responses did not differ between sites for this species (Analysis S1), indicating that responses are similar at both experimental sites, which is in line with previous studies (*e.g.* Schnabel *et al.* (2021)). Finally, we selected the most parsimonious trait-independent neighbourhood model through backward elimination of fixed and random effects. For further details see Method S2.

Second, we examined how focal tree traits and neighbour traits modulate growth and $\delta^{13}\text{C}$ responses to the interactive

effects of NSR and climate. To understand the effect of focal tree traits, we included interactions between NSR, climate and either focal tree resistance-acquisition or stomatal control traits into the models of step 1. Similarly, to understand the effect of neighbour traits, we included the interaction between climate and either neighbour resistance-acquisition or stomatal control traits into the models of step 1. We selected the most parsimonious focal tree trait and neighbour trait models through 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 $\delta^{13}\text{C}$ 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.

As we were interested in relative and not in absolute differences between species, we standardised basal area increment values by dividing each value by its species' mean and $\delta^{13}\text{C}$ values by subtracting its species' mean in all mixed-effect models to reduce total variance in the data, referred to as ba_{std} and $\Delta\delta^{13}\text{C}$, 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 *et al.* 2015) and lmerTest (Kuznetsova *et al.* 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.

RESULTS

Across the 15 species examined, we observed large species-specific differences in focal tree growth and particularly in $\delta^{13}\text{C}$ (Fig. 3). Species responses to the interactive effects of NSR and climate were highly variable (Fig. 3). To elucidate general trends, while accounting for confounding effects such as a tree's or a plot's location, we employed mixed-effect models. Using trait-independent models, we found that focal tree growth, measured as basal area increment, increased logarithmically with tree size ($t = 5.01$, $P < 0.001$), decreased with competition by neighbouring trees ($t = -5.91$, $P < 0.001$), and increased by 11.4% from 1-species to 4-species neighbourhoods ($t = 2.29$, $P = 0.024$) (Fig. 4, Table S5). The effects of NSR on growth were consistent across different annual climatic conditions, and we did not observe an absolute difference in growth between the wet (2016), intermediate (2017) and dry year (2018). When examining the trait-independent models for carbon isotope ratios ($\delta^{13}\text{C}$) in the wood of focal trees, we found a linear decrease in $\delta^{13}\text{C}$ from the wet to the dry year ($t = -9.06$, $P < 0.001$; Figure S6, Table S6). Neither tree size, competition, NSR, nor the interaction between NSR and year significantly affected $\delta^{13}\text{C}$ (Tables S6 and S7).

The effect of drought-tolerance traits on tree growth

Using trait-dependent models, we found that the resistance-acquisition traits of focal trees significantly modulated the relationship between tree growth and two factors: NSR and climate

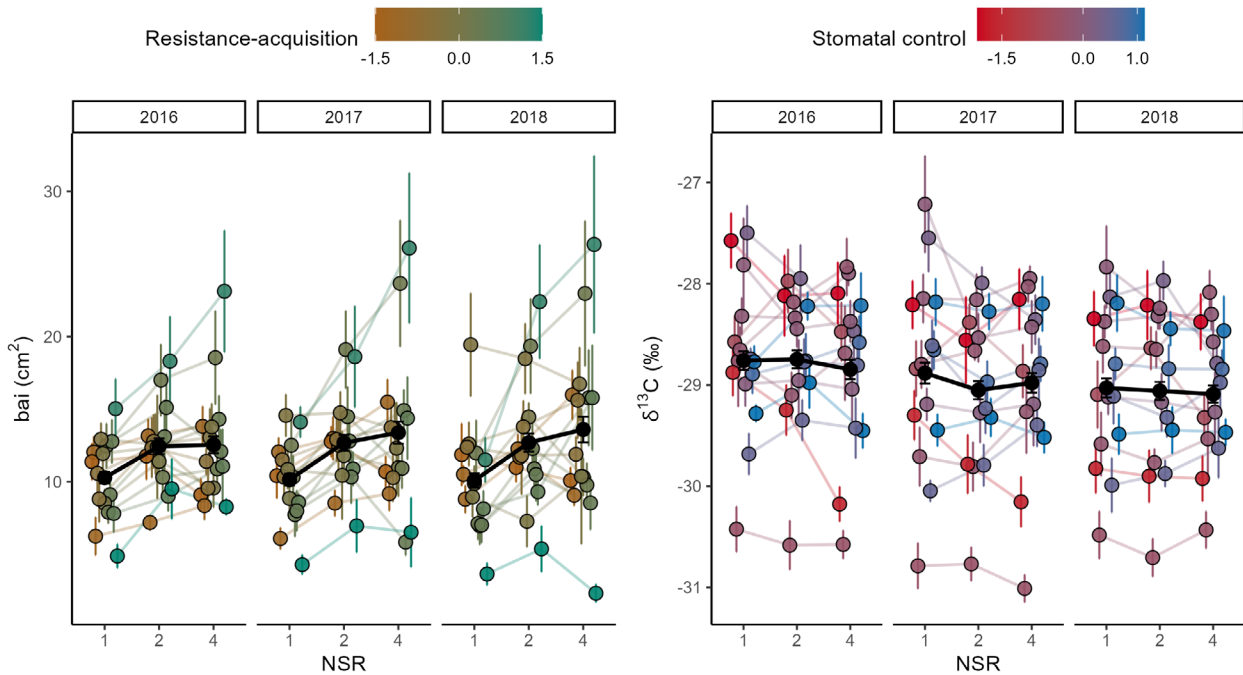


Fig. 3. Measured values of focal tree basal area increment (bai) and carbon isotope ratio ($\delta^{13}\text{C}$) per species, year and neighbourhood species richness (NSR) level. Points show mean values per species ($N = 15$) and error bars respective standard errors of the mean with lines illustrating trends from 1-species to 4-species neighbourhoods. Points, error bars and lines are coloured according to the species' trait value on either the resistance–acquisition gradient for growth or the stomatal control gradient for $\delta^{13}\text{C}$ (see Fig. 1B for trait values and species identities). Black points, error bars and lines represent an overall mean and standard error of the mean across species.

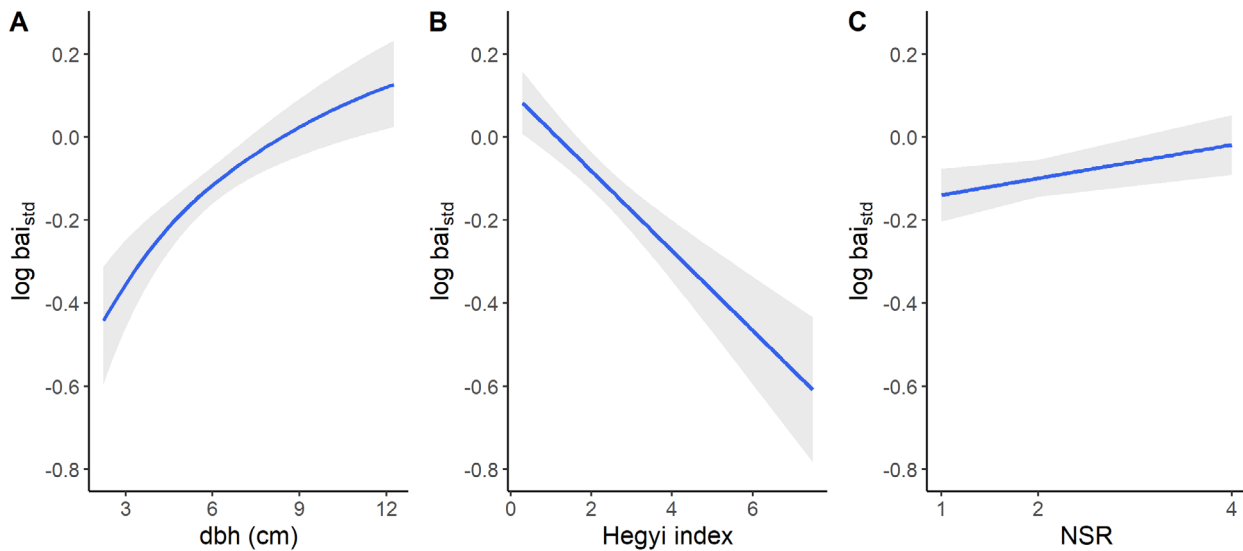


Fig. 4. Effects of tree size (dbh; A), neighbourhood competition (Hegyi index; B) and neighbourhood species richness (NSR; C) on the logarithm of focal tree basal area increment (bai_{std}). The blue lines are mixed-effects model fits and grey bands show a 95% confidence interval. See Table S5 for details on the fitted model.

(Fig. 5A, B, Table 1). With increasing NSR, acquisitive species grew 29.7% more in 4-species compared to 1-species neighbourhoods. On the other hand, resistant species experienced a 8.9% decrease in growth in 4-species compared to 1-species neighbourhoods ($\text{NSR} \times \text{focal tree resistance-acquisition traits}$, $t = 2.45$, $P = 0.015$; Fig. 5A). Furthermore, from the wet to the

dry year, growth increased for resistant species but declined for acquisitive species ($\text{year} \times \text{focal tree resistance-acquisition traits}$, $t = -6.84$, $P < 0.001$; Fig. 5B). We also found that resistance–acquisition traits of focal trees had contrasting effects on the relationship between NSR, climate, and growth, although this three-way interaction was only marginally

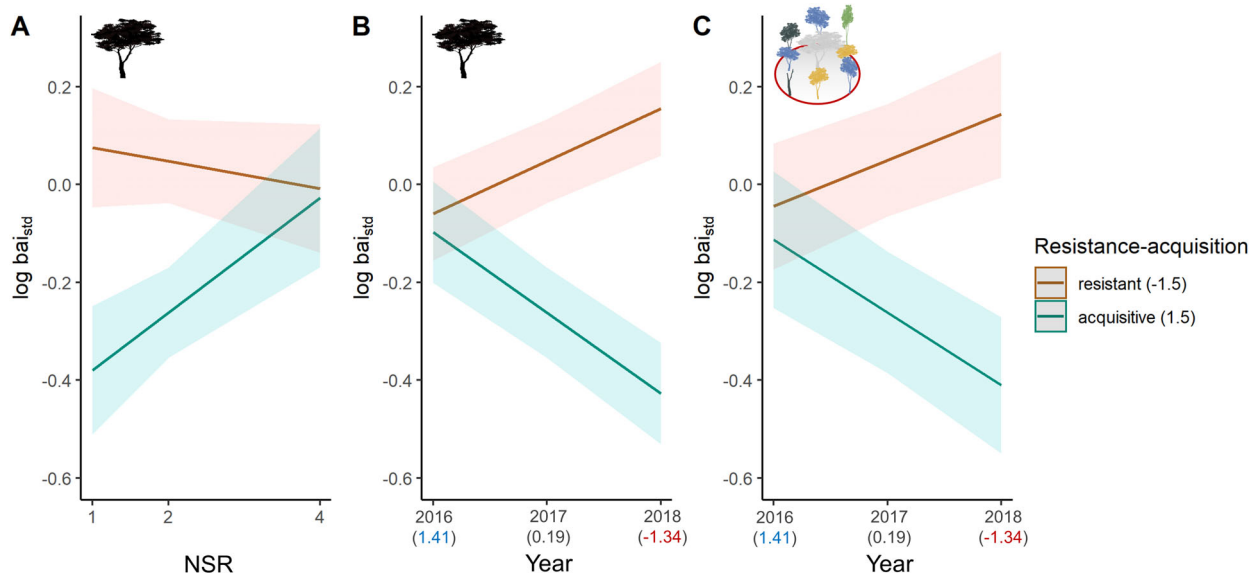


Fig. 5. Modulation of the relationship between neighbourhood species richness (NSR) and growth, and between climate and growth by resistance–acquisition traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant effects of 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 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 Figs 1 and 2 for details on the study design and Table 1 for the fitted models.

Table 1. Mixed-effect model statistics for effects of tree size, competition by neighbours, neighbourhood species richness (NSR), year and drought-tolerance traits and interactions on the basal area increment and $\delta^{13}\text{C}$ of focal trees.

Source of variation	Resistance–acquisition				Stomatal control			
	Focal tree traits		Neighbour traits		Focal tree traits		Neighbour traits	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Basal area increment (bai_{std})								
Size	5.8	<0.001	5.6	<0.001	5.0	<0.001	5.0	<0.001
Competition	−6.1	<0.001	−6.1	<0.001	−5.9	<0.001	−5.9	<0.001
NSR	2.4	0.018	2.1	0.036	2.3	0.024	2.2	0.027
Year	−1.8	0.074	−1.8	0.080	−1.8	0.078	−1.7	0.082
Trait	−0.3	0.758	1.1	0.282	3.4	0.001	2.6	0.011
NSR × year	–	–	–	–	–	–	–	–
NSR × trait	2.5	0.015	–	–	–	–	–	–
Year × trait	−6.8	<0.001	−4.2	<0.001	−5.1	<0.001	−3.0	0.002
NSR × year × trait	–	–	–	–	–	–	–	–
Carbon isotope ratio ($\Delta\delta^{13}\text{C}$)								
Size	–	–	–	–	–	–	–	–
Competition	–	–	–	–	–	–	–	–
NSR	–	–	–	–	−0.9	0.351	–	–
Year	43.6	<0.001	44.0	<0.001	−4.8	<0.001	−9.1	<0.001
Trait	0.0	0.847	0.2	0.649	−2.8	0.005	−2.2	0.028
NSR × year	–	–	–	–	0.5	0.610	–	–
NSR × trait	–	–	–	–	2.3	0.024	–	–
Year × trait	6.2	0.002	9.4	<0.001	3.7	<0.001	3.4	0.001
NSR × year × trait	–	–	–	–	−2.7	0.008	–	–

See Figs 1 and 2 for details on the study design and Tables S8–S15 for details on the fitted models. Models were fit for resistance–acquisition or stomatal control traits using either focal tree traits or neighbour traits; individual models are separated by grey shading. *t* and *F* indicate *t* and *F* statistics based on Satterthwaite's method and *P* the *P*-value of the significance test. *P*-values < 0.05 are printed in bold. Only the most parsimonious models are presented; parameters dropped during model selection are indicated with '–'.

significant (NSR \times year \times focal tree resistance–acquisition traits, $t = -1.75$, $P = 0.080$; Figure S7, Table S16): In the wet year, acquisitive species benefited from higher NSR, while resistant species grew less. In the dry year, the effects were weaker but predominately positive, with acquisitive species still growing more with higher NSR, while resistant species were unaffected by NSR. Notably, the resistance–acquisition traits of neighbours significantly influenced growth responses. Focal trees in a neighbourhood dominated by resistant species grew more from the wet to the dry year, while those in an acquisitive neighbourhood grew less (year \times NWM of resistance–acquisition, $t = -4.17$, $P < 0.001$; Fig. 5C, Table 1).

The stomatal control traits of focal trees significantly modulated the relationship between climate and growth, but not the relationship between NSR and growth nor between NSR, climate and growth (Fig. 6A, Table 1). Specifically, water-saving species increased in their growth, while water-spending species decreased in their growth from the wet to the dry year (year \times focal tree stomatal control traits, $t = -5.10$, $P < 0.001$; Fig. 6A). Furthermore, the stomatal control traits of neighbours significantly influenced the climate–growth relationship: Focal trees in a neighbourhood dominated by water-saving species grew better from the wet to the dry year, while growth of focal trees in a water-spending neighbourhood declined (year \times NWM of stomatal control, $t = -3.04$, $P = 0.002$; Fig. 6B, Table 1). The growth responses, as found for basal area increment, were similar for tree-ring width, except for a general decline in tree-ring width from 2016 to 2018 and with tree size,

presumably due to an age trend (Figures S8–10). For tree-ring width, the three-way interaction between NSR, year and the resistance–acquisition traits of focal trees was significant ($t = -2.21$, $P = 0.027$; Figure S9).

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

Using trait-dependent models to explain variations in $\delta^{13}\text{C}$ in the wood of focal trees, we found significant interactions of resistance–acquisition traits with climate, with a stronger influence observed from neighbour traits compared to focal tree traits (Fig. 7, Table 1). In both the intermediate and dry year, we observed a tendency towards higher $\delta^{13}\text{C}$ (indicating higher water stress) in focal trees located in acquisitive neighbourhoods compared to resistant neighbourhoods (Fig. 7B). However, in the wet year, lower $\delta^{13}\text{C}$ (indicating lower water stress) occurred in focal trees situated in acquisitive neighbourhoods (year \times NWM of resistance–acquisition, year as a categorical fixed effect, $F = 9.45$, $P < 0.001$; Fig. 7B). The difference between focal trees in resistant *versus* acquisitive neighbourhoods was most prominent during the year with intermediate water availability (2017; Fig. 7B).

The stomatal control traits of focal trees played a significant role in modulating the relationship between NSR, climate and $\delta^{13}\text{C}$ (NSR \times year \times focal tree stomatal control traits, $t = -2.66$, $P = 0.008$; Fig. 8, Table 1): We found contrasting NSR effects on $\delta^{13}\text{C}$ for water-saving and water-spending species, which weakened as climate conditions transitioned from wet to dry

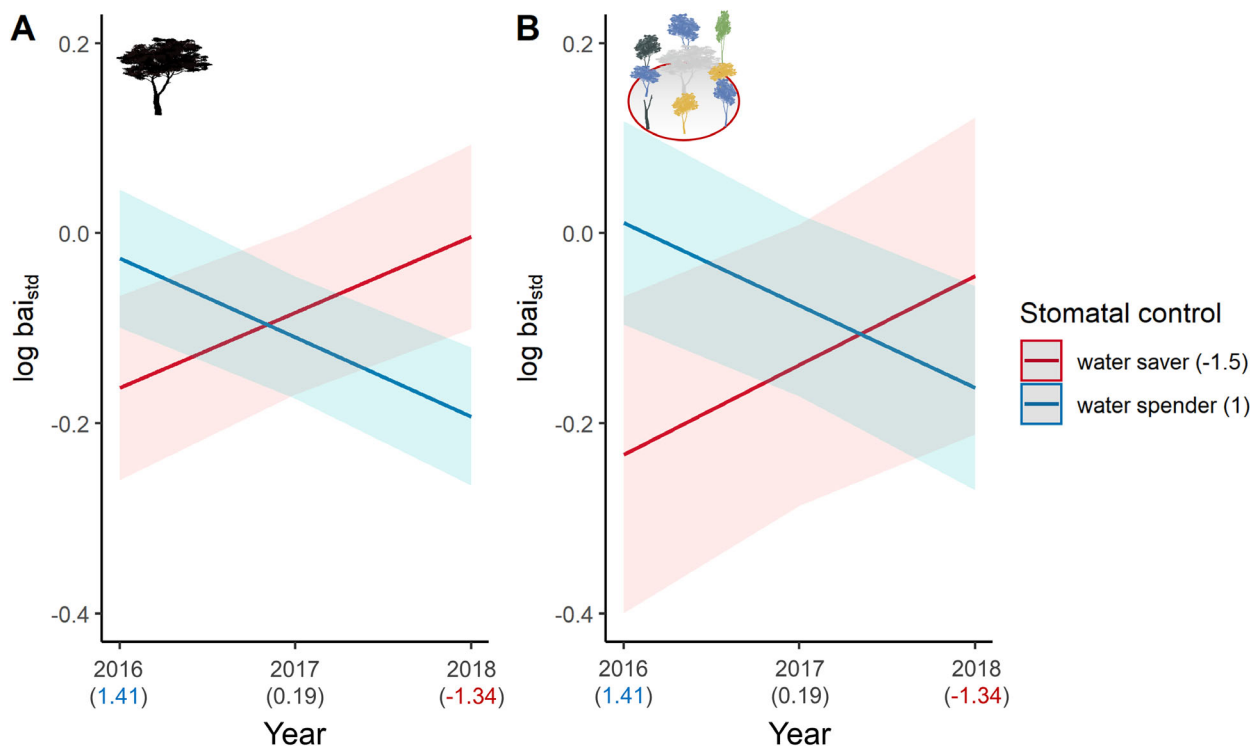


Fig. 6. Modulation of the relationship between climate and growth by stomatal control traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant effects of study year (2016–2018 with wet to dry climate, SPEI values in brackets) 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 Figs 1 and 2 for details on the study design and Table 1 for the fitted models.

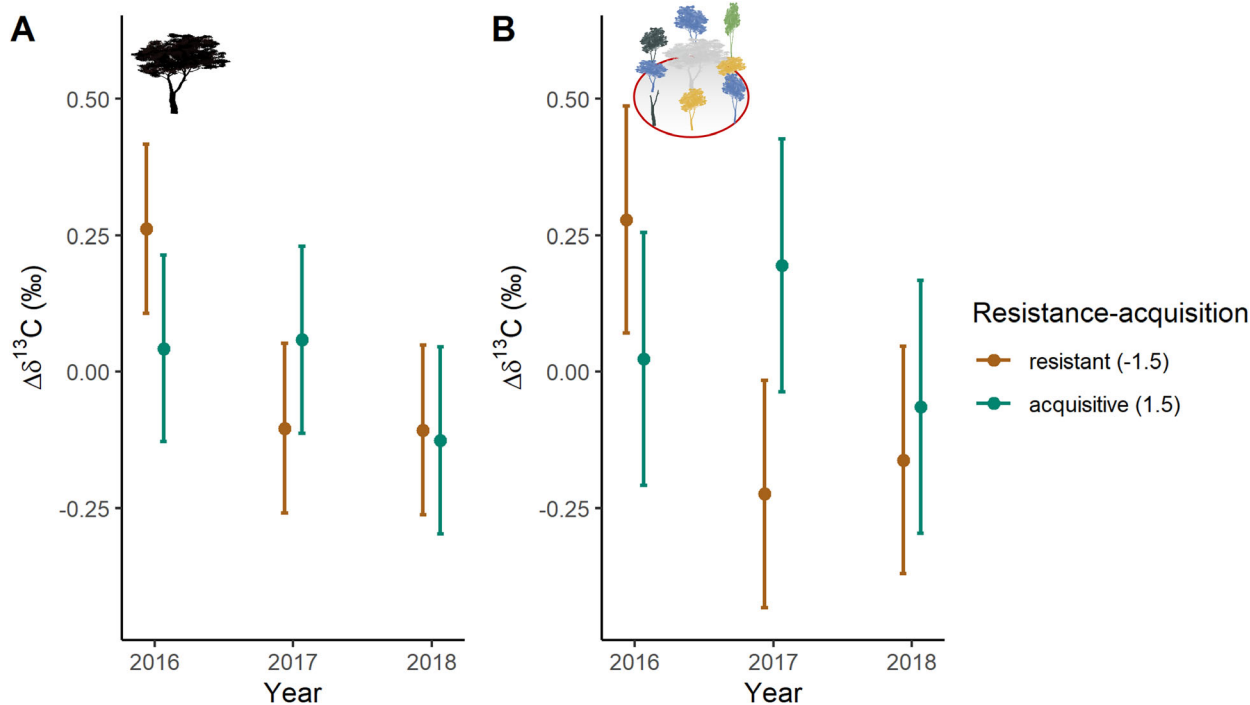


Fig. 7. Modulation of the relationship between climate and $\delta^{13}\text{C}$ by resistance-acquisition traits. Points represent linear mixed-effects model fits and error bars show a 95% confidence interval. The models depict significant effects of study year (2016–2018 with wet to dry climate, SPEI values in brackets) on $\delta^{13}\text{C}$ in the wood of focal trees predicted for 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 Figs 1 and 2 for details on the study design and Table 1 for the fitted models.

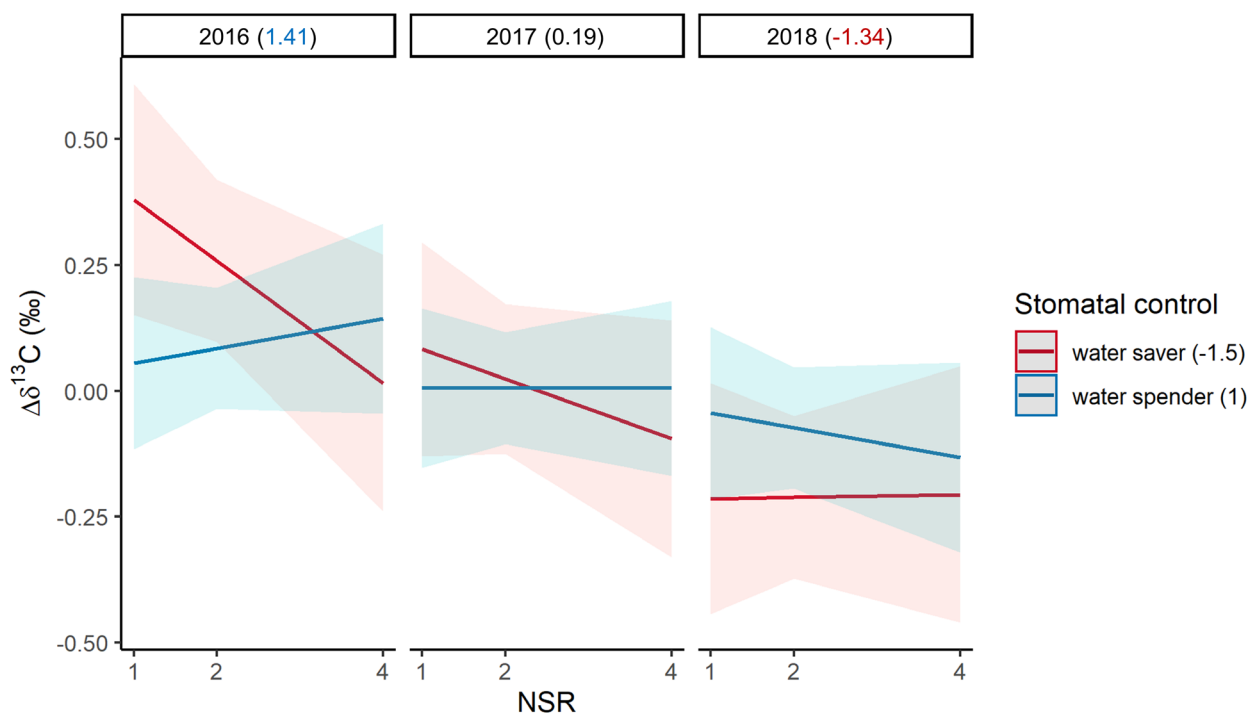


Fig. 8. Modulation of the relationship between neighbourhood species richness (NSR), climate and $\delta^{13}\text{C}$ by stomatal control traits. Lines represent linear mixed-effects model fits and coloured bands show a 95% confidence interval. The models depict significant, interactive effects of NSR and study year (2016–2018 with wet to dry climate, SPEI values in brackets) on $\delta^{13}\text{C}$ in the wood of focal trees predicted for water-savers (PC2 value of -1.5) and water-spenders (PC2 value of 1.0). See Figs 1 and 2 for details on the study design and Table 1 for the fitted model.

(Fig. 8). In the wet year, water-saving species exhibited a decrease in $\delta^{13}\text{C}$ with increasing NSR. However, this positive diversity effect declined in the dry year, resulting in similar $\delta^{13}\text{C}$ across NSR levels. In contrast, water-spending species tended to show an increase in $\delta^{13}\text{C}$ with increasing NSR in the wet year, but a decrease in $\delta^{13}\text{C}$ with increasing NSR in the dry year. Hence, water-saving species benefited from more species-rich neighbourhoods (NSR) by experiencing lower water stress during wet conditions. In contrast, water-spending species tended to benefit from higher NSR during dry climatic conditions, although the effect sizes were relatively small. Finally, the stomatal control traits of neighbours influenced the $\delta^{13}\text{C}$ in the wood of focal trees (year \times NWM of stomatal control, $t = 3.43$, $P = 0.001$; Figure S11, Table 1). Focal trees surrounded by water-saving neighbours had lower $\delta^{13}\text{C}$ in the dry year compared to the wet year, but this effect may have been enhanced by the overall decline in $\delta^{13}\text{C}$ from the wet to the dry year (Figure S6).

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 isotope ratios in the wood of focal trees ($\delta^{13}\text{C}$), which we considered as a proxy of neighbourhood-scale water availability (Grossiord *et al.* 2014; Jucker *et al.* 2017). Moreover, the strength of the relationship between NSR and growth and between NSR and $\delta^{13}\text{C}$ did not increase from wet to dry climatic conditions. Instead, relationships between NSR, climate and growth or $\delta^{13}\text{C}$ were modulated by drought-tolerance traits of focal trees and their neighbours regarding cavitation resistance *versus* resource acquisition and stomatal control. The biotic context (*i.e.* focal tree and neighbour traits) thus determined the strength and nature of BEF relationships in the examined tree communities. Resistance-acquisition traits primarily modulated NSR and climate effects on growth, whereas stomatal control traits primarily influenced wood $\delta^{13}\text{C}$. As expected, growth was thus more strongly related to the leaf economics spectrum (Reich 2014), while $\delta^{13}\text{C}$ was controlled by stomatal aperture (Farquhar *et al.* 1989).

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 (Schnabel *et al.* 2019; Guillemot *et al.* 2020; 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. 3; *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).

Contrary to our expectation (H1) and an earlier study on twig $\delta^{13}\text{C}$ in our experiment conducted during the particularly

wet year 2015 (Fig. 1A; Jansen *et al.* 2021), we did not detect a general enhancement of water availability in more diverse tree neighbourhoods. Similarly, other studies found mixed results and no universal decrease in $\delta^{13}\text{C}$ in mixtures compared to monocultures (Grossiord 2020; Haberstroh & Werner 2022). The net negative effect of NSR on $\delta^{13}\text{C}$ in Jansen *et al.* (2021) is likely due to increased shading at high NSR, which reduces photosynthesis rates, and not due to enhanced water availability. Our assumption is based on the fact that Jansen *et al.* (2021) found the strongest NSR effects for trees with a high degree of crown competition from neighbours. In contrast, our $\delta^{13}\text{C}$ values should be primarily influenced by NSR- and climate-induced changes in neighbourhood-scale water availability as we only studied (co-)dominant trees with slight shading. This notion is supported by the non-significant effect of competition indices on $\delta^{13}\text{C}$.

To understand the abiotic context dependency of BEF relationships, we selected years to represent a gradient from wet to dry climatic conditions (SPEIs; Figure S1). Contrary to our expectation (H1), we did not observe a consistent increase in diversity effects with increasing dryness (SPEIs; Figure S1) nor an overall decline in tree growth and decreasing $\delta^{13}\text{C}$ values from the wet to the dry year. This suggests that water was not limiting (even though the examined dry year had similar SPEIs as past drought years; Figure S2) or that drought impacts were buffered through the mobilisation of reserves (McDowell *et al.* 2022). Alternatively, light may have been the primary limiting factor (Forrester & Bauhus 2016). Particularly for $\delta^{13}\text{C}$, the use of stored carbon *versus* freshly fixed C for wood formation by the trees and the timing of drought may have affected our ability to detect tree responses to the interactive effects of drought and diversity. Since $\delta^{13}\text{C}$ captures the balance between net CO_2 assimilation and stomatal conductance during the time of carbon fixation, the $\delta^{13}\text{C}$ found in wood may not only contain the climatic signal of the time of wood formation but also of previous periods, if stored carbon (*e.g.* starch in the parenchyma) from previous years is used for wood formation. Here, we analysed the effects of a drought year that was preceded by year(s) with average climatic conditions to prevent negative carry-over effects of drought. However, positive carry-over effects may have attenuated $\delta^{13}\text{C}$ responses if the wood in the drought year was (partly) formed from carbon reserves built under average climatic conditions. Moreover, we could not separate between early- and latewood due to the complex wood anatomy of the 15 examined subtropical tree species (see Figure S4). As earlywood may be influenced more by the mobilisation of reserves than latewood (Offermann *et al.* 2011), analysing them together may have reduced our ability to capture climatic signals in $\delta^{13}\text{C}$. Both points may explain why we observed relatively small, albeit significant, trait-mediated changes in $\delta^{13}\text{C}$ across the 15 species examined. 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). Likewise, additional analyses, such as the separation of early- and latewood, or the inclusion of $\delta^{18}\text{O}$ as an additional proxy (Gessler *et al.* 2014), may allow us to better infer trait-mediated responses along gradients in neighbourhood tree species richness and climatic conditions in the future.

Other studies reported stronger diversity effects during dry (Schnabel *et al.* 2019; Fichtner *et al.* 2020) and during wet (Belluau *et al.* 2021) years. Similarly, positive, neutral and negative effects of species richness on growth and $\delta^{13}\text{C}$ have been reported under drought (Grossiord 2020). An important difference between these former results and our study is that we examined a balanced trait sample (in terms of species and number of individuals) along both drought-tolerance trait gradients (Fig. 1B). Given that species with contrasting drought-tolerance traits showed opposite responses to NSR and climate in our study, it is not surprising that we detected a net zero or only a weak overall effect of NSR on focal tree responses to drought. In contrast, the non-balanced trait sample in former studies may explain their mixed results on the modulation of drought impacts on trees and forests by tree diversity. Hence, the contrasting water-use strategies of focal trees and their neighbours may be one fundamental missing link for understanding the role of tree diversity during drought. Here, we attempted to address this by considering the biotic context dependency of BEF relationships, which we quantified in terms of their modulation by drought-tolerance traits of focal trees and their neighbours.

The importance of focal tree traits

Consistent with H2, we found that during drought, NSR increased growth and decreased wood $\delta^{13}\text{C}$ of acquisitive and water-spending focal tree species. In contrast, resistant and water-saving species did not respond to NSR, presumably because species interactions did not aid their strategies to cope with drought. Hence, high neighbourhood diversity supported the more vulnerable species in the forest community during drought (Fichtner *et al.* 2020). In general, the presence of heterospecific neighbours is more likely with increasing NSR. These heterospecific neighbours can influence focal tree responses by enhancing or reducing competition or promoting facilitation (Forrester & Pretzsch 2015; Forrester 2017). In our study, acquisitive species likely grew better due to their ability to acquire and use resources and the lower inter- compared to intraspecific competition for water at high NSR (Fichtner *et al.* 2017; Fichtner *et al.* 2020). Similarly, it is conceivable that NSR may have relieved water stress for water-spending species during drought by increasing the likelihood of having water-saving neighbours, which transpire less water, thereby increasing local soil water availability (Forrester 2017). The lower physiological water stress (lower $\delta^{13}\text{C}$) 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). The growth decline we observed for resistant and water-saving species from the wet to the dry year could be related to higher degrees of embolism in the vessels of acquisitive species (which are sensitive to cavitation) and higher risks for such cavitation in water-spending species (McDowell *et al.* 2008). In contrast, their less vulnerable counterparts may have been able to grow better under drought.

The importance of neighbour traits

Consistent with H3, we found that the drought-tolerance traits of tree neighbours consistently changed the nature of

focal tree growth and $\delta^{13}\text{C}$ 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. As expected, 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 $\delta^{13}\text{C}$ 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 (Grossiord *et al.* 2014; Forrester 2017) 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.

Overall, 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 (Reich 2014; Guillemot *et al.* 2022) and between water-spending and water-saving stomatal control (Martínez-Vilalta & García-Forner 2017). We discuss this and potential relationships between resistance–acquisition and stomatal control traits in detail in Discussion S1. However, despite our consideration of multiple traits that were measured within our experiment, future studies could foster a more holistic understanding of tree drought responses and their modulation by functional traits by accounting for plastic changes in traits with environmental conditions (Guo *et al.* 2020; Kannenberg *et al.* 2022) and through examining traits not considered here, such as the storage of non-structural carbohydrates (Hajek *et al.* 2022; McDowell *et al.* 2022) or attributes of the root system (Weigelt *et al.* 2021). Moreover, in cases where both focal tree and neighbour traits influenced observed responses, our modelling approach does not allow us to mechanistically disentangle their relative contributions. Future studies could improve our ability to do so by sampling (or planting) trees along orthogonal gradients in focal tree and neighbour traits.

Outlook

Trait-based neighbourhood models have been used to understand tree growth, survival and community assembly

(Uriarte *et al.* 2010; Kunstler *et al.* 2012; Yang *et al.* 2021), and in few cases to understand how focal tree traits modulate tree growth responses to species richness 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 accounted here, for the first time, for the influence of focal tree and neighbour traits on BEF relationships in experimental tree communities. Our results extend research on the modulation of drought impacts on forests by tree diversity beyond observational studies in comparably species-poor forests (Grossiord 2020) to include species-rich tree communities featuring contrasting drought-tolerance traits, which are grown under experimental conditions. This approach enabled the establishment of causality while minimising confounding factors, such as environmental variation. Still, despite the rapid tree growth in the subtropics that enabled us to study fairly large trees (25% of the experimental communities had grown taller than 10 m; Schnabel *et al.* 2021), the juvenile growth trajectories may not have revealed trends that become apparent only at an older age. Overall, we could derive 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 *versus* 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 generalise 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 TreeDi funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 319936945/GRK2324 and the University of Chinese Academy of Sciences. Open Access funding enabled and organized by Projekt DEAL.

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.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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>). 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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Climate-based characterisation of the study years 2016 (wet), 2017 (intermediate) and 2018 (dry).

Figure S2. A long-term perspective on standardized climatic water balances at our study site.

Figure S3. Intra-annual climatic water balances at our study site.

Figure S4. Wood anatomy of the 15 tree species sampled in this study.

Figure S5. Comparison of focal tree tree-ring width (trw, mm) and basal area increment (bai, cm²) series.

Figure S6. Effect of study year on $\delta^{13}\text{C}$ in wood of focal trees.

Figure S7. Modulation of the relationship between neighbourhood species richness (NSR), climate and growth by resistance-acquisition traits.

Figure S8. Effects of tree size (dbh), neighbourhood competition (Hegyí index), neighbourhood species richness (NSR) and study year on the logarithm of tree-ring width (trw_{std}) of focal trees.

Figure S9. Modulation of the relationship between neighbourhood species richness (NSR), climate and growth by resistance-acquisition traits using tree-ring width (trw_{std}) of focal trees instead of basal area increment (bai_{std}) as indicator of growth.

Figure S10. Modulation of the relationship between climate and growth by the neighbourhood-weighted mean (NWM) of resistance-acquisition traits using tree-ring width (trw_{std}) of focal trees instead of basal area increment (bai_{std}) as indicator of growth.

Figure S11. Modulation of the relationship between climate and $\delta^{13}\text{C}$ by the neighbourhood-weighted mean (NWM) of stomatal control traits.

Table S1. The 40 broadleaved evergreen and deciduous tree species planted in BEF-China.

Table S2. Resistance-acquisition and stomatal control traits were used in this study (adapted from Schnabel *et al.* (2021)).

Table S3. Description of competition indices.

Table S4. Comparison of competition indices (Table S3) for the growth linear mixed-effects model (Table S4) against a null model without a competition index.

Table S5. Best-fitting trait-independent linear mixed-effects model after model selection.

Table S6. Best-fitting trait-independent linear mixed-effects model after model selection.

Table S7. Comparison of competition indices (Table S3) for the $\delta^{13}\text{C}$ linear mixed-effects model (Table S6) against a null model without a competition index.

Table S8. Best-fitting linear mixed-effects model of focal tree resistance-acquisition traits after model selection.

Table S9. Best-fitting linear mixed-effects model of neighbour resistance-acquisition traits after model selection.

Table S10. Best-fitting linear mixed-effects model of focal tree stomatal control traits after model selection.

Table S11. Best-fitting linear mixed-effects model of neighbour stomatal control traits after model selection.

Table S12. Best-fitting linear mixed-effects model of focal tree resistance-acquisition traits after model selection.

Table S13. Best-fitting linear mixed-effects model of neighbour resistance-acquisition traits after model selection.

Table S14. Best-fitting linear mixed-effects model of focal tree stomatal control traits after model selection.

Table S15. Best-fitting linear mixed-effects model of neighbour stomatal control traits after model selection.

Table S16. Linear mixed-effects model of focal tree resistance-acquisition traits that still includes the marginally significant 3-way interaction between year, neighbourhood species richness (NSR) and resistance-acquisition traits.

Table S17. Full linear mixed-effects model for growth of the species *Schima superba* exploring the influence of experimental site (A or B).

Table S18. Full linear mixed-effects model for growth of the species *Schima superba* exploring the influence of experimental site (A or B).

Method S1. Focal tree selection.

Method S2. Trait-independent neighbourhood models.

Analysis S1. Potential site-specific differences.

Discussion S1. Coordination of drought-tolerance traits.

REFERENCES

- Anderegg W.R.L., Trugman A.T., Badgley G., Anderson C.M., Bartuska A., Ciais P., Cullenward D., Field C.B., Freeman J., Goetz S.J., Hicke J.A., Huntzinger D., Jackson R.B., Nickerson J., Pacala S., Randerson J.T. (2020) Climate-driven risks to the climate mitigation potential of forests. *Science*, **368**, eaaz7005.
- Barry K.E., Mommer L., van Ruijven J., Wirth C., Wright A.J., Bai Y., Connolly J., De Deyn G.B., De Kroon H., Isbell F., Milcu A., Roscher C., Scherer-Lorenzen M., Schmid B., Weigelt A. (2019) The future of complementarity: disentangling causes from consequences. *Trends in Ecology & Evolution*, **34**, 167–180.
- Bates D., Mächler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Bauhus J., Forrester D.I., Gardiner B., Jactel H., Vallejo R., Pretzsch H. (2017) Ecological stability of mixed-species forests. In: Pretzsch H., Forrester D.I., Bauhus J. (Eds), *Mixed-species forests: ecology and management*. Springer Nature, Berlin, Germany, pp 337–382.
- 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**, 1790–1803.
- Bertness M.D., Callaway R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
- 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**, 81–96.
- Böhnke M., Kreibitz N., Kröber W., Fang T., Bruelheide H. (2012) Wood trait–environment relationships in a secondary forest succession in South-East China. *Trees*, **26**, 641–651.
- Bongers F.J., Schmid B., Bruelheide H., Bongers F., Li S., Oheimb G., von Li Y., Cheng A., Ma K., Liu X. (2021) Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nature Ecology & Evolution*, **5**, 1594–1603.
- Brancalion P.H.S., Niamir A., Broadbent E., Crouzeilles R., Barros F.S.M., Almeida Zambrano A.M., Baccini A., Aronson J., Goetz S., Reid J.L., Strassburg B.B.N., Wilson S., Chazdon R.L. (2019) Global restoration opportunities in tropical rainforest landscapes. *Science Advances*, **5**, eaav3223.
- Bruelheide H., Nadrowski K., Assmann T., Bauhus J., Both S., Buscot F., Chen X.-Y., Ding B., Durka W., Erfmeier A., Gutknecht J.L.M., Guo D., Guo L.-D., Härdtle W., He J.-S., Klein A.-M., Kühn P., Liang Y., Liu X., Michalski S., Niklaus P.A., Pei K., Scherer-Lorenzen M., Scholten T., Schuldt A., Seidler G., Trogisch S., Oheimb G., von Welk E., Wirth C., Wubet T., Yang X., Yu M., Zhang S., Zhou H.-Z., Fischer M., Ma K., Schmid B. (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution*, **5**, 74–89.
- Bunn A.G., Korpela M., Biondi F., Campelo F., Mérian P., Qeadan F., Zang C. (2020) dplR: dendrochronology program library in R. Available from <https://CRAN.R-project.org/package=dplR>
- Choat B., Jansen S., Brodribb T.J., Cochard H., Delzon S., Bhaskar R., Bucci S.J., Feild T.S., Gleason S.M., Hacke U.G., Jacobsen A.L., Lens F., Maherali H., Martínez-Vilalta J., Mayr S., Mencuccini M., Mitchell P.J., Nardini A., Pittermann J., Pratt R.B., Sperry J.S., Westoby M., Wright I.J., Zanne A.E. (2012) Global convergence in the vulnerability of forests to drought. *Nature*, **491**, 752–755.
- 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**, 2538–2560.
- 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**, 2439–2441.
- Craven D., Eisenhauer N., Pearse W.D., Hautier Y., Isbell F., Roscher C., Bahn M., Beierkuhnlein C., Bönisch G., Buchmann N., Byun C., Catford J.A., Cerabolini B.E.L., Cornelissen J.H.C., Craine J.M., De Luca E., Ebeling A., Griffin J.N., Hector A., Hines J., Jentsch A., Kattge J., Kreyling J., Lanta V., Lemoine N., Meyer S.T., Minden V., Onipchenko V., Polley H.W., Reich P.B., van Ruijven J., Schamp B., Smith M.D., Soudzilovskaia N.A., Tilman D., Weigelt A., Wilsey B., Manning P. (2018) Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*, **2**, 1579–1587.
- Dunn P.J.H., Malinovsky D., Holcombe G., Cowen S., Goenaga-Infante H. (2021) Guidance for characterization of in-house reference materials for light element stable isotope analysis. *Rapid Communications in Mass Spectrometry*, **35**, e9177.
- 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**, 503–537.
- Fichtner A., Härdtle W., Bruelheide H., Kunz M., Li Y., von Oheimb G. (2018) Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nature Communications*, **9**, 1144.
- Fichtner A., Härdtle W., Li Y., Bruelheide H., Kunz M., von Oheimb G. (2017) From competition to facilitation: how tree species respond to neighbourhood diversity. *Ecology Letters*, **20**, 892–900.
- Fichtner A., Schnabel F., Bruelheide H., Kunz M., Mausolf K., Schuldt A., Härdtle W., von Oheimb G. (2020) Neighbourhood diversity mitigates drought impacts on tree growth. *Journal of Ecology*, **108**, 865–875.
- Forrester D.I. (2017) Ecological and physiological processes in mixed versus monospecific stands. In: Pretzsch H., Forrester D.I., Bauhus J. (Eds), *Mixed-species forests: ecology and management*. Springer Nature, Berlin, Germany, pp 73–115.
- Forrester D.I., Bauhus J. (2016) A review of processes behind diversity–Productivity relationships in forests. *Current Forestry Reports*, **2**, 45–61.
- 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.
- 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**, 1062–1070.
- 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**, 85–92.
- Gessler A., Ferrio J.P., Hommel R., Treyde K., Werner R.A., Monson R.K. (2014) Stable isotopes in tree rings: towards a mechanistic understanding of isotope fractionation and mixing processes from the leaves to the wood. *Tree Physiology*, **34**, 796–818.

- Gheyret G., Zhang H.-T., Guo Y., Liu T.-Y., Bai Y.-H., Li S., Schmid B., Bruehlheide H., Ma K., Tang Z. (2021) Radial growth response of trees to seasonal soil humidity in a subtropical forest. *Basic and Applied Ecology*, **55**, 74–86.
- Grams T.E.E., Kozovits A.R., Häberle K.-H., Matyssek R., Dawson T.E. (2007) Combining delta ¹³C and delta ¹⁸O analyses to unravel competition, CO₂ and O₃ effects on the physiological performance of different-aged trees. *Plant, Cell and Environment*, **30**, 1023–1034.
- Grossiord C. (2020) Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytologist*, **228**, 42–49.
- Grossiord C., Granier A., Ratcliffe S., Bouriaud O., Bruehlheide H., Checko E., Forrester D.I., Dawud S.M., Finer L., Pollastrini M., Scherer-Lorenzen M., Valladares F., Bonal D., 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**, 14812–14815.
- Guillemot J., Kunz M., Schnabel F., Fichtner A., Madson C.P., Gebauer T., Härdtle W., von Oheimb G., Potvin C. (2020) Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. *New Phytologist*, **228**, 1256–1268.
- Guillemot J., Martin-StPaul N., Bulascoschi L., Poorter L., Morin X., Pinho B.X., Le Maire G., Bittencourt P., Oliveira R.S., Bongers F., Brouwer R., Pereira L., Melo G.A.G., Boonman C.C.F., Brown K.A., Cerabolini B.E.L., Niinemets Ü., Onoda Y., Schneider J.V., Sheremetiev S., Brancalion P.H.S. (2022) Small and slow is safe: on the drought tolerance of tropical tree species. *Global Change Biology*, **28**, 2622–2638.
- Guo J.S., Hultine K.R., Koch G.W., Kropp H., Ogle K. (2020) Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. *New Phytologist*, **225**, 713–726.
- Haberstroh S., Werner C. (2022) The role of species interactions for forest resilience to drought. *Plant Biology*, **24**, 1098–1107.
- Hajek P., Link R.M., Nock C.A., Bauhus J., Gebauer T., Gessler A., Kovach K., Messier C., Paquette A., Saurer M., Scherer-Lorenzen M., Rose L., Schuldt B. (2022) Mutually inclusive mechanisms of drought-induced tree mortality. *Global Change Biology*, **28**, 3365–3378.
- 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**, 109.
- Hartmann H., Bastos A., Das A.J., Esquivel-Muelbert A., Hammond W.M., Martínez-Vilalta J., McDowell N.G., Powers J.S., Pugh T.A.M., Ruthrof K.X., 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*, **73**, 673–702.
- Huang Y., Chen Y., Castro-Izaguirre N., Baruffol M., Brezzi M., Lang A., Li Y., Härdtle W., von Oheimb G., Yang X., Liu X., Pei K., Both S., Yang B., Eichenberg D., Assmann T., Bauhus J., Behrens T., Buscot F., Chen X.-Y., Chesters D., Ding B.-Y., Durka W., Erfmeier A., Fang J., Fischer M., Guo L.-D., Guo D., Gutknecht J.L.M., He J.-S., He C.-L., Hector A., Hönig L., Hu R.-Y., Klein A.-M., Kühn P., Liang Y., Li S., Michalski S., Scherer-Lorenzen M., Schmidt K., Scholten T., Schuldt A., Shi X., Tan M.-Z., Tang Z., Trogisch S., Wang Z., Welk E., Wirth C., Wubet T., Xiang W., Yu M., Yu X.-D., Zhang J., Zhang S., Zhang N., Zhou H.-Z., Zhu C.-D., Zhu L., Bruehlheide H., Ma K., Niklaus P.A., Schmid B. (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science*, **362**, 80–83.
- IPCC (2022) *Climate change 2022: impacts, adaptation, and vulnerability: contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp 3056.
- Jansen K., von Oheimb G., Bruehlheide 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 of the Royal Society B: Biological Sciences*, **288**, 20203100.
- Jucker T., Avacaritei D., Barnoiea I., Duduman G., Bouriaud O., Coomes D.A. (2016) Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, **104**, 388–398.
- Jucker T., Bouriaud O., Avacaritei D., Coomes D.A. (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters*, **17**, 1560–1569.
- 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**, 706.
- Kannenberg S.A., Guo J.S., Novick K.A., Anderegg W.R.L., Feng X., Kennedy D., Konings A.G., Martínez-Vilalta J., Matheny A.M. (2022) Opportunities, challenges and pitfalls in characterizing plant water-use strategies. *Functional Ecology*, **36**, 24–37.
- Kröber W., Bruehlheide H. (2014) Transpiration and stomatal control: a cross-species study of leaf traits in 39 evergreen and deciduous broadleaved subtropical tree species. *Trees*, **28**, 901–914.
- Kröber W., Zhang S., Ehmg M., Bruehlheide 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**, e109211.
- Kunstler G., Lavergne S., Courbaud B., Thuiller W., Vieilledent G., Zimmermann N.E., Kattge J., Coomes D.A. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, **15**, 831–840.
- Kuznetsova A., Brockhoff P.B., Christensen R.H.B. (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, **82**, 1–26.
- Li Y., Kröber W., Bruehlheide H., Härdtle W., von Oheimb G. (2017) Crown and leaf traits as predictors of subtropical tree sapling growth rates. *Journal of Plant Ecology*, **10**, 136–145.
- Martínez-Vilalta J., García-Fornier N. (2017) Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant, Cell and Environment*, **40**, 962–976.
- McDowell N.G., Pockman W.T., Allen C.D., Breshears D.D., Cobb N., Kolb T., Plaut J., Sperry J., West A., Williams D.G., Yezpey E.A. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.
- McDowell N.G., Sapes G., Pivovarov A., Adams H.D., Allen C.D., Anderegg W.R.L., Arend M., Breshears D.D., Brodrick T., Choat B., Cochard H., De Cáceres M., De Kauwe M.G., Grossiord C., Hammond W.M., Hartmann H., Hoch G., Kahmen A., Klein T., Mackay D.S., Mantova M., Martínez-Vilalta J., Medlyn B.E., Mencuccini M., Nardini A., Oliveira R.S., Sala A., Tissue D.T., Torres-Ruiz J.M., Trowbridge A.M., Trugman A.T., Wiley E., Xu C. (2022) Mechanisms of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit. *Nature Reviews Earth and Environment*, **3**, 294–308.
- Messier C., Bauhus J., Sousa-Silva R., Auge H., Baeten L., Barsoum N., Bruehlheide H., Caldwell B., Cavender-Bares J., Dhiedt E., Eisenhauer N., Ganade G., Gravel D., Guillemot J., Hall J.S., Hector A., Hérault B., Jactel H., Koricheva J., Kreft H., Meru S., Muys B., Nock C.A., Paquette A., Parker J.D., Perring M.P., Ponette Q., Potvin C., Reich P.B., Scherer-Lorenzen M., Schnabel F., Verheyen K., Weih M., Wollni M., Zemp D.C. (2021) For the sake of resilience and multifunctionality, let's diversify planted forests! *Conservation Letters*, **15**, e12829.
- Offermann C., Ferrio J.P., Holst J., Grote R., Siegwolf R., Kayler Z., Gessler A. (2011) The long way down – Are carbon and oxygen isotope signals in the tree ring uncoupled from canopy physiological processes? *Tree Physiology*, **31**, 1088–1102.
- van der Plas F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, **94**, 1220–1245.
- Reich P.B. (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.
- Schnabel F., Liu X., Kunz M., Barry K.E., Bongers F.J., Bruehlheide H., Fichtner A., Härdtle W., Li S., Pfaff C.-T., Schmid B., Schwarz J.A., Tang Z., Yang B., Bauhus J., von Oheimb G., Ma K., Wirth C. (2021) Species richness stabilizes productivity via asynchrony and drought-tolerance diversity in a large-scale tree biodiversity experiment. *Science Advances*, **7**, eabk1643.
- Schnabel F., Purucker S., Schmitt L., Engelmann R.A., Kahl A., Richter R., Seele-Dilbat C., Skiadasis G., Wirth C. (2022) Cumulative growth and stress responses to the 2018–2019 drought in a European floodplain forest. *Global Change Biology*, **28**, 1870–1883.
- 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**, 4257–4272.
- 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-annual variation of delta ¹³C in tree rings. *Tree Physiology*, **24**, 1193–1201.
- Schwarz J.A., Skiadasis 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.
- Schweingruber F.H. (1996) *Tree rings and environment: dendroecology*. Paul Haupt AG Bern, Berne, Switzerland, pp 609.

- 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**, 1710–1720.
- Sohn J.A., Kohler M., Gessler A., Bauhus J. (2012) Interactions of thinning and stem height on the drought response of radial stem growth and isotopic composition of Norway spruce (*Picea abies*). *Tree Physiology*, **32**, 1199–1213.
- Stoll P., Newbery D.M. (2005) Evidence of species-specific neighborhood effects in the dipterocarpaceae of a Bornean rain forest. *Ecology*, **86**, 3048–3062.
- Trogisch S., Liu X., Rutten G., Xue K., Bauhus J., Brose U., Bu W., Cesarz S., Chesters D., Connolly J., Cui X., Eisenhauer N., Guo L., Haider S., Härdtle W., Kunz M., Liu L., Ma Z., Neumann S., Sang W., Schuldt A., Tang Z., van Dam N.M., von Oheimb G., Wang M.-Q., Wang S., Weinhold A., Wirth C., Wubet T., Xu X., Yang B., Zhang N., Zhu C.-D., Ma K., Wang Y., Bruelheide H. (2021) The significance of tree–tree interactions for forest ecosystem functioning. *Basic and Applied Ecology*, **55**, 33–52.
- Uriarte M., Swenson N.G., Chazdon R.L., Comita L.S., John Kress W., Erickson D., Forero-Montaña J., Zimmerman J.K., 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**, 1503–1514.
- 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**, 1696–1718.
- 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**, 1215–1229.
- 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**, 76–87.
- Weigelt A., Mommer L., Andrzejak K., Iversen C.M., Bergmann J., Bruelheide H., Fan Y., Freschet G.T., Guerrero-Ramírez N.R., Kattge J., Kuyper T.W., Laughlin D.C., Meier I.C., van der Plas F., Poorter H., Roumet C., van Ruijven J., Sabatini F.M., Semchenko M., Sweeney C.J., Valverde-Barrantes O.J., York L.M., McCormack M.L. (2021) An integrated framework of plant form and function: the below-ground perspective. *New Phytologist*, **232**, 42–59.
- Werner R.A., Brand W.A. (2001) Referencing strategies and techniques in stable isotope ratio analysis. *Rapid Communications in Mass Spectrometry: RCM*, **15**, 501–519.
- Yang J., Song X., Zambrano J., Chen Y., Cao M., Deng X., Zhang W., Yang X., Zhang G., Tang Y., Swenson N.G. (2021) Intraspecific variation in tree growth responses to neighbourhood composition and seasonal drought in a tropical forest. *Journal of Ecology*, **109**, 26–37.
- Yang X., Bauhus J., Both S., Fang T., Härdtle W., Kröber W., Ma K., Nadrowski K., Pei K., Scherer-Lorenzen M., Scholten T., Seidler G., Schmid B., von Oheimb G., Bruelheide H. (2013) Establishment success in a forest biodiversity and ecosystem functioning experiment in subtropical China (BEF-China). *European Journal of Forest Research*, **132**, 593–606.