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Neighbourhood diversity mitigates drought impacts on tree growth

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Abstract

1. Biodiversity is considered to mitigate detrimental impacts of climate change on the functioning of forest ecosystems, such as drought-induced decline in forest productivity. However, previous studies produced controversial results and experimental evidence is rare. Specifically, the biological mechanisms underlying mitigation effects remain unclear, as existing work focuses on biodiversity effects related to the community scale.
2. Using trait-based neighbourhood models, we quantified changes in above-ground wood productivity of 3,397 trees that were planted in a large-scale tree diversity experiment in subtropical China across gradients of neighbourhood diversity and climatic conditions over a 6-year period. This approach allowed us to simultaneously assess to what extent functional traits of a focal tree and biodiversity at the local neighbourhood scale mediate the growth response of individual trees to drought events.
3. We found that neighbourhood tree species richness can mitigate for drought-induced growth decline of young trees. Overall, positive net biodiversity effects were strongest during drought and increased with increasing taxonomic diversity of neighbours. In particular, drought-sensitive species (i.e. those with a low cavitation resistance) benefitted the most from growing in diverse neighbourhoods, suggesting that soil water partitioning among local neighbours during drought particularly facilitated most vulnerable individuals. Thus, diverse neighbourhoods may enhance ecosystem resistance to drought by locally supporting drought-sensitive species in the community.
4. *Synthesis*. Our findings demonstrate that mechanisms operating at the local neighbourhood scale are a key component for regulating forests responses to drought

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and improve insights into how local species interactions vary along stress gradients in highly diverse tree communities.

KEYWORDS
biodiversity, climate change, drought resistance, ecosystem functioning, forest, functional traits, species interactions, stress-gradient hypothesis

1 | INTRODUCTION

Forests store immense amounts of carbon (Pan et al., 2011), and carbon sequestration by trees is assumed to be an important measure to remove carbon dioxide from the atmosphere (Griscom et al., 2017). However, the expected increase in severity and frequency of drought events (IPCC, 2018) might have detrimental impacts on forest ecosystem functions (e.g. biomass production), services (e.g. carbon sequestration), species composition and diversity (Choat et al., 2018; Zhang, Niinemets, Sheffield, & Lichstein, 2018). Conversely, biodiversity has a positive effect on forest productivity (Duffy, Godwin, & Cardinale, 2017), as mixed-species forest communities have been demonstrated to be more productive (Huang et al., 2018; Liang et al., 2016) and more consistent in productivity over time than monocultures (del Río et al., 2017; Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Morin, Fahse, de Mazancourt, Scherer-Lorenzen, & Bugmann, 2014; Schnabel et al., 2019), resulting in higher amounts of carbon stored above- and below-ground in species-rich forests (Liu et al., 2018). Yet, despite advances in our understanding of biodiversity–productivity relationships (BPRs), the role of biodiversity in mitigating adverse effects of climate change on the functioning of forest ecosystems remains controversial (Ammer, 2019; González de Andrés, 2019; Grossiord, 2019; Hisano, Chen, Searle, & Reich, 2019; Hisano, Searle, & Chen, 2018), making predictions of ecosystem responses to climate change challenging. For example, it has been shown that the strength of BPRs at the community scale was higher in forest types or at forest sites associated with adverse climatic conditions (Jucker et al., 2016; Paquette & Messier, 2011), but the opposite response was revealed for forest sites along a global precipitation gradient (Jactel et al., 2018). In contrast, a recent study showed that functional tree diversity enhanced community productivity during normal, but not during warmer climatic conditions (Paquette, Vayreda, Coll, Messier, & Retana, 2018). Similarly, interannual variation in climate has been demonstrated to have no consistent effect on the strength of community BPRs within a given forest site (Jucker et al., 2016). This indicates that we currently lack a general understanding of mitigation effects (i.e. the potential of biodiversity in attenuating climate change impacts on ecosystem functioning, such as drought-induced decline in growth) in long-lived plant communities, such as forests.

Biodiversity-mediated effects on ecosystem functioning can result from species interactions, leading to competitive reduction or facilitation, thereby promoting ecosystem functions (Barry et al., 2019). The existing controversies regarding mitigation effects might therefore be reconciled when considering the relevant scale for species interactions, that is, the local neighbourhood (Stoll & Weiner, 2000). Such biodiversity-mediated interactions among local neighbours are a key component for regulating productivity in diverse tree communities (Fichtner et al., 2018), suggesting that the potential of biodiversity in mitigating the impact of drought on tree growth largely depends on how species interact at the local neighbourhood scale. In this context, the stress-gradient hypothesis (SGH) predicts that competitive plant–plant interactions become less important in favour of facilitative ones with increasing environmental stress (Bertness & Callaway, 1994). Consequently, BPRs at the local neighbourhood scale should become stronger during periods of water deficits, meaning that the relative importance of biodiversity effects increases during drought (Figure 1a,b). The few evidence on climate–growth relationships in response to local neighbourhood conditions comes from observational studies performed in less diverse temperate forests with a limited taxonomic tree diversity (Jourdan, Kunstler, & Morin, 2020), and most of these studies accounted for neighbourhood diversity using a contrast of neighbourhood composition (conspecific vs. heterospecific neighbours; Mölder & Leuschner, 2014; Vitali, Forrester, & Bauhus, 2018) or neighbourhood competition (intraspecific vs. interspecific competition; Aussenac, Bergeron, Gravel, & Drobyshev, 2019). Similarly, one recent experimental study explored drought resistance of tropical tree seedlings in response to neighbourhood composition (conspecific vs. heterospecific neighbours; O'Brien, Reynolds, Ong, & Hector, 2017). Improving mechanistic insight into mitigation effects therefore requires experimental evidence on how local neighbourhood interactions alter the response of individual trees to drought across biodiversity levels (i.e. along a gradient of neighbourhood diversity), particularly in highly diverse tree communities.

Refined versions of the SGH additionally suggest that the outcome of local neighbourhood interactions may depend on the stress tolerance and diversity of the interacting species (Maestre, Callaway, Valladares, & Lortie, 2009; Soliveres, Smit, & Maestre, 2015). In a previous study, we showed that the mode (competitive reduction and facilitation) and intensity of biodiversity-mediated neigbourhood interactions in subtropical tree communities is closely related to the functional traits of the focal species (Fichtner et al., 2017). Moreover, there is evidence that the diversity in hydraulic traits of component trees within a community play an important role for regulating forest ecosystem resilience to drought (Anderegg et al., 2018). Thus, it is further conceivable that functional traits

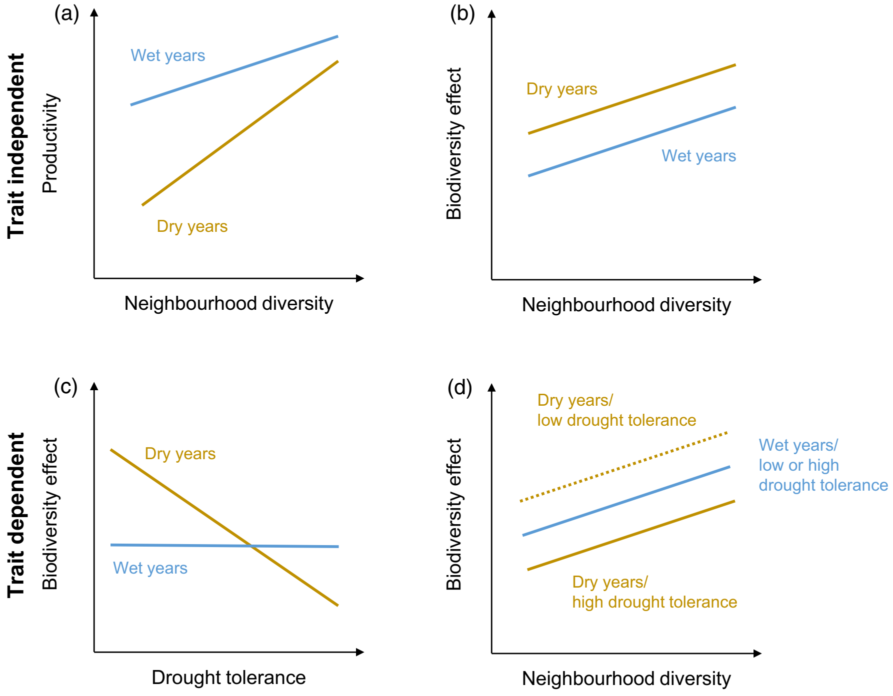

FIGURE 1 Neighbourhood interactions and climate change. (a) Across different tree species (trait-independent response), neighbourhood diversity is assumed to mitigate negative impacts of climate change on individual tree productivity, resulting in a positive biodiversity–productivity relationship during drought. Moreover, the relative importance of neighbourhood diversity in mitigating drought-induced growth decline is expected to increase during drought, thus (b) the magnitude (effect size) of biodiversity effects should become stronger. (c) Alternatively, the magnitude of biodiversity effects might depend on the species' functional traits associated with drought tolerance (trait-dependent response). (d) Biodiversity effects are, thus, expected to become stronger for drought-sensitive species during unfavourable climatic conditions (in dry years), while they should become stronger for drought-tolerant species during favourable climatic conditions (in wet years). Consequently, the relative importance (effect size) of neighbourhood diversity in modulating climate change impacts should critically depend on species' functional traits [Colour figure can be viewed at wileyonlinelibrary.com]

that predict the species' response to water limitations and therefore its drought tolerance mediate the magnitude of biodiversity effects (effect size) at the local neighbourhood scale during drought (Figure 1c,d).

Here, we used growth and trait data of young subtropical trees planted in a large-scale biodiversity–ecosystem functioning experiment in China (BEF-China; Bruelheide et al., 2014) to explore how climate variability (years with and without water deficits) modulates biodiversity effects on tree growth at the local neighbourhood scale (using species richness as a measure for biodiversity). In this study, we define the term 'biodiversity effect' as the net effect of all intra- and interspecific interactions within the neighbourhood of a single focal tree, while the neighbourhood is defined as the total number of closest trees surrounding the focal tree (i.e. the local neighbourhood). Note that this definition differs from the one in Loreau and Hector (2001), where the diversity effect refers to the whole community. Our tree communities cover a long diversity gradient, ranging from monocultures to 24-species mixtures and from conspecific neighbourhoods to species-rich neighbourhoods with a maximum of eight heterospecific neighbours. Specifically, we quantified growth responses of 3,397 focal trees, belonging to 25 species, to climate events along an experimentally manipulated gradient of local neighbourhood diversity over a 6-year period. Using trait-based neighbourhood models, we tested whether neighbourhood diversity mitigates drought-induced growth decline. We hypothesized (a) that positive biodiversity effects become stronger during years with water deficits and (b) that the focal trees' drought tolerance (using cavitation resistance as a key physiological trait that predicts the species' response to water limitations) mediate the importance of biodiversity effects at the local neighbourhood scale.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

In this study, we used data from 228 study plots (25.8 × 25.8 m^2) of a 26.6-ha experimental site (site A; 29.125°N, 117.908°E) established in southeast subtropical China as part of the BEF-China tree diversity experiment (Bruelheide et al., 2014). The study site is located on sloped terrain (average slope 27.5°) between 105 and 275 m above sea level. The climate of the study area is characterized as subtropical summer monsoon (mean annual temperature of 16.7°C and mean precipitation of 1,821 mm/year, averaged from 1971 to 2000; Yang et al., 2013) with the wet season lasting from April to August. The mean annual temperature for the study period (2010–2016; based on available data from the closest weather station Jingdezhen, CMA, 2019) was 18.4°C and the mean precipitation was 2,111 mm/year. The mean monthly temperatures ranged from 2.9°C (winter) to 34.8°C (summer) and the mean monthly precipitation ranged from 25 mm/month (winter) to 492 mm/month (summer). Prevailing soil types are Cambisols, Regosols and Colluvissols (Scholten et al., 2017). In March 2009, each study plot was planted with 400 1- to 2-year-old tree saplings (20 × 20 individuals) with a horizontal planting distance of 1.29 m (Bruelheide et al., 2014). Based on a species pool of 40 native broad-leaved tree species, a long diversity gradient was created by manipulating the number of tree species within a plot (monocultures and mixed communities of 2, 4, 8, 16 and 24 tree species), where species and tree diversity levels were randomly assigned to planting positions and plots. All saplings that died during the first growing season were replanted in November 2009 (deciduous species) and March 2010 (evergreen species). More detailed information on the experimental design is provided by Bruelheide et al. (2014).

2.2 | Tree data

For all trees within a plot, species identity, stem diameter (measured 5 cm above-ground) and tree height (measured from the stem base to the apical meristem) were recorded. To avoid confounding effects between experimental treatments and planting, tree measurements started in autumn (September–October) 2010. Here, we used growth data of 3,397 trees that were assigned to the central planting positions within a plot (hereafter: focal trees) and that survived during the 6-year (2010–2016) study period (i.e. tree measurements were available in each year; Table S1). All other trees within a plot were treated as neighbour-only trees (Figure S1). For each focal tree, above-ground wood volume was calculated by multiplying the arithmetic product of tree basal area and tree height with a factor of 0.5412 (an average value for young subtropical trees obtained from our study species; Huang et al., 2018) to account for the deviation of the theoretical volume of a cylinder from actual tree volume (Pretzsch, 2009). Annual growth rates were calculated for each year of the study period as $V_t - V_{t-1}$, where V is the above-ground wood volume in a specific year (t) with t = 2010, ..., 2016. To avoid potential bias in model estimates, we excluded those trees that exhibited negative growth rates in a given census intervals (7.3%) that can result from stochastic processes (e.g. mechanical tree damage due to falling large-sized branches or falling stones or browsing) or measurement errors (e.g. different measurement positions between the censuses due to trees with trunk irregularities). Note that the likelihood of such processes increases with time. To account for variation in tree size, growth rates were standardized by dividing annual above-ground wood productivity by the initial volume of the focal tree in the respective annual census interval (AWP; $\text{cm}^3\ \text{cm}^{-3}\ \text{year}^{-1}$).

2.3 | Climate data

We used the standardized precipitation-evapotranspiration index (SPEI) to identify climate events. The drought index captures the monthly climatic water balance (precipitation minus potential evapotranspiration), where negative values indicate periods with water deficits (negative climatic water balance) and positive values conditions with ample water supply (positive climatic water balance; Vicente-Serrano, Beguería, & López-Moreno, 2010). We considered annual water balances (calculated for a 12-month timescale, $\text{SPEI}_{12\text{-Oct}}$) to link observed annual growth rates with interannual variation in climatic conditions, as they have been shown to capture well variation in tree demography in response to climate events in humid biomes (Hutchison, Gravel, Guichard, & Potvin, 2018; Vicente-Serrano et al., 2013). SPEI data with a 0.5° (latitude/longitude) resolution were calculated with the R code for generating the global SPEI database (Beguería, 2017) based on updated precipitation and potential evapotranspiration data (CRU TS v4.03; Harris, Jones, Osborn, & Lister, 2014) to cover the study period (Figure S2).

2.4 | Functional trait data

Functional trait data for our study species were obtained from trait assessments conducted at our study site (Kröber, Zhang, Ehmig, & Bruelheide, 2014). We focused on hydraulic traits, as they allow for an advanced mechanistic understanding of plant responses to changes in water availability (Griffin-Nolan et al., 2018). To examine the role of inter-specific trait variation in regulating neighbourhood interactions during climate events, we used the water potential at which 50% of xylem hydraulic conductivity is lost (Ψ_{50}; Figure S3) as an indicator for species' drought tolerance (Choat et al., 2012). Vulnerability to cavitation is considered a key physiological trait determining species' response to water limitations, where increasing (less negative) Ψ_{50} values indicate a higher risk of cavitation (Choat et al., 2018; Maherali, Pockman, & Jackson, 2004). In our study, drought-tolerant species (those with lower Ψ_{50} values) were associated with a high leaf toughness (r: −.58, p = .002) and leaf thickness (r: −.41, p = .041). In contrast, specific leaf area (r: .37, p = .070) and wood density (r: −.12, p = .555) were not significantly related to Ψ_{50}.

2.5 | Data analysis

We used linear mixed-effects models to test the effects of local neighbourhood conditions, climatic fluctuations (expressed as the drought index, SPEI) over a 6-year study period (2010–2016) and focal tree's drought tolerance (DT) on individual tree productivity. We were primarily interested to explore changes in local biodiversity-mediated neighbourhood interactions along climatic gradients independently from temporal changes in growth rates (note that in general, growth rates of young trees increase through time; thus, annual growth variation might not inevitable be linked to changes in annual climatic conditions). To avoid confounding effects between year (i.e. the calendrical interval of a census) and drought index (SPEI), we therefore removed the temporal trend in AWP (cm^3 cm^{-3} year^{-1}) by dividing AWP of a given focal tree (*i*) in a specific census interval (*k*) by the average AWP (using the 50% quantile of AWP) of the respective census *k*:

$$\mathrm{SAWP}_{i,k} = \left(\mathrm{AWP}_{i,k} \Big/ \overline{\mathrm{AWP}_k} \right), \tag{1}$$

where SAWP denotes the standardized annual above-ground wood productivity (dimensionless) of a focal tree in an annual census interval.

Neighbourhood conditions were characterized as the relative abundance of neighbours (expressed as the neighbourhood competition index, NCI) and number of heterospecific (different species identity as the focal tree) tree species (NSR) in the local neighbourhood of a focal tree. For each focal tree *i*, NCI was calculated as the focal trees' basal area relative to the total basal area of closest neighbours *j* ($\sum_{j \neq i} \pi D_j^2/4$, where *D* is the measured ground diameter) in a given study year. NSR was calculated as the total number of closest heterospecific neighbour species ($\sum_{j \neq i} N_j$, where *N* is the recorded species number) in given study year. NSR represents the net effect of neighbouring trees on the growth of a focal tree and is, as expected, positively related to log-tree species richness at the community level (r = .82, p < .001). We excluded the maximum of NSR (8), as this level was only realized once across study years.

The focal trees' species identity (to account for effects of species identity), neighbourhood species composition (to account for compositional differences of neighbouring trees), total number of living neighbours (to account for effects of neighbour mortality) and the focal tree nested in study plot (to account for small-scale variation in abiotic site conditions and repeated measurements) were used as crossed random effects. To allow for temporal variation in species identity effects, we additionally included a random slope of study year (continuous variable corresponding to the six consecutive census intervals) depending on species identity, which significantly improved the fit of the initial model (ΔAIC: 334.22; χ^2 = 337.39, p < .001).

First, we determined the optimal random-effects structure based on restricted maximum likelihood (REML) estimation, considering additive and interactive effects. Second, we determined the optimal fixed-effects structure using the maximum likelihood (ML) method (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In this study, we were primarily interested to understand how net biodiversity effects at the local neighbourhood scale vary in the magnitude and direction of their responses to drought and how these effects are mediated by the focal trees' functional traits. To test for trait-independent and trait-dependent responses, we therefore considered the three-way interaction among NSR, SPEI and DT, where a significant three-way interaction would indicate a trait dependency of the NSR-SPEI relationship and vice versa. Additionally, we included NCI as a main effect in our neighbourhood model to account for the impacts of neighbour abundance on individual tree productivity. To simplify the model structure, and thus allowing for a biologically plausible interpretation of parameter estimates, we did not include interaction terms with NCI in the subsequent analyses (note that the difficulty of interpreting interactions increases with the number of predictors involved; Zuur, Ieno, & Smith, 2007). Importantly, results from a neighbourhood model accounting for a three-way interaction between NCI, SPEI and DT were qualitatively the same (Table 1; Table S2), suggesting that our parameter estimates had an adequate power to explore the link between NSR, SPEI and DT. Different competing models were evaluated by sequential comparison based on the Akaike Information Criterion (AIC). The model with the lowest AIC and highest Akaike weights (i.e. the likelihood of being the best-fitting model based on AIC values; Burnham & Anderson, 2002) was chosen as the most parsimonious model (Table S3). Parameter estimates of the best-fitting model were based on restricted maximum likelihood (REML) estimation (Zuur et al., 2009). For each census interval (2010–2011, 2011–2012, 2012–2013, 2013–2014, 2014–2015, 2015–2016), we used the initial values of NCI and NSR. All predictors were standardized (*M* = 0, *SD* = 1) before analysis; SAWP and NCI were log-transformed (using the natural logarithm) to meet model assumptions. There was no critical correlation between

TABLE 1 Best-fitting mixed-effects model of the effects of neighbourhood conditions, drought index and drought tolerance on individual tree growth (standardized above-ground wood productivity, SAWP). Regression coefficients are standardized and significant terms (p < .05) are highlighted in bold. See Table S5 for variance components

	Estimate	*SE*	*df*	*t* value	*p* value
Intercept	0.136	0.126	15.9	1.08	.295
Neighbourhood competition index (NCI, log)	−0.258	0.008	4,970.0	−33.30	**<.001**
Neighbourhood tree species richness (NSR)	0.026	0.013	1,134.0	2.02	**.043**
Drought index (SPEI)	0.008	0.007	10,800.0	1.13	.261
Drought tolerance (DT)	−0.143	0.066	20.8	−2.17	**.042**
NSR × SPEI	0.003	0.005	15,500.0	0.53	.598
NSR × DT	0.023	0.008	2,869.0	2.76	**.006**
SPEI × DT	−0.020	0.007	8,892.0	−2.83	**.005**
NSR × SPEI × DT	−0.015	0.006	15,590.0	−2.74	**.006**

Abbreviations: *df*, degrees of freedom; *SE*, standard error.

covariates (collinearity), as indicated by the variance inflation factors (all VIFs <1.03). Model assumptions were checked and confirmed according to Zuur et al. (2009). In addition, we fitted an alternative model that accounted for variation in topography (slope and elevation) to test the robustness of our parameter estimates (Table 1; Table S4). This was confirmed and is in line with the previously reported weak impacts of topography and soil chemical properties on tree growth rates (Kröber et al., 2015) and community productivity (Fichtner et al., 2018) at our study site.

To assess the impact of climate on biodiversity effects, we used growth predictions (based on fixed-effects estimates) from our best-fitting model (Table 1). Specifically, we quantified climate-induced changes in annual tree productivity of a focal tree growing in conspecific (NSR = 0) compared to heterospecific neighbourhoods (NSR ≥ 1). Changes in the net biodiversity effect (NE) for a given NSR-level *j* were quantified using a measure of relative effect sizes (i.e. neighbour-effect index with additive symmetry; Díaz-Sierra, Verwijmeren, Rietkerk, de Dios, & Baudena, 2017):

$$\mathrm{NE}_j = 2\frac{\left(\mathrm{SAWP}_{h,j} - \mathrm{SAWP}_c\right)}{\mathrm{SAWP}_c + \left|\left(\mathrm{SAWP}_{h,j} - \mathrm{SAWP}_c\right)\right|}, \qquad (2)$$

where SAWP denotes the predicted annual standardized above-ground wood productivity (back-transformed from logarithmic scale) of a focal tree and *c* indicates conspecific and *h* heterospecific neighbours with *j* = 1, …, 7 species. The effect size measure is standardized, symmetrical around zero and bounded between −1 and +2. Negative values indicate underyielding (higher SAWP in conspecific relative to heterospecific neighbourhoods), while positive values imply overyielding (higher SAWP in heterospecific relative to conspecific neighbourhoods). NE was then related to species richness of the local neighbourhood, for each species (across species approach; trait-independent response) or separately for low, average and high drought tolerance (DT; trait-dependent response). For each focal tree, we predicted SAWP at low (80% quantile of species-specific Ψ_{50}; note that Ψ_{50} values are negative), average (50% quantile) and high (20% quantile) DT. We did this for every level of NSR, while keeping NCI fixed at its mean and keeping SPEI fixed at values of −1.5 (severely dry), −0.8 (moderately dry), 0.8 (moderately wet) or 1.5 (severely wet). In this way, our function-derived growth rates allowed us to explore how neighbourhood-scale biodiversity effects vary in the mode and intensity during climate events. All analyses were conducted in R (version 3.5.1; R Core Team, 2018) using the packages lme4 (Bates, Maechler, Bolker, & Walker, 2015), lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016) and MuMIn (Bartón, 2016).

3 | RESULTS

Across species, neighbourhood tree species richness (NSR) promoted individual tree growth (standardized above-ground

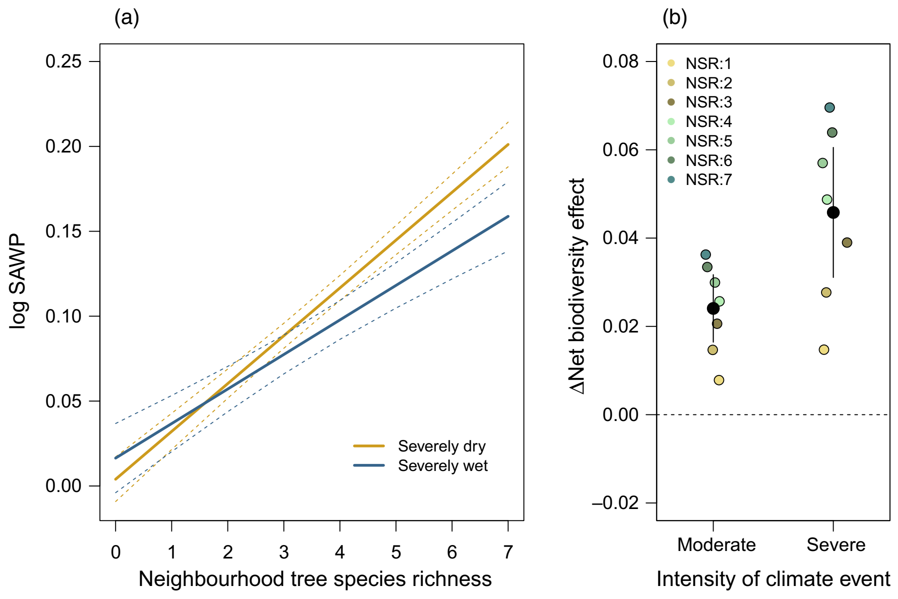

FIGURE 2 Variation in trait-independent (averaged across species) biodiversity effects at the local neighbourhood scale on individual tree growth (standardized above-ground wood productivity, SAWP) with neighbourhood tree species richness (NSR) and climate conditions. (a) Changes in local biodiversity–productivity relationships (BPRs). Lines correspond to the fitted BPRs of a mixed-effects model, with dotted lines representing the 95% confidence interval of the prediction. NSR = 0 indicate conspecific and NSR ≥ 1 heterospecific neighbourhoods. (b) Changes in the magnitude (standardized effect size) of net biodiversity effects (Δ net biodiversity effects; mean and 95% confidence interval) on SAWP with the intensity of climate events. Severe event: difference in Δ net biodiversity effects between severely dry (SPEI = −1.5) and severely wet (SPEI = 1.5) years; moderate event: difference in Δ net biodiversity effects between moderately dry (SPEI = −0.8) and moderately wet (SPEI = 0.8) years. Positive values indicate higher biodiversity effects in dry relative to wet years and negative values indicate higher biodiversity effects in wet relative to dry years. Transparent points represent Δ net biodiversity effects predicted for each NSR level. NSR-specific values are jittered to facilitate visibility [Colour figure can be viewed at wileyonlinelibrary.com]

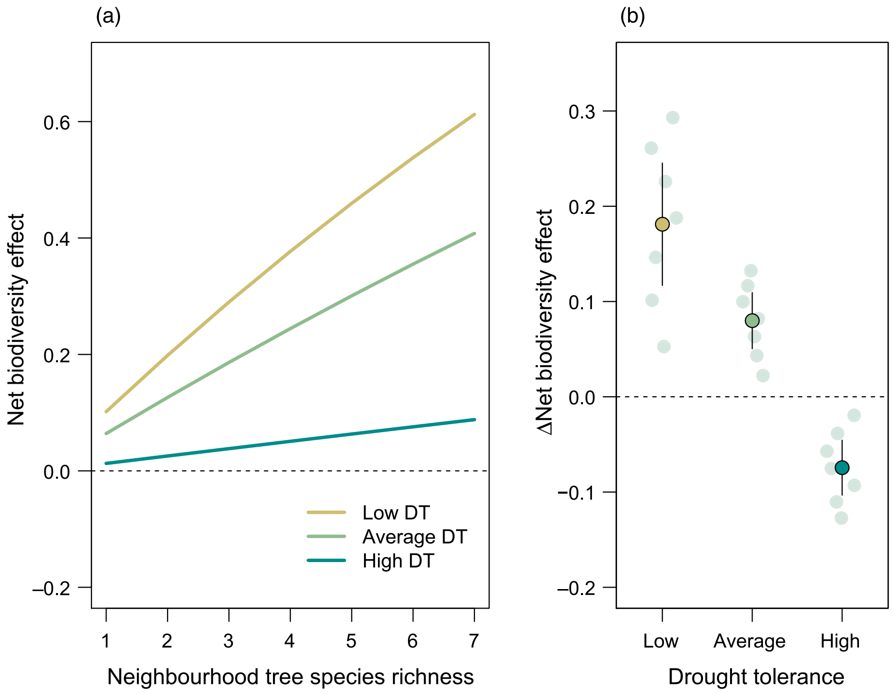

FIGURE 3 Trait-mediated biodiversity effects during climate events. (a) Variation in the magnitude (standardized effect size) of net biodiversity effects on individual tree growth (standardized above-ground wood productivity, SAWP) with neighbourhood tree species richness (NSR) and the focal trees' drought tolerance (DT) during a severe drought (SPEI = −1.5). Lines are mixed-effects model fits for each drought tolerance category. Positive values of the standardized effect size indicate overyielding (higher productivity in heterospecific; NSR ≥ 1, relative to conspecific, NSR = 0, neighbourhoods) and negative values indicate underyielding (higher productivity in conspecific relative to heterospecific neighbourhoods). (b) Trait-dependent differences in net biodiversity effects (Δ net biodiversity effects, mean and 95% confidence interval) between severely dry (SPEI = −1.5) and severely wet (SPEI = 1.5) years. Transparent points represent Δ net biodiversity effects predicted for each NSR level. NSR-specific values are jittered to facilitate visibility. See Figure 2 for further information [Colour figure can be viewed at wileyonlinelibrary.com]

wood productivity, SAWP) both in dry and wet years (Figure 2a; Figure S4). Overall, positive biodiversity effects increased with increasing NSR (Figure S5), but were on average 15% (moderate event) and 30% (severe event) stronger in dry compared to wet years (severe event: $t = 6.10$, $p < .001$; moderate event: $t = 6.18$, $p < .001$; Figure 2b). Importantly, the magnitude of biodiversity effects (and thus their potential for climate change mitigation) critically depended on the focal trees' hydraulic traits, as indicated by the significant three-way interaction between NSR, drought index and drought tolerance (DT; Table 1). Specifically, drought-sensitive species benefitted the most from growing with heterospecific neighbours during drought, with biodiversity effects here being on average about 0.5 and 6 times higher than for species with an average or high DT, respectively (Figure 3a). In contrast, differences in drought tolerance of the focal tree had little impact on the magnitude of biodiversity effects during favourable conditions (wet years; Figure S6). As a result, the magnitudes of biodiversity effects promoting growth of drought-sensitive species and those with average DT were significantly higher in dry than wet years (low DT: $t = 5.53$, $p = .001$; average DT: $t = 5.33$, $p = .002$). Contrarily, drought-tolerant species benefitted less from growing in diverse neighbourhoods in dry compared to wet years ($t = -5.07$, $p = .002$; Figure 3b). This was consistent with significantly higher SAWP for species with low and average DT during drought, while the opposite was evident for species with high DT (low DT: $t = 3.23$, $p = .014$; average DT: $t = 2.71$, $p = .030$; high DT: $t = -4.98$, $p = .002$; Figure S7).

4 | DISCUSSION

We found that positive biodiversity effects at the local neighbourhood scale persist and became stronger in years with water deficits, indicating that neighbourhood diversity has a strong potential to mitigate adverse impacts of climate change on tree growth. This confirms our first hypothesis and theoretical considerations of positive species interactions and biodiversity effects becoming more important during adverse climatic conditions (Brooker, 2006; Hisano et al., 2018; Wright, Wardle, Callaway, & Gaxiola, 2017). There are multiple mechanisms by which tree–tree interactions could mitigate drought-induced growth decline. Overall, tree responses to drought largely depend on the amount of plant-available soil water remaining during a drought event, but soil water availability, in turn, is strongly altered by species interactions (Forrester, 2014). Species interactions can lead to higher water availability and water-uptake efficiency via competitive reduction or facilitation and thereby mitigate trees' water stress (Forrester & Bauhus, 2016). For example, reduced competition for water among heterospecific neighbours was recently shown as a mechanism maintaining growth rates of tropical tree seedlings under drought (O'Brien et al., 2017). Thus, trees might be more productive in diverse neighbourhoods during periods of water deficits by benefitting from enhanced fine root growth and interspecific variation in rooting strategies, and hence from an improved access to soil water (Brassard et al., 2013; Sun et al., 2017). Moreover, soil water availability is determined by the water use behaviour of coexisting species. It is therefore conceivable that the observed mitigation effects of neighbourhood diversity additionally result from interspecific differences in stomatal regulation strategies (Forrester, 2017; Kröber & Bruelheide, 2014). Next to resource partitioning, microclimate amelioration via facilitative neighbourhood interactions might act as a further mechanism by which the water demand of a focal tree growing in diverse neighbourhoods is decreased. For example, increasing tree species diversity at the local neighbourhood scale allows for more complex structured and densely packed canopies by shifts in wood volume allocation in favour of branches over time (Kunz et al., 2019). This, in turn, can reduce irradiance, air and soil surface temperature as well as vapour pressure deficits at the leaf surface and the evaporative demand of whole trees (Montgomery, Reich, & Palik, 2010), therefore improving abiotic growing conditions during drought. Biotic facilitation via mycorrhizal networks might be a further reason why trees growing with functional diverse neighbours are more resistant to drought. For example, such common mycorrhizal mycelium links the roots of trees by which coexisting tree species can transfer substantial amounts of carbon below-ground (Klein, Siegwolf, & Körner, 2016), suggesting that below-ground transfers of water and nutrients become increasingly important in a changing climate (Simard et al., 2012). Our finding of consistently higher biodiversity effects in more diverse neighbourhoods during drought suggests that positive neighbourhood interactions can improve the local soil water availability or microclimate for a given focal tree, thereby becoming particularly important during periods of water deficits. Positive neighbourhood interactions can also arise through biotic feedbacks (Barry et al., 2019). Reduced conspecific neighbour density and the presence of heterospecific neighbours can decrease host-specific damage by herbivores and pathogens (Barbosa et al., 2009; Hantsch et al., 2014; Johnson, Beaulieu, Bever, & Clay, 2012). These effects might be particularly pronounced during dry conditions (e.g. Lin, Comita, Zheng, & Cao, 2012), and beneficial effects of a diverse neighbourhood might therefore be more notable, because drought stress can weaken trees and make them particularly susceptible to enemy attack (Jactel et al., 2012). Although we were not able to assess the importance of potential mechanisms underlying mitigation effects, our results indicate that processes operating at the local neighbourhood scale are a key component that contribute to the role of biodiversity in mitigating impacts of drought on forest ecosystems.

Based on a large-scale biodiversity experiment, our study shows mitigation effects of neighbourhood diversity on drought-induced growth decline, but the magnitude of mitigation was dependent on the focal trees' hydraulic traits. This supports our second hypothesis of changes in trait-mediated neighbourhood interactions across biodiversity levels during climatic events. Given that a focal trees' drought tolerance was negatively related to the magnitude of biodiversity effects, the relative importance of neighbourhood diversity was higher for drought-sensitive species, but lower for species with a high drought tolerance in dry compared to wet years. Thus, our results suggest that both neighbourhood diversity and the focal trees' traits related to hydraulic function have a dominant role in mediating drought responses of individual trees. In our study system, neighbourhood tree species richness promotes individual tree productivity of species with an acquisitive resource-use strategy by competitive reduction (Fichtner et al., 2017), and those species with the lowest cavitation resistance are associated with acquisitive functional traits (Figure S3). We therefore conclude that shifts in neighbourhood interactions towards less intense competition for soil water among local heterospecific neighbours largely explain why drought-sensitive species benefitted the most from growing with diverse neighbours during drought. Our results are in contrast to findings from temperate forests, where Jucker, Bouriaud, Avacaritei, Dănilă, et al. (2014) demonstrated the strongest decline in biodiversity effects (relative to community tree species richness) during dry years for species associated with the lowest drought tolerance. Similarly, the proportion of heterospecific neighbours was shown to positively affect drought resilience of drought-tolerant species (*Quercus pubescens*), while a neutral (*Fagus sylvatica*) and negative (*Abies alba*) effect was evident for less drought-tolerant species (Jourdan et al., 2020). These differences might be largely attributed to differences in biomes (level of tree species diversity, climate and soil conditions). Finally, favourable light- or nutrient-related species interactions are assumed to become more important in wet years or at sites associated with high precipitation (Jactel et al., 2018), which could explain why trees with favourable traits to tolerate drought benefitted more from growing in species-rich neighbourhoods in wet than in dry years.

The strong effects of neighbourhood diversity in mediating individual tree productivity has important consequences for climate-change mitigation, as our experimental findings clearly show that more diverse neighbourhoods are able to mitigate the negative impacts of drought on individual tree productivity. Importantly, we observed a stronger biodiversity effect for drought-sensitive species in dry years. This implies that water-related neighbourhood relationships are primarily beneficial for trees with unfavourable traits to tolerate drought. In this way, diverse local neighbourhoods can act as a 'welfare net' by providing greatest support for most vulnerable individuals in the community. Our results suggest that neighbourhood diversity can increase ecosystem resistance against adverse impacts of climate change via strengthening the weakest components of the system. Although there might be trade-offs between mixed-species forest productivity and high-quality timber production or harvesting systems (Coll et al., 2018), our findings emphasize the importance of promoting tree species richness at the local neighbourhood scale in current afforestation and forest restoration strategies to secure high forest productivity and carbon sequestration even during periods of drought.

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AUTHORS' CONTRIBUTIONS

G.v.O., W.H. and H.B. conceived and designed the study; M.K., K.M. and F.S. compiled the data; A.F. analysed the data with support of F.S. and H.B. A.S. contributed to the discussion of the results. A.F. wrote the manuscript with substantial input from all co-authors.

DATA AVAILABILITY STATEMENT

All data are available on the BEF-China project database: https://china.befdata.biow.uni-leipzig.de/datasets/614 (Fichtner et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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