Abstract

Taxonomic diversity effects on forest productivity and response to climate extremes range from positive to negative, suggesting a key role for complex interactions among neighbouring trees. To elucidate how neutral interactions, hierarchical competition and resource partitioning between neighbours shape tree growth and climate response in a highly diverse Amazonian forest, we combined 30 years of tree censuses with measurements of water and carbon related traits. We modelled individual tree growth response to climate and neighbourhood to disentangle the relative effect of neighbourhood densities, trait hierarchies and dissimilarities. While neighbourhood densities consistently decreased tree growth, trait dissimilarity increased it, and both influenced climate response. Greater water conservatism provided a competitive advantage to focal trees in normal years, but water spender neighbours reduced this effect in dry years. By underlining the importance of density and trait-mediated neighbourhood interactions, our study offers a way towards improving predictions of forest response to climate change.

Introduction

Climate extremes such as heat waves, high atmospheric evaporative demands and low soil water availability (i.e drought stress sensu lato), negatively affect forest productivity and functioning (Allen *et al.*, 2010; Bauman *et al.*, 2022a,b). These events are predicted to increase in frequency and intensity with ongoing climate change (Shukla *et al.*, 2022), which can alter global carbon dynamics (Higgins *et al.*, 2023). At the global scale, tree taxonomic diversity is an important driver of forest productivity (Liang *et al.*, 2016), and can increase forest resistance to drought (Anderegg *et al.*, 2018). However, at local scales, the magnitude and even the sign of the effect of diversity on productivity can vary from site to site, depending on the local context (e.g. climate and disturbance regimes, stand structure and composition: Ammer 2019; Belote *et al.* 2011; Crawford *et al.* 2021) and temporal variations in resource availability or climate (Forrester & Bauhus, 2016). Increasing evidence further suggests that diversity does not always increase forest resistance to droughts locally (Grossiord, 2020; Pardos *et al.*, 2021). Uncovering the mechanisms that underlie diversity effects on forest productivity and its response to climate is needed to better understand these context-dependent effects (Grossiord, 2020) and improve our ability to predict forest responses to climate change.

Complementarity in resource use among co-occurring species has been proposed to explain increased forest productivity (Liang *et al.*, 2015; Morin *et al.*, 2011) and resistance to environmental fluctuations, such as climate extremes (Loreau & de Mazancourt, 2013) in species diverse stands. As competition for resources takes place at the neighbourhood scale, evidence for such an effect and its signature should be found in the influence of neighbours' identity on individual tree growth (Yu *et al.*, 2024) and its response to climate. Neighbourhood species richness has been shown to influence individual functioning under various conditions (Fichtner *et al.*, 2018, 2020). However, this taxonomic diversity lens only offers limited insights into the mechanisms that drive the effects of neighbourhood diversity, and especially whether complementarity actually plays a major role in the mitigation of negative climate effects (Grossiord, 2020; Jucker *et al.*, 2014).

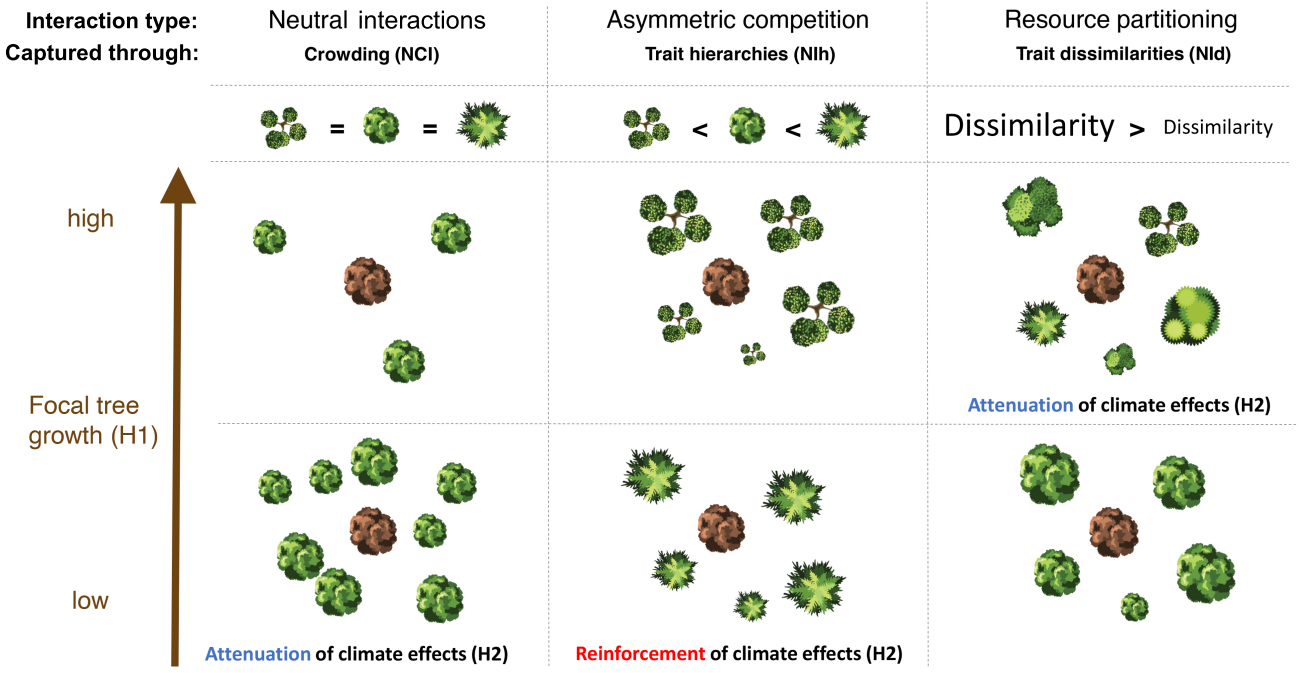

Figure **1.** Conceptual illustration of different types of neighbourhood interactions, including neutral interactions, asymmetric competition and resource partitioning between a focal tree (brown) and its neighbouring trees (green). Neutral interactions can be captured by neighbourhood crowding indices (NCI), which depend solely on neighbourhood densities (i.e. the number, size and distance of neighbours). Asymmetric competition and resource partitioning can be respectively captured by the use of neighbourhood indices (NIh and NId) that include functional differences in the form of trait hierarchies (i.e. relative trait differences) or trait dissimilarities (i.e. absolute trait differences) between the focal tree and its neighbours. The expected effect of different types of neighbourhood interactions on individual tree growth (H1) and response to climate stress (H2), correspond to our hypotheses.

Neighbourhood effects on individual tree growth are the net outcome of simultaneous negative and positive interactions, which can be captured by different neighbourhood indices (Fig. 1) and whose relative importance may change when heat and drought stress occur (Grossiord, 2020). Negative neighbourhood effects can result from density dependent (i.e. neutral) interactions for shared resources (Jucker *et al.*, 2016; Pommerening & Sánchez Meador, 2018). While denser neighbourhoods can reinforce drought effects (Bottero *et al.*, 2017), for instance through increased consumption of water, they can simultaneously shelter trees from atmospheric climate extremes (Nemetschek *et al.*, 2024). Interactions may additionally be asymmetric, suggesting that differences in functional strategies between tree species can result into competitive hierarchies between neighbours (Canham *et al.*, 2004; Pommerening & Sánchez Meador, 2018). Water spender neigh-

bours that exert strong pressure on the common water resource may have greater negative impacts on drought stress experienced by water conservative trees than conservative species have on them. Conversely, positive neighbourhood effects may result from facilitation (Brooker *et al.*, 2007) or greater functional dissimilarity indicating resource partitioning (Pommerening & Sánchez Meador, 2018), which could alleviate climate stress experienced by individual trees. Previous work on the relative contributions of different neighbourhood interactions on tree growth, captured by different indices, showed a key role of traits related to space, light and nutrients use (Fortunel *et al.*, 2016; Kunstler *et al.*, 2016; Uriarte *et al.*, 2010). As these traits offer little insights on water-use strategies and responses to water limitations (Maréchaux *et al.*, 2019; Wagner *et al.*, 2014), traits related to water relations may offer additional insight into neighbourhood interactions for water and elucidate their role in shaping individual response to droughts (Brodribb, 2017; Grossiord, 2020).

In a highly diverse Amazonian forest, we investigated how species differences in traits pertaining to plant-water relations and carbon use drive interactions between neighbouring trees and modulate individual growth response to heat and drought stress. We used hierarchical Bayesian models to evaluate the separate and interactive effects of i) climate variables indicating heat, atmospheric and soil water drought stress and ii) neighbourhood indices capturing the effects of neighbourhood crowding, trait hierarchies and dissimilarities on individual tree growth. Our analyses leveraged trait and 30-year long census data for 89 species from 15 permanent plots, some of which were subjected to initial selective logging and thinning, leading to contrasting neighbourhood structure, composition and dynamics. This long-term census data and its high temporal resolution (biennial) provides a broad range of neighbourhood and climatic conditions (Fig. S1) needed to study neighbourhood effects on climate responses of individual tree growth. We hypothesised that:
(H1) An individuals' growth is lower when surrounded by more neighbours (higher density), by superior competitors (stronger trait hierarchy) and more similar neighbours (lower trait dissimilarity) (Table 1).
(H2) Neighbourhood is more likely to buffer negative climate effects when trait dissimilarity is high or when being composed of more water conservative species. Conversely, high densities of

water-spender and dehydration tolerant species are more likely to accentuate negative drought-related climate effects (Table 1).

Materials and Methods

Study site and inventory data

This study leverages 30 years of spatially-explicit inventory data from the CIRAD permanent forest plots of the Paracou research station (5°18'N, 52°53'W) in French Guiana. Paracou is a tropical lowland forest site with an annual precipitation of 3102 mm yr^{-1} and a pronounced 3-month dry season (<100 mm mo^{-1}) spanning from mid-August to mid-November, during which wood production is reduced, and at the end of which water becomes limiting. Additionally a shorter dry season can be observed in March (Aguilos *et al.*, 2019).

The plot network was established between 1984 and 1990 and consists of fifteen 6.25 ha forest plots, covering 93.75 ha of predominantly terra-firme forest. In 1987, nine plots were subjected to three intensities of silvicultural treatments including thinning, poison-girdling and selective logging. These treatments resulted in 12–56% loss of above-ground biomass (Gourlet-Fleury *et al.*, 2004), and led to contrasting community composition (Mirabel *et al.*, 2020) and neighbourhood densities (Nemetschek *et al.*, 2024) between plots and years. Since then, tree inventories took place every two years, during which the spatial location (precision 0.5 m), status (alive/dead) and circumference (precision 0.5 cm, from which we calculated DBH), of each tree $\geq$ 10 cm DBH (diameter at breast height, i.e. 1.3 m) was recorded (Derroire *et al.*, 2022b; Gourlet-Fleury *et al.*, 2004). More than 590 species and subspecies, from 227 genera and 63 families have been measured at the site (mean 142 species per hectare), with the dominant families being Fabaceae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae (Hérault *et al.*, 2011).

We calculated individual annualised absolute diameter growth rate (AGR, cm/yr) from DBH at the end *t* and the start *t-2* of 15 two-year census intervals between 1991 and 2021, excluding

aberrant and uncertain growth measurements (see Supplementary Methods S1 for details).

$$AGR_{i,s,t} = \frac{DBH_{i,s,t} - DBH_{i,s,t-2}}{2} \quad \text{(eqn 1)}$$

Although most trees at Paracou were botanically identified, some individuals (<10%) only received a vernacular name, mainly due to tree death before botanical identification could take place. To infer the most likely association between the botanical and vernacular name for a given individual, we used the vernabota R package (Derroire *et al.* 2022a, see Supplementary Methods S2 for details). While tree individuals with gapfilled species information were removed from the focal tree data, they were kept in the neighbourhood data (see section Neighbourhood indices).

Climate data

To study the separate and interactive effects of climate and neighbours, we extracted mean monthly averages of three climate variables from the high-resolution global TerraClimate data set (Abatzoglou *et al.*, 2018): maximum temperature (Tmax), vapour pressure deficit (VPD) and climatic water deficit (CWD), which have been shown to capture tropical tree responses to different aspects of climate stress (Bauman *et al.*, 2022a; Nemetschek *et al.*, 2024). Specifically, these climate indices respectively capture heat stress, atmospheric evaporative demands and soil water availability, the latter by relating precipitation to evapotranspiration. We expressed inter-annual variation in these indices as the mean of monthly climate anomalies over each of the two-year census intervals, as follows (CA_t, Fig. S1): For each climate index and month, we calculated their deviations from their respective 30-year monthly mean for the 1991-2021 period, before dividing them by their 30-year monthly standard deviation. We then averaged these standardised monthly climate anomalies over the 24 months prior to each census t (Bauman *et al.* 2022a; Nemetschek *et al.* 2024; Rifai *et al.* 2018, see Methods S3). Doing so allowed us to directly interpret climate induced growth variations as responses to higher climate stress than usual.

Trait data

To capture species water relations (Table 1), we measured leaf water potential at turgor loss point (π_{tlp}), leaf minimum conductance (g_{min}) and leaf saturated water content (LSWC) in the dry seasons of 2020 and 2021 (Nemetschek *et al.*, 2024). We selected target species according to their abundance to maximise neighbourhood coverage for our growth models. In addition, we combined our three water-related traits with data from previous field campaigns at Paracou (Levionnois *et al.*, 2021; Maréchaux *et al.*, 2015, 2019; Ziegler *et al.*, 2019). We further compiled data on bulk leaf carbon isotope composition ($\delta^{13}C$), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}) and wood specific gravity (WSG) from previous work conducted in French Guiana (Baraloto *et al.*, 2010; Fortunel *et al.*, 2012; Vleminckx *et al.*, 2021). We subsequently calculated species mean trait values from individual trait measurements. Our final trait dataset includes complete trait information on 89 species (from 71 genera and 34 families), that together represent 77% of all unique individual stems and 78% of growth measurements at Paracou. For more information on the different traits and data sources see Table 1 and Nemetschek *et al.* (2024).

Table **1.** Functional traits used in the study, and their functional significance. We additionally provide the sources from which data on each trait was compiled.

Organ	Trait	Abbreviation (Unit)	Function	Description	References	Data Source
Traits pertaining to plant water relations						
Leaf	Bulk leaf carbon stable isotope	$\delta^{13}C$ (‰)	Carbon-water use	High $\delta^{13}C$ translates into high intrinsic water-use efficiency (i.e. high photosynthetic rates relative to stomatal conductance) and therefore greater water conservation.	Farquhar et al. 1989, Cernusak et al. 2013, Scheidegger et al. 2000	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021
Leaf	Water potential at turgor loss point	π_{tlp} (MPa)	Drought tolerance or water conservation	Low π_{tlp} translates into a greater ability to tolerate dehydration thereby maintaining stomatal conductance, hydraulic conductance and photosynthetic gas exchange at lower soil water potential. Conversely, high (i.e. less negative) π_{tlp} indicates early stomatal closure during drought, which allows avoiding dehydration through water conservation.	Bartlett et al. 2012, Martin St-Paul et al. 2017	Maréchaux et al. 2015, Maréchaux et al. 2019, Nemetschek et al. 2024, Ziegler et al. 2019
Leaf	Minimum conductance	g_{min} (mmol m^{-2} s^{-1})	Water conservation	Low g_{min} translates into low residual water loss after stomatal closure through leaf cuticle and incompletely closed stomata, thereby avoiding dehydration through water conservation.	Blackman et al. 2019, Duursma et al. 2019, Machado et al. 2021	Levionnois et al. 2021, Nemetschek et al. 2024
Leaf	Leaf saturated water content	LSWC (%)	Water storage	High LSWC translates into leaf water reserves that may allow maintenance of leaf water potential when water supply becomes limited.	Blackman et al.2019, Gleason et al. 2014, Luo et al. 2021	Nemetschek et al. 2024
Traits pertaining to carbon use						
Leaf	Leaf area	LA (cm^2)	Light capture	Large leaves intercept more light, have thick leaf boundary layer that limit heat exchange with surrounding air, but also higher transpiration rates.	Wright et al. 2017	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021
Leaf	Specific leaf area	SLA (m^2 kg^{-1})	Resource capture and defense	High SLA reflects greater allocation of dry mass to light interception than physical resistance and leaf lifespan and indicates aquisitive carbon-use strategy.	Osnas et al. 2013, Wright et al. 2004	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021
Leaf	Leaf thickness	L_{thick} (mm)	Resource capture and defense	High L_{thick} reflects greater allocation of dry mass to structural support, physical resistance and leaf lifespan and indicates conservative carbon-use strategy.	Vile et al. 2005	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021
Leaf	Leaf toughness	L_{tough} (N)	Resource capture and defense	High L_{tough} reflects greater allocation of dry mass to structural support, physical resistance and leaf lifespan and indicates conservative carbon-use strategy.	Kitajima and Poorter 2010	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021
Wood	Stem wood specific gravity	WSG	Stem transport, structure and defense	High wood specific gravity reflects greater allocation of dry mass to mechanical strength and resistance to abiotic and biotic threats, and indicates conservative carbon-use strategy and slow growth.	Chave et al. 2009, Poorter et al. 2010,	Baraloto et al. 2010, Fortunel et al. 2012, Vleminckx et al. 2021

Neighbourhood indices

For each individual focal tree i at the start of the growth census interval $t-2$, we calculated three neighbourhood indices within a radius of 10 m around the focal tree (Fortunel *et al.*, 2018; Lasky *et al.*, 2014). To capture neighbourhood densities we calculated a neutral neighbourhood crowding index (NCI) as:

$$NCI_{i,t-2} = \sum_{\substack{j=1 \\ j \neq i}}^{J} \frac{DBH_{j,t-2}^2}{d_{i,j}} \qquad \text{(eqn 2)}$$

where J is the number of neighbours within the 10-m radius and the influence of a given neighbour j on the focal tree i is proportional to its basal area (DBH_j^2) and declines linearly with its distance (d_{ij}) from the focal tree i.

To respectively capture the effects of trait hierarchies and dissimilarities between the focal tree and its neighbours we calculated NIh and NId as the weighted average of trait hierarchies and dissimilarities between the focal tree and all its neighbours within the neighbourhood radius as:

$$NIh_{i,t-2} = \frac{1}{NCI_{i,t-2}} \times \left(\sum_{k=1}^{K} \lambda_{s,k} \sum_{\substack{j=1 \\ j \neq i}}^{J(k)} \frac{DBH_{j,t-2}^2}{d_{i,j}} \right) \qquad \text{(eqn 3)}$$

$$NId_{i,t-2} = \frac{1}{NCI_{i,t-2}} \times \left(\sum_{k=1}^{K} |\lambda_{s,k}| \sum_{\substack{j=1 \\ j \neq i}}^{J(k)} \frac{DBH_{j,t-2}^2}{d_{i,j}} \right) \qquad \text{(eqn 4)}$$

where trait hierarchies are relative trait differences ($\lambda_{s,k} = trait_s - trait_k$) and trait dissimilarities are absolute trait differences ($|\lambda_{s,k}| = |trait_s - trait_k|$) between the species s of focal tree i and the species k of its $J(k)$ neighbours j. $\lambda_{s,k}$ increasingly differs from 0 with increasing relative (hierarchical) and absolute (dissimilarities) trait differences (Lasky *et al.*, 2014). The contribution of trait differences ($\lambda_{s,k}$) between the focal tree and each neighbour j to NIh and NId is weighted by the squared diameter of j and its inverse distance d_{ij} to the focal tree i (i.e. its contribution

to the NCI). For a given focal tree, NIh therefore increases when the focal tree has a relatively higher trait value in comparison to its neighbour and decreases when the focal tree has a relatively lower trait value in comparison to its neighbour. NId increases with increasing absolute trait differences (dissimilarities) between the focal and its neighbour, and these two indices are not influenced by the density of neighbours (see Table S3).

The 89 species for which complete information for all nine traits was available constitute our focal species. As NIh and NId require trait information for all neighbours within the neighbourhood, we gapfilled missing trait information for all remaining species using the year and plot specific community weighted mean. To reduce the influence of missing species trait information on neighbourhood effect estimates, we only selected focal trees for which at least 75% of their NCI belonged to species with available trait information. For more detailed information on neighbourhood indices and subsetting of focal individuals see Methods S4.

Models

We evaluated the separate and interactive effects of climate anomalies and neighbourhood indices (NCI, NIh and NId) on individual absolute growth rates (AGR) using hierarchical Bayesian models. To manage model complexity, we fitted models separately for each combination of (i) trait hierarchies (NIh) and dissimilarities (NId), (ii) the three climate variables (Tmax, VPD and CWD) and (iii) the nine functional traits, resulting in a total of 54 models. The model hierarchy consists of a community-level regression and a species-level response. The community-level regression models AGR responses to covariates via hyperparameters (i.e. statistical distributions from which species-level intercepts and slope coefficients arose), whereas the species-level captures species deviations from the community average parameters.

To reduce the influence of outliers and heteroscedasticity of the growth data, and to represent the multiplicative effects of covariates, we modelled the natural logarithm of absolute growth rates $log(AGR)$ (Fortunel *et al.*, 2018; Hérault *et al.*, 2011; Kunstler *et al.*, 2016). As we assumed tree growth to have a non-linear relationship with DBH (Canham *et al.*, 2004), NCI (Fortunel *et al.*,

2016), NIh and NId, we log-transformed DBH and all three neighbourhood indices prior to standardisation (Fortunel *et al.*, 2018; Kunstler *et al.*, 2016). To allow for direct comparison of parameter estimates within and between models and ease the assignment of plausible weakly-informative prior to the parameters (McElreath, 2020), $log(AGR)$ and all covariates were standardised to mean zero and unit standard deviation, except for climate anomalies (Bauman *et al.*, 2022a; Nemetschek *et al.*, 2024). As our focal species cover a wide range of mean tree sizes, we standardised DBH to mean zero and unit standard deviation within species, to prevent confounding species differences in growth response to tree size with inter-specific variation in mean DBH (Fortunel *et al.*, 2018). For further details on variable transformation see Methods S5.

For each individual i of species s in plot p between censuses *t-2* and t, we modelled the logarithm of tree growth with a normal distribution:

$$\log(AGR_{i,s,t,p}) \sim \mathcal{N}(\mu_{i,s,t,p}, \sigma^2) \qquad \text{(eqn 5a)}$$

where the mean $\mu_{i,s,t,p}$ is a linear function of tree size at the beginning of the census interval ($DBH_{i,t\text{-}2}$), monthly climate anomalies averaged over the census interval (CA_t), neutral neighbourhood crowding index ($NCI_{i,t\text{-}2}$), one of the non-neutral neighbourhood index ($NI_{i,t\text{-}2}$) capturing either trait hierarchies ($NIh_{i,t\text{-}2}$) or trait dissimilarities ($NId_{i,t\text{-}2}$) at the beginning of the census interval, and their interactive effects with climate anomalies ($CA_t \times NCI_{i,t-2}$ and $CA_t \times NI_{i,t-2}$):

$$\begin{aligned}\mu_{i,s,t,p} = {} & \alpha_s + \beta_{1s} \times \log(DBH_{i,t-2}) + \beta_{2s} \times CA_t \\ & + \beta_{3s} \times \log(NCI_{i,t-2}) + \beta_{4s} \times \log(NI_{i,t-2}) \\ & + \beta_{5s} \times CA_t \times \log(NCI_{i,t-2}) + \beta_{6s} \times CA_t \times \log(NI_{i,t-2}) \\ & + \gamma_p + \epsilon_i\end{aligned} \qquad \text{(eqn 5b)}$$

α_s and β_{1-6s} are species-specific coefficients representing intrinsic AGR (α_s), and species responses

to tree size (β_{1s}), climate anomalies (β_{2s}), neighbourhood crowding (β_{3s}), hierarchical or dissimilarity neighbourhood index (β_{4s}) as well as interactive effect of climate anomalies with neighbourhood crowding index (β_{5s}), or with hierarchical or dissimilarity neighbourhood index (β_{6s}). We further allowed intercepts to vary by plots γ_p and individuals ϵ_i, to capture part of the unexplained growth variation related to plots and individuals (Bauman *et al.*, 2022a; Fortunel *et al.*, 2018).

Species intrinsic AGR α_s and AGR response to covariates β_{1-6s} for the s species were modelled using a multivariate normal distribution:

$$\begin{pmatrix} \alpha_s \\ \beta_{1s} \\ \vdots \\ \beta_{6s} \end{pmatrix} \sim MVNormal \left[\begin{pmatrix} \alpha \\ \beta_1 \\ \vdots \\ \beta_6 \end{pmatrix}, S \right] \quad \text{(eqn 5c)}$$

where α represents the community level intrinsic growth rate, β_{1-6} the overall effect of covariates on AGR across all species and S is a covariance matrix. Modelling all species-level parameters as a multivariate normal distribution allows sharing information across species, thus improving the fit for poorly represented species, while preventing overfitting (McElreath, 2020). For the full model equation and the specified weakly informative priors see Methods S6.

Models were fitted in the R environment (R Core Team, 2021; RStudio Team, 2020) on the Meso@LR HPC cluster using the package brms (Bürkner, 2017). Bayesian updating of parameters was performed via the No-U-Turn Sampler (NUTS) in Stan (Carpenter *et al.*, 2017) using CmdStanR (Stan Development Team, 2022). We used four chains and 3000 iterations (1500 warm up) per chain. Chains of all models mixed well and generally converged within 1500 iterations (Rhat between 1 and 1.05). Model parameter posteriors were summarised through their median and 90% highest posterior density interval (HPDI) using the packages tidyverse (Wickham *et al.*, 2019) and tidybayes (Kay, 2022). To assess the model goodness of fit, we calculated conditional and marginal R^2, which represent respectively the fraction of variance explained by the fixed and random terms and by the fixed terms only, using the bayes_R2() function of the brms package

(Bürkner, 2017). The function calculates a Bayesian version of R^2 for regression models (Gelman *et al.*, 2019). Our models had high a explanatory power, with a mean conditional R^2 of 61% and showed to be stable across climate-trait model combinations. For detailed information on conditional and marginal R^2 values for each model fit see Table S1 and for model stability see Methods S7.

Results

Tree growth response to neighbourhood indices

Individual tree growth strongly declined (negative β_3) with increasing NCI, while effect sizes were smaller for both NIh and NId (Fig. 2). Greater NIh can both increase (positive β_4) or reduce (negative β_4) tree growth, while increasing NId consistently increased (positive β_4) tree growth. More specifically, higher NIh in $\delta^{13}C$ and SLA increased growth, indicating that focal trees grew faster when their intrinsic water-use efficiency and specific leaf area was higher than those of their neighbours. On the other hand, growth declined with increasing NIh in π_{tlp}, g_{min}, LA, L_{thick}, L_{though} or WSG, indicating that focal trees grew slower when they had higher water potential at turgor loss point, higher minimum conductance, larger, thicker or tougher leaves as well as higher wood specific gravity than that of their neighbours. Lastly, higher NId in $\delta^{13}C$, π_{tlp}, LSWC, g_{min}, LA, SLA, L_{thick} and WSG positively influenced tree growth, indicating trees grew faster when their neighbours were more dissimilar in these trait values.

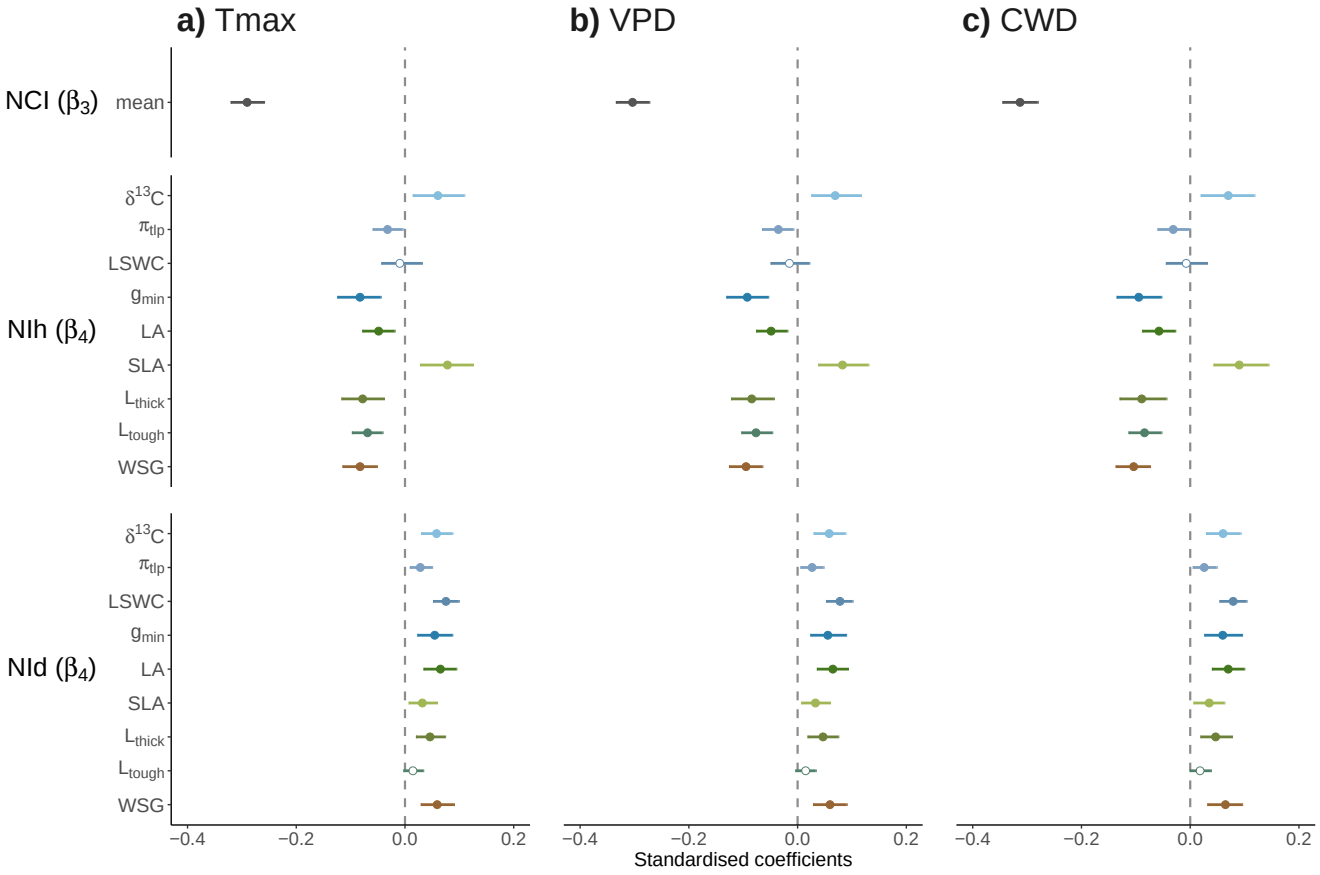

Figure **2.** Community-level effect of neutral neighbourhood crowding (NCI, β_3), hierarchical (NIh, β_4) and dissimilarity (NId, β_4) neighbourhood index on tree growth. Standardised coefficients from a) Tmax, b) VPD and c) CWD models are shown for NCI as mean estimates across the two NI and nine trait models (see Fig. S2 and S3 for separate estimates) and for NIh and NId separately for each of the nine trait models: carbon ($\delta^{13}C$) isotope composition, water potential at turgor loss point (π_{tlp}), leaf saturated water content (LSWC), minimum conductance (g_{min}), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}) and wood specific gravity (WSG). Circles show posterior medians of standardised coefficients, and lines indicate 90% HPDIs. Model covariates were considered to have a clear effect when the slope coefficients 90%-HPDIs did not encompass zero. Filled circles indicate clear negative and positive effects (i.e. slope coefficient 90% HPDI not encompassing zero) and empty circles indicate no clear effects. Positive β_{3-4} values indicate faster growth with increasing neighbourhood index, while negative β_{3-4} values indicate slower growth with increasing neighbourhood index (details in Table S2).

Tree growth response to interactive effects of climate anomalies and neighbourhood indices

Positive anomalies in maximum temperature (Tmax), vapour pressure deficit (VPD) and climatic water deficit (CWD) reduced tree growth (negative β_2). Moreover, higher NCI led to a clear buffering (positive β_5, Fig. 3) of negative effects of Tmax, while also showing a strong trend to

buffer negative effects of VPD and CWD. Only a few trait differences between the focal tree and its neighbours led to a clear modulation of growth through trait hierarchies (NIh) or dissimilarities (NId), and these effects depended on the climate variable. More specifically, negative effects of Tmax were reinforced (negative β_6) for trees with relatively higher $\delta^{13}C$ (higher NIh) than their neighbours and buffered (positive β_6) for trees with relatively higher π_{tlp} and g_{min} than their neighbourhood (higher NIh). Furthermore, negative effects of Tmax were reinforced (negative β_6) with increasing trait dissimilarities (higher NId) in LSWC but attenuated (positive β_6) for trees surrounded by more dissimilar neighbours regarding $\delta^{13}C$, L_{thick} and L_{though}. While increasing trait hierarchies in LA, L_{thick} and L_{though} reinforced the negative effects of VPD on tree growth (negative β_6), increasing trait hierarchies in π_{tlp} and greater dissimilarity (higher NId) in L_{though} led to significant buffering (positive β_6). Lastly, focal trees suffered lower growth declines (positive β_6) from higher CWD when having relatively higher LA than their neighbours (higher NIh) or having more dissimilar neighbours regarding π_{tlp} (higher NId). However, greater dissimilarities in $\delta^{13}C$ (higher NId) accentuated negative effects of CWD (negative β_6).

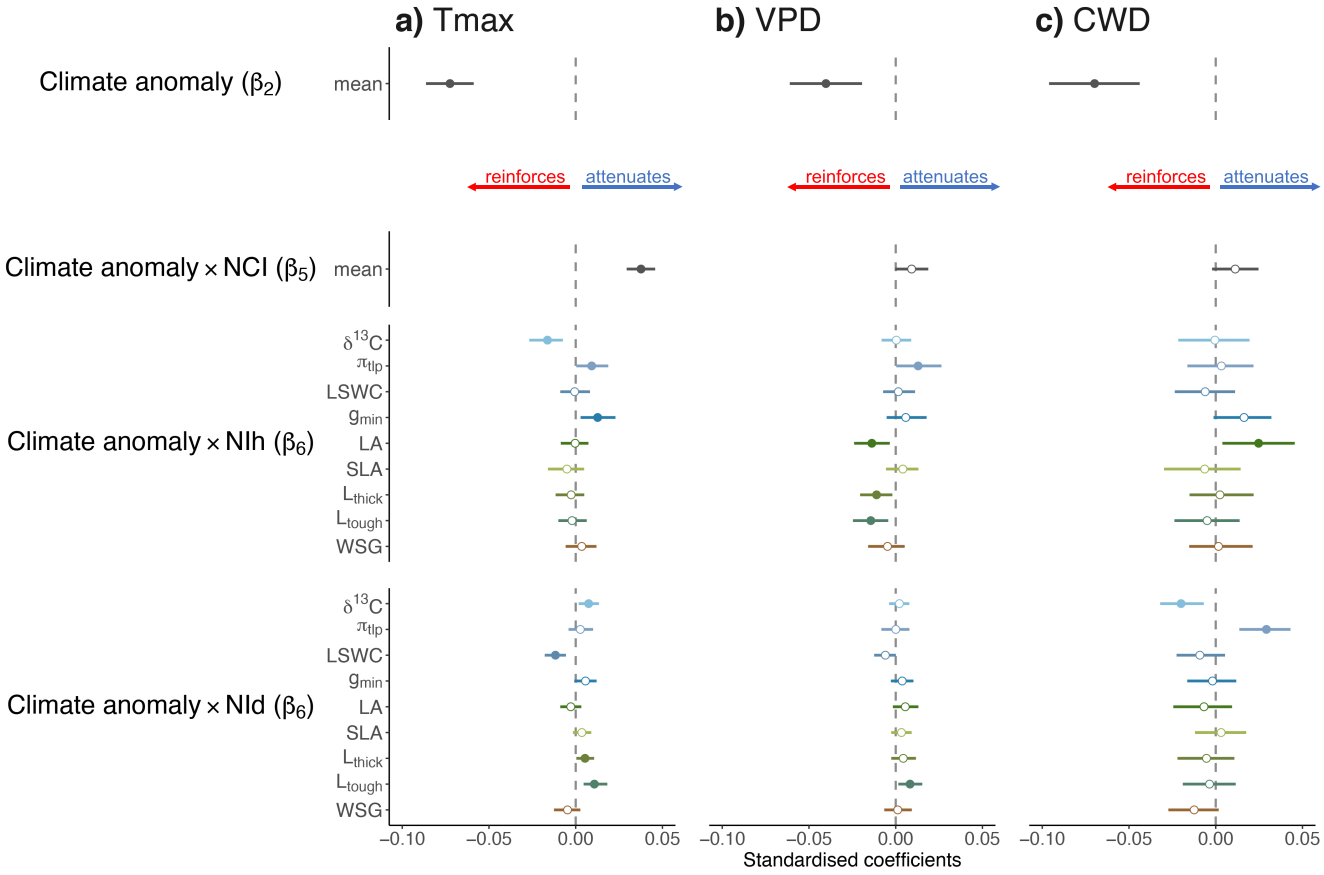

Figure **3.** Community-level effects of climate anomaly (β_2), and the interactions between climate anomaly and neutral neighbourhood crowding (Climate anomaly×NCI, β_5), hierarchical (Climate anomaly×NIh, β_6) and dissimilarity (Climate anomaly×NId, β_6) neighbourhood index on tree growth. Standardised coefficients from a) Tmax, b) VPD and c) CWD models are shown for climate anomalies and its interaction with NCI as mean estimates across the two NI and nine trait models (see Fig. S2 and S3 for separate estimates) and for the interaction between climate anomaly and NIh and NId separately for each of the nine trait models: carbon ($\delta^{13}C$) isotope composition, water potential at turgor loss point (π_{tlp}), leaf saturated water content (LSWC), minimum conductance (g_{min}), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}) and wood specific gravity (WSG). Circles show posterior medians of standardised coefficients, and lines indicate 90% HPDIs. Model covariates were considered to have a clear effect when the slope coefficients 90%-HPDIs did not encompass zero. Filled circles indicate clear negative and positive effects (i.e. slope coefficient 90%-HPDI not encompassing zero) and empty circles indicate no clear effects. Positive β_{5-6} values indicate a buffering effect of either NCI or NI, while negative β_{5-6} values indicate an accentuating effect of either NCI or NI (details in Table S2).

Discussion

Using 30 years of high temporal resolution census data in a highly diverse tropical forest, we studied how the neighbourhood context influences tree growth in 89 tree species and its responses to heat as well as atmospheric and soil water drought stress. Our results reveal that neutral and asymmetric

competition act in concert with resource partitioning to shape tropical tree growth (Fig. 1 and 2). We further show that the local neighbourhood context can both attenuate or reinforce the negative effects of heat (Tmax), atmospheric (VPD) and soil water drought (CWD) stress (Fig. 2, see Nemetschek *et al.* 2024 for detailed discussion on effects of climate anomalies). Our analyses integrate for the first time trait differences of a broad suite of functional traits pertaining to plant water-relations and carbon-use (Table 1). This provides novel insights on the potential mechanisms that underlie negative and positive neighbourhood interactions mediated by trait differences both in normal and anomalous climate years.

Neighbourhood crowding (NCI), capturing neighbourhood density, strongly reduced individual tree growth (Fig. 1) and had by far the largest effect size of any of the six tested model covariates. This suggests that competition for shared space and resources is a key driver of tree growth at Paracou (Nemetschek *et al.*, 2024), and that competitive interactions between neighbouring trees are foremost driven by their size and proximity in space (Laurans *et al.*, 2014; Moravie *et al.*, 1997). Previous studies have shown that neighbourhood taxonomic diversity can positively influence tree performance, likely through increased functional dissimilarity between neighbours promoting resource partitioning (Ammer, 2019; Forrester & Bauhus, 2016). Our results provide direct and strong support of this hypothesis as greater dissimilarity in all nine tested traits consistently stimulated individual tree growth at our site (Fig. 2. Greater dissimilarity between neighbours in traits related to carbon use and root strategies have also previously been shown to increase tropical and subtropical tree performance (Fortunel *et al.*, 2016; Huang *et al.*, 2022; Lasky *et al.*, 2014; Uriarte *et al.*, 2010). Here we show for the first time that this extends to traits pertaining to leaf water relations ($\delta^{13}C$, π_{tlp}, LSWC, g_{min}), uncovering the importance of complementary water-use and drought response strategies even in predominantly light- rather than water-limited tropical forests such as Paracou (Wagner *et al.*, 2016). This complementarity may be especially beneficial when a shift from light- to water-limitation can be observed (Meng *et al.*, 2022).

Providing further evidence for the importance of interactions for water at the neighbourhood scale, we show that greater trait hierarchies, which capture asymmetric neighbourhood interactions (Fig. 1), in water-related traits significantly influence tree growth (Fig. 2). Our results suggest that

a higher water use efficiency (higher $\delta^{13}C$), a greater ability to maintain physiological functioning under decreasing water availability (more negative π_{tlp}) and conserve water under drought stress (lower g_{min}) than its neighbours may provide a competitive advantage, as reflected by faster growth. Contrasting to our findings for water-related traits and previous research (Fortunel *et al.*, 2016; Kunstler *et al.*, 2016), greater conservatism in carbon use relative to neighbours (lower SLA and greater L_{thick}, L_{tough} and WSG) was consistently associated to reduced tree growth. This highlights that greater resource conservatism in comparison to neighbours does not always result in a competitive advantage in tropical forests. Having more conservative carbon-use strategies than one's neighbours implies being surrounded by more resource acquisitive neighbours that may faster deplete common resources (Garbowski *et al.*, 2020; Goldberg, 1990). Specifically, faster growth at the expense of less mechanically resistant leaf and wood tissue (Chave *et al.*, 2009; Reich, 2014) promotes fast colonisation of forest gaps both vertically and horizontally (Westoby *et al.*, 2002), which constitutes a strong competitive advantage in disturbed plots making up 51% of growth observations at Paracou.

Beside its importance in shaping tree growth in normal years, our results clearly show that the neighbourhood context has the potential to modulate individual growth responses to climate stress (Fig. 3). In line with our previous study (Nemetschek *et al.*, 2024), we found that denser neighbourhoods consistently attenuate negative climate effects on tree growth. Denser neighbourhoods can physically shelter trees from extreme atmospheric climate stress, thereby improving local microclimatic conditions (De Frenne *et al.*, 2019; Tymen *et al.*, 2017; Wright, 2024). Simultaneously, neighbourhood taxonomic diversity can influence growth responses to drought (Grossiord, 2020). If resource partitioning is a key driver of positive diversity effects on drought resistance, their magnitude should depend on the functional identity of focal trees (Fichtner *et al.*, 2020), that of their neighbours and ultimately on their functional differences. Here we showed that greater trait dissimilarities can indeed increase individual growth resistance to climate stress. However, this effect can differ across traits and climate variables. Greater dissimilarities in leaf economics traits tended to buffer negative effects of the atmospheric climate variables Tmax (for L_{thick} and L_{tough}) and VPD (for L_{thick}). Increased complementarity in leaf morphology can indicate greater canopy

space filling (Forrester & Bauhus 2016, but see Hildebrand *et al.* 2021), which likely increases thermal insulation (De Frenne *et al.*, 2019; Zhang *et al.*, 2022). Conversely, greater dissimilarities in tlp mitigated negative effects of soil water stress (CWD). π_{tlp} is a key drought tolerance trait (Bartlett *et al.*, 2012) and a strong predictor of leaf water potential at stomatal closure (Martin-StPaul *et al.*, 2017; Rodriguez-Dominguez *et al.*, 2016). In line with our findings, complementarity in stomatal regulation and drought response strategies have previously been suggested to reduce plant water stress via its positive effect on local soil moisture status (Grossiord, 2020; Moreno *et al.*, 2023). In contrast to our expectations, we showed that greater trait dissimilarities also hold the potential to reinforce climate stress depending on the climatic stressors. For instance, complementarity in water-use efficiency ($\delta^{13}C$), which increased tree growth in normal years, attenuated negative effects of heat stress (Tmax), but reinforced negative effects of soil water stress (CWD). This suggests that rather than greater dissimilarity in certain traits capturing water-use strategies, greater overall water conservation at the neighbourhood scale may be beneficial under water limited conditions.

In line with this assumption, our results indicate that the competitive advantage of water-conservative species observed in normal years decreases in extreme climate years, as the negative effect of a higher consumption of water by the neighbourhood becomes more important (Fig. 2 and 3). For instance, greater water use efficiency (higher $\delta^{13}C$) relative to neighbours benefited individual tree growth in normal years, but reinforced negative effects of temperature stress (Tmax). Higher temperatures can lead to increased evapotranspiration, hence greater abundances of relatively less water conservative neighbours likely exert greater pressure on local soil water resources when temperature stress occurs (Grossiord *et al.*, 2014; Mas *et al.*, 2024). Conversely, greater water spenders relative to their neighbours tended to be more buffered: trees with higher residual water loss (g_{min}) or larger LA relative to their neighbours grew slower in normal years but suffered less from negative effects of either temperature (Tmax) or soil water (CWD) stress. Larger leaves require more cooling through (higher) transpiration rates, which necessitates greater water supply per unit leaf area (Wright *et al.*, 2017). Our results therefore provide strong evidence for the positive effect of water conservative species on local soil water availability during drought and heat waves, which

may particularly benefit water spender species (Mas *et al.*, 2024; Moreno *et al.*, 2023). These findings can also provide mechanistic insights to why species with low drought tolerance profit most from neighbourhood diversity during drought, as shown by Fichtner *et al.* 2020. Conversely our results indicate that water spender tree neighbours decrease water resources to the detriment of the focal tree (Garbowski *et al.*, 2020; Goldberg, 1990), increasing the climate stress experienced particularly for water conservative species.

As forest ecosystems are increasingly likely to experience environmental conditions beyond their normal range, understanding if currently observed biotic interactions will hold in a changing climate is crucial (Grossiord *et al.*, 2019). By considering neighbourhood differences in water-related traits in addition to carbon-related ones, our study shows that the consistent positive effect of resource partitioning observed under normal conditions becomes more complex in climatically stressful years. Similarly, trees profit from greater conservatism in water use in normal years, but as climate stress increases, become increasingly affected by their neighbours' overall water consumption. Our findings suggest that climate-change adapted forest management should carefully consider species' water-use strategies and their interactions (Forrester *et al.*, 2016). We also stress the importance of moving beyond the taxonomic diversity lens to understand how different types of neighbourhood interactions affect tree performance in these new conditions. This provides a promising way forward to assess the productivity and resilience of entire forest ecosystems under climate change.

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List of Supporting Information

In file SupportingInformation_1.pdf

Figure S1. Adapted figure from Nemetschek et al. (2024): Mean standardised climate anomalies at Paracou for the two-year census intervals over the study period.

Figure S2. Standardised regression coefficients of community level parameter estimates from NIh models.

Figure S3. Standardised regression coefficients of community level parameter estimates from NId models.

Methods S1. Corrections of tree inventory data.

Methods S2. Gapfilling of missing species information.

Methods S3. Calculation of climate anomalies.

Methods S4. Additional information on neighbourhood indices.

Methods S5. Transformation of response variable and model covariates.

Methods S6. Full model equation.

Methods S7. Information on model stability.

In file SupportingInformation_2.xlsx

Table S1. Conditional and marginal R2 estimates models.

Table S2. Standardised regression coefficients of community level parameters and group-level sigmas.

Table S3. Pairwise Pearson correlation coefficients between neighbourhood indices.

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