

Love thy neighbour? Tropical tree growth and its response to climate anomalies is mediated by neighbourhood hierarchy and dissimilarity in carbon and water related traits.

Daniela Nemetschek¹, Claire Fortunel², Eric Marcon³, Johanna Auer⁴, Vincyane Badouard³, Christopher Baraloto⁵, Marion Boisseaux⁶, Damien Bonal⁷, Sabrina Coste⁶, Elia Dardevette³, Patrick Heuret³, Peter Hietz⁸, Sebastien Levionnois³, Isabelle Maréchaux³, Clément Stahl⁶, Jason Vleminckx⁹, Wolfgang Wanek⁴, Camille Ziegler⁶, and Geraldine Derroire¹⁰

¹University of Bristol

²Botanique et Modélisation de l'Architecture des Plantes et des Végétations

³Botanique et Modélisation de l'Architecture des Plantes et des Végétations

⁴University of Vienna

⁵Florida International University

⁶ECOFOG

⁷Université de Lorraine

⁸University of Natural Resources and Life Sciences Vienna

⁹Universite Libre de Bruxelles

¹⁰CIRAD Departement Environnements et Societes

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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 highlighting the importance of density and trait-mediated neighbourhood interactions, our study offers a way towards improving predictions of forest response to climate change.

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Daniela Nemetschek^{1,2,3}, Claire Fortunel¹, Eric Marcon^{1,2}, Johanna Auer⁴, Vinciane Badouard^{1,2}, Christopher Baraloto^{2,5}, Marion Boisseaux², Damien Bonal⁶, Sabrina Coste², Elia Dardevet¹, Patrick Heuret^{1,2}, Peter Hietz⁷, Sébastien Levionnois^{1,2}, Isabelle Maréchaux¹, Clément Stahl², Jason Vleminckx⁸, Wolfgang Wanek³, Camille Ziegler^{2,6}, and Géraldine Derroire⁹

¹UMR AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

²UMR EcoFoG (AgroParistech, CIRAD, CNRS, INRAE, Université des Antilles, Université de la Guyane), Kourou, France

³School of Biological Sciences, University of Bristol, Bristol, UK

⁴Center of Microbiology and Environmental Systems Science, University of Vienna, Vienna, Austria

⁵Institute of Environment, Department of Biological Sciences, Florida International University, Miami, FL, USA

⁶INRAE, Université de Lorraine, AgroParisTech, UMR SILVA, Nancy, France

⁷Institute of Botany, University of Natural Resources and Life Sciences, Vienna, Austria

⁸Université Libre de Bruxelles, Brussels, Belgium

⁹Cirad, UMR EcoFoG (AgroParistech, CNRS, INRAE, Université des Antilles, Université de la Guyane), France

Statement of authorship:

DN, GD, CF and EM designed the study. DN, MB, JA, VB, CB, QLB, DBo, SC, ED, CF, PH, SL, IM, CS, JV, WW and CZ collected or contributed trait data. DN formatted and vetted the plot census, climate and functional trait data, with help from GD, CF, EM and MB. DN, GD, CF and EM designed the tree growth models. DN performed the analyses, with help from GD, CF and EM. DN and GD led the interpretation of the results, and DN wrote the first draft, with frequent discussions with GD and inputs from CF and EM. All authors contributed substantially to revisions and gave final approval for publication.

Authors email addresses:

Daniela Nemetschek, daniela.nemetschek@gmail.com

Claire Fortunel, claire.fortunel@ird.fr

Eric Marcon, eric.marcon@agroparistech.fr

Johanna Auer, johanna-auer@live.de

Vincyane Badouard, vincyane.badouard@gmail.com

Christopher Baraloto, cbaralot@fiu.edu

Marion Boisseaux, marionboisseaux@gmail.com

Damien Bonal, damien.bonal@inrae.fr

Sabrina Coste, sabrina.coste@univ-guyane.fr

Elia Dardevet, eliadardevette@gmail.com

Patrick Heuret, Patrick.Heuret@inrae.fr

Peter Hietz, peter.hietz@boku.ac.at

Sébastien Levionnois, sebastien.levionnois.pro@gmail.com

Isabelle Maréchaux, isabelle.marechaux@inrae.fr

Clément Stahl, clement.stahl@inrae.fr

Jason Vleminckx, jasvix86@gmail.com

Wolfgang Wanek, wolfgang.wanek@univie.ac.at

Camille Ziegler, camille.ziegler9@gmail.com

Géraldine Derroire, geraldine.derroire@cirad.fr

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To whom correspondence should be addressed:

Daniela Nemetschek

daniela.nemetschek@gmail.com, danielakrebber@gmail.com

+43 6603885176; +44 7508371490

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1 **Abstract**

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3 positive to negative, suggesting a key role for complex interactions among neighbouring trees.
4 To elucidate how neutral interactions, hierarchical competition and resource partitioning between
5 neighbours shape tree growth and climate response in a highly diverse Amazonian forest, we com-
6 bined 30 years of tree censuses with measurements of water and carbon related traits. We modelled
7 individual tree growth response to climate and neighbourhood to disentangle the relative effect
8 of neighbourhood densities, trait hierarchies and dissimilarities. While neighbourhood densities
9 consistently decreased tree growth, trait dissimilarity increased it, and both influenced climate
10 response. Greater water conservatism provided a competitive advantage to focal trees in normal
11 years, but water spender neighbours reduced this effect in dry years. By underlining the impor-
12 tance of density and trait-mediated neighbourhood interactions, our study offers a way towards
13 improving predictions of forest response to climate change.

14 Introduction

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

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

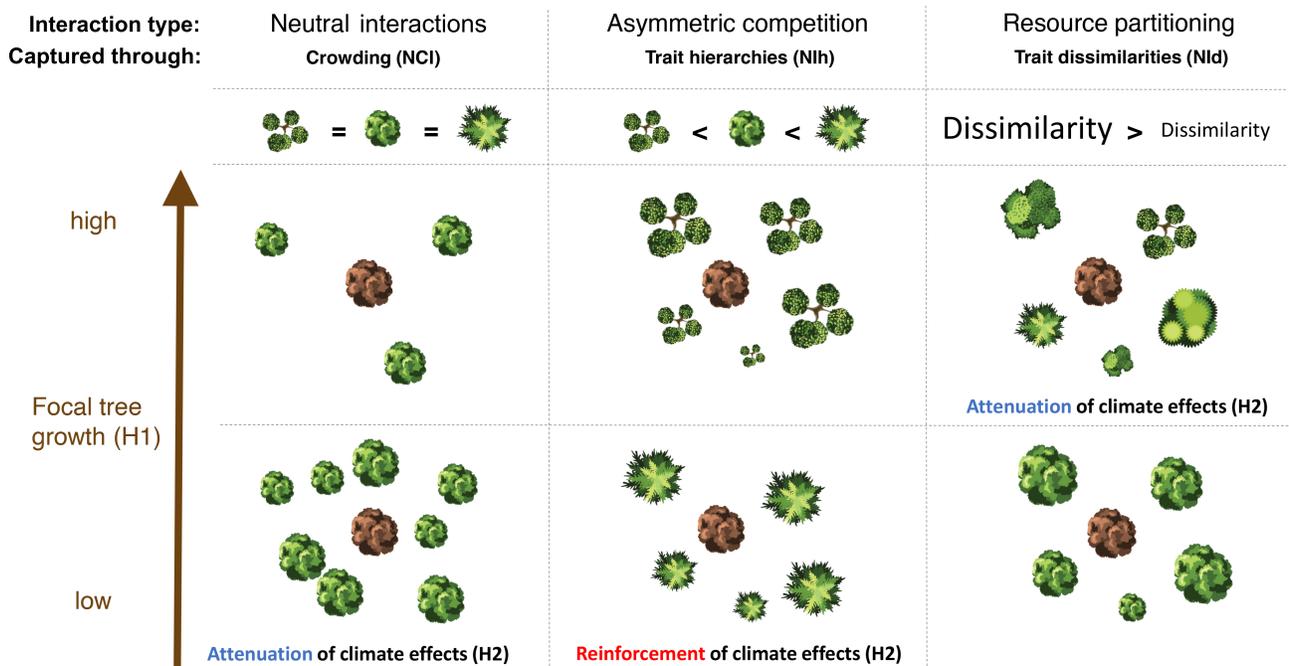


Figure 1. Conceptual illustration of different types of neighbourhood interactions, including neutral interactions, asymmetric competition and resource partitioning between a focal tree (brown) and its neighbouring trees (green). Neutral interactions can be captured by neighbourhood crowding indices (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 (NI_h and NI_d) 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.

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

50 hours that exert strong pressure on the common water resource may have greater negative impacts
51 on drought stress experienced by water conservative trees than conservative species have on them.
52 Conversely, positive neighbourhood effects may result from facilitation (Brooker *et al.*, 2007) or
53 greater functional dissimilarity indicating resource partitioning (Pommerening & Sánchez Meador,
54 2018), which could alleviate climate stress experienced by individual trees. Previous work on the
55 relative contributions of different neighbourhood interactions on tree growth, captured by differ-
56 ent indices, showed a key role of traits related to space, light and nutrients use (Fortunel *et al.*,
57 2016; Kunstler *et al.*, 2016; Uriarte *et al.*, 2010). As these traits offer little insights on water-use
58 strategies and responses to water limitations (Maréchaux *et al.*, 2019; Wagner *et al.*, 2014), traits
59 related to water relations may offer additional insight into neighbourhood interactions for water
60 and elucidate their role in shaping individual response to droughts (Brodribb, 2017; Grossiord,
61 2020).

62 In a highly diverse Amazonian forest, we investigated how species differences in traits pertaining to
63 plant-water relations and carbon use drive interactions between neighbouring trees and modulate
64 individual growth response to heat and drought stress. We used hierarchical Bayesian models to
65 evaluate the separate and interactive effects of i) climate variables indicating heat, atmospheric
66 and soil water drought stress and ii) neighbourhood indices capturing the effects of neighbourhood
67 crowding, trait hierarchies and dissimilarities on individual tree growth. Our analyses leveraged
68 trait and 30-year long census data for 89 species from 15 permanent plots, some of which were
69 subjected to initial selective logging and thinning, leading to contrasting neighbourhood structure,
70 composition and dynamics. This long-term census data and its high temporal resolution (bien-
71 nial) provides a broad range of neighbourhood and climatic conditions (Fig. S1) needed to study
72 neighbourhood effects on climate responses of individual tree growth. We hypothesised that:

73 (H1) An individuals' growth is lower when surrounded by more neighbours (higher density), by
74 superior competitors (stronger trait hierarchy) and more similar neighbours (lower trait dissimi-
75 larity) (Table 1).

76 (H2) Neighbourhood is more likely to buffer negative climate effects when trait dissimilarity is
77 high or when being composed of more water conservative species. Conversely, high densities of

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

80

81 **Materials and Methods**

82 **Study site and inventory data**

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

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

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

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

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

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

110 Climate data

111 To study the separate and interactive effects of climate and neighbours, we extracted mean monthly
112 averages of three climate variables from the high-resolution global TerraClimate data set (Abat-
113 zoglou *et al.*, 2018): maximum temperature (Tmax), vapour pressure deficit (VPD) and climatic
114 water deficit (CWD), which have been shown to capture tropical tree responses to different aspects
115 of climate stress (Bauman *et al.*, 2022a; Nemetschek *et al.*, 2024). Specifically, these climate indices
116 respectively capture heat stress, atmospheric evaporative demands and soil water availability, the
117 latter by relating precipitation to evapotranspiration. We expressed inter-annual variation in these
118 indices as the mean of monthly climate anomalies over each of the two-year census intervals, as fol-
119 lows (CA_t , Fig. S1): For each climate index and month, we calculated their deviations from their
120 respective 30-year monthly mean for the 1991-2021 period, before dividing them by their 30-year
121 monthly standard deviation. We then averaged these standardised monthly climate anomalies over
122 the 24 months prior to each census t (Bauman *et al.* 2022a; Nemetschek *et al.* 2024; Rifai *et al.*
123 2018, see Methods S3). Doing so allowed us to directly interpret climate induced growth variations
124 as responses to higher climate stress than usual.

125 Trait data

126 To capture species water relations (Table 1), we measured leaf water potential at turgor loss point
127 (π_{tlp}), leaf minimum conductance (g_{min}) and leaf saturated water content (LSWC) in the dry
128 seasons of 2020 and 2021 (Nemetschek *et al.*, 2024). We selected target species according to their
129 abundance to maximise neighbourhood coverage for our growth models. In addition, we combined
130 our three water-related traits with data from previous field campaigns at Paracou (Levionnois *et al.*,
131 2021; Maréchaux *et al.*, 2015, 2019; Ziegler *et al.*, 2019). We further compiled data on bulk leaf
132 carbon isotope composition ($\delta^{13}\text{C}$), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}),
133 leaf toughness (L_{tough}) and wood specific gravity (WSG) from previous work conducted in French
134 Guiana (Baraloto *et al.*, 2010; Fortunel *et al.*, 2012; Vleminckx *et al.*, 2021). We subsequently
135 calculated species mean trait values from individual trait measurements. Our final trait dataset
136 includes complete trait information on 89 species (from 71 genera and 34 families), that together
137 represent 77% of all unique individual stems and 78% of growth measurements at Paracou. For
138 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
<u>Traits pertaining to plant water relations</u>						
Leaf	Bulk leaf carbon stable isotope	$\delta^{13}\text{C}$ (‰)	Carbon-water use	High $\delta^{13}\text{C}$ 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_{tip} (MPa)	Drought tolerance or water conservation	Low π_{tip} 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_{tip} 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
<u>Traits pertaining to carbon use</u>						
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 acquisitive 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

139 **Neighbourhood indices**

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

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

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

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

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

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

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

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

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

168 Models

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

178 To reduce the influence of outliers and heteroscedasticity of the growth data, and to represent the
179 multiplicative effects of covariates, we modelled the natural logarithm of absolute growth rates
180 $\log(\text{AGR})$ (Fortunel *et al.*, 2018; Hérault *et al.*, 2011; Kunstler *et al.*, 2016). As we assumed tree
181 growth to have a non-linear relationship with DBH (Canham *et al.*, 2004), *NCI* (Fortunel *et al.*,

182 2016), *NIh* and *NId*, we log-transformed DBH and all three neighbourhood indices prior to stan-
 183 dardisation (Fortunel *et al.*, 2018; Kunstler *et al.*, 2016). To allow for direct comparison of param-
 184 eter estimates within and between models and ease the assignment of plausible weakly-informative
 185 prior to the parameters (McElreath, 2020), $\log(AGR)$ and all covariates were standardised to mean
 186 zero and unit standard deviation, except for climate anomalies (Bauman *et al.*, 2022a; Nemetschek
 187 *et al.*, 2024). As our focal species cover a wide range of mean tree sizes, we standardised DBH to
 188 mean zero and unit standard deviation within species, to prevent confounding species differences
 189 in growth response to tree size with inter-specific variation in mean DBH (Fortunel *et al.*, 2018).
 190 For further details on variable transformation see Methods S5.

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

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

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

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

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

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

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

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

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

211 Models were fitted in the R environment (R Core Team, 2021; RStudio Team, 2020) on the
 212 Meso@LR HPC cluster using the package brms (Bürkner, 2017). Bayesian updating of param-
 213 eters was performed via the No-U-Turn Sampler (NUTS) in Stan (Carpenter *et al.*, 2017) using
 214 CmdStanR (Stan Development Team, 2022). We used four chains and 3000 iterations (1500 warm
 215 up) per chain. Chains of all models mixed well and generally converged within 1500 iterations
 216 (Rhat between 1 and 1.05). Model parameter posteriors were summarised through their median
 217 and 90% highest posterior density interval (HPDI) using the packages tidyverse (Wickham *et al.*,
 218 2019) and tidybayes (Kay, 2022). To assess the model goodness of fit, we calculated conditional
 219 and marginal R^2 , which represent respectively the fraction of variance explained by the fixed and
 220 random terms and by the fixed terms only, using the bayes_R2() function of the brms package

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

226 Results

227 Tree growth response to neighbourhood indices

228 Individual tree growth strongly declined (negative β_3) with increasing NCI , while effect sizes were
229 smaller for both NIh and NId (Fig. 2). Greater NIh can both increase (positive β_4) or reduce
230 (negative β_4) tree growth, while increasing NId consistently increased (positive β_4) tree growth.
231 More specifically, higher NIh in $\delta^{13}C$ and SLA increased growth, indicating that focal trees grew
232 faster when their intrinsic water-use efficiency and specific leaf area was higher than those of their
233 neighbours. On the other hand, growth declined with increasing NIh in π_{tlp} , g_{min} , LA, L_{thick} ,
234 $L_{thorough}$ or WSG, indicating that focal trees grew slower when they had higher water potential at
235 turgor loss point, higher minimum conductance, larger, thicker or tougher leaves as well as higher
236 wood specific gravity than that of their neighbours. Lastly, higher NId in $\delta^{13}C$, π_{tlp} , LSWC, g_{min} ,
237 LA, SLA, L_{thick} and WSG positively influenced tree growth, indicating trees grew faster when their
238 neighbours were more dissimilar in these trait values.

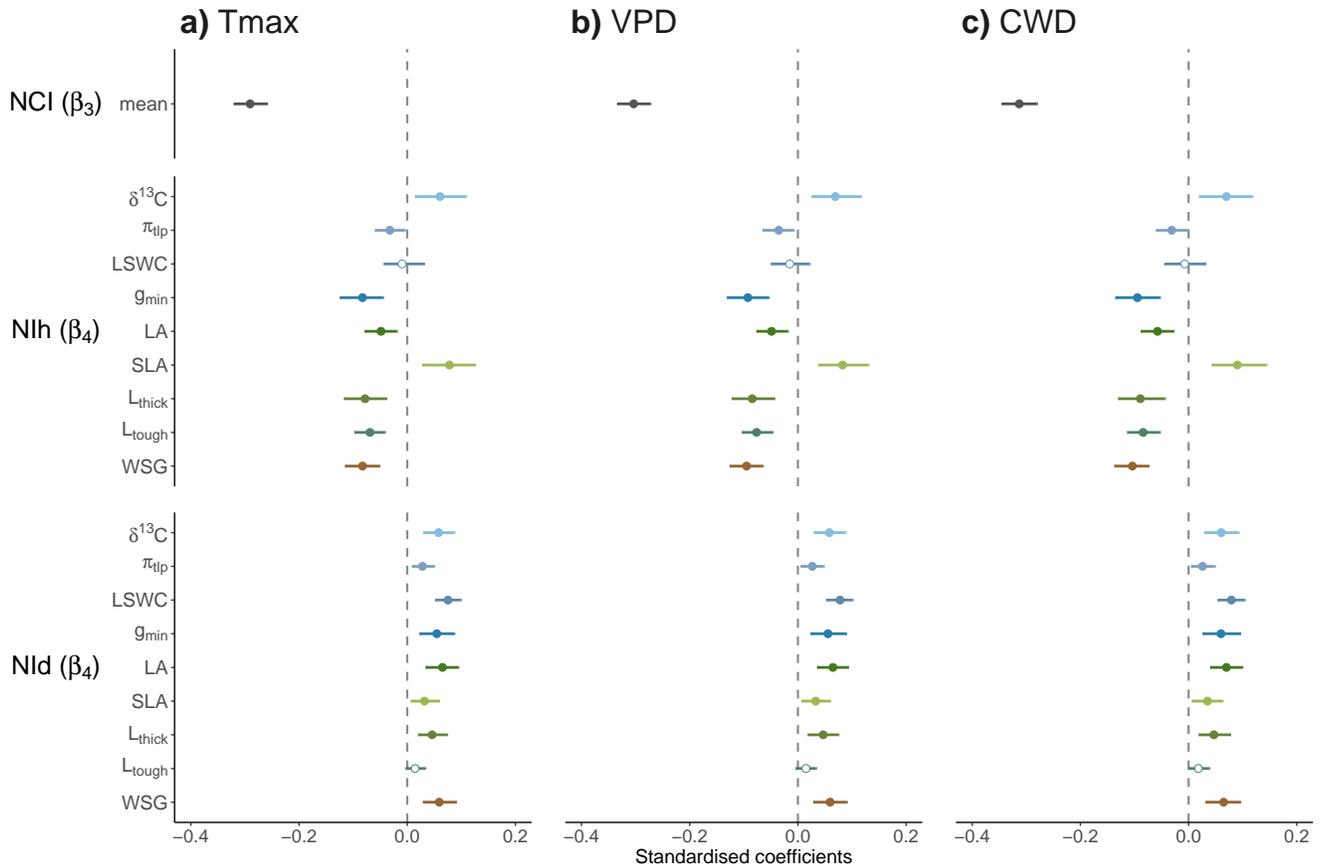


Figure 2. Community-level effect of neutral neighbourhood crowding (NCI, β_3), hierarchical (NIh, β_4) and dissimilarity (NId, β_4) neighbourhood index on tree growth. Standardised coefficients from a) Tmax, b) VPD and c) CWD models are shown for NCI as mean estimates across the two NI and nine trait models (see Fig. S2 and S3 for separate estimates) and for NIh and NId separately for each of the nine trait models: carbon ($\delta^{13}\text{C}$) 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_{tough}) 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).

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

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

244 buffer negative effects of VPD and CWD. Only a few trait differences between the focal tree and its
245 neighbours led to a clear modulation of growth through trait hierarchies (*NTh*) or dissimilarities
246 (*NId*), and these effects depended on the climate variable. More specifically, negative effects
247 of Tmax were reinforced (negative β_6) for trees with relatively higher $\delta^{13}\text{C}$ (higher *NTh*) than
248 their neighbours and buffered (positive β_6) for trees with relatively higher π_{tlp} and g_{min} than their
249 neighbourhood (higher *NTh*). Furthermore, negative effects of Tmax were reinforced (negative β_6)
250 with increasing trait dissimilarities (higher *NId*) in LSWC but attenuated (positive β_6) for trees
251 surrounded by more dissimilar neighbours regarding $\delta^{13}\text{C}$, L_{thick} and L_{through} . While increasing
252 trait hierarchies in LA, L_{thick} and L_{through} reinforced the negative effects of VPD on tree growth
253 (negative β_6), increasing trait hierarchies in π_{tlp} and greater dissimilarity (higher *NId*) in L_{through}
254 led to significant buffering (positive β_6). Lastly, focal trees suffered lower growth declines (positive
255 β_6) from higher CWD when having relatively higher LA than their neighbours (higher *NTh*) or
256 having more dissimilar neighbours regarding π_{tlp} (higher *NId*). However, greater dissimilarities in
257 $\delta^{13}\text{C}$ (higher *NId*) accentuated negative effects of CWD (negative β_6).

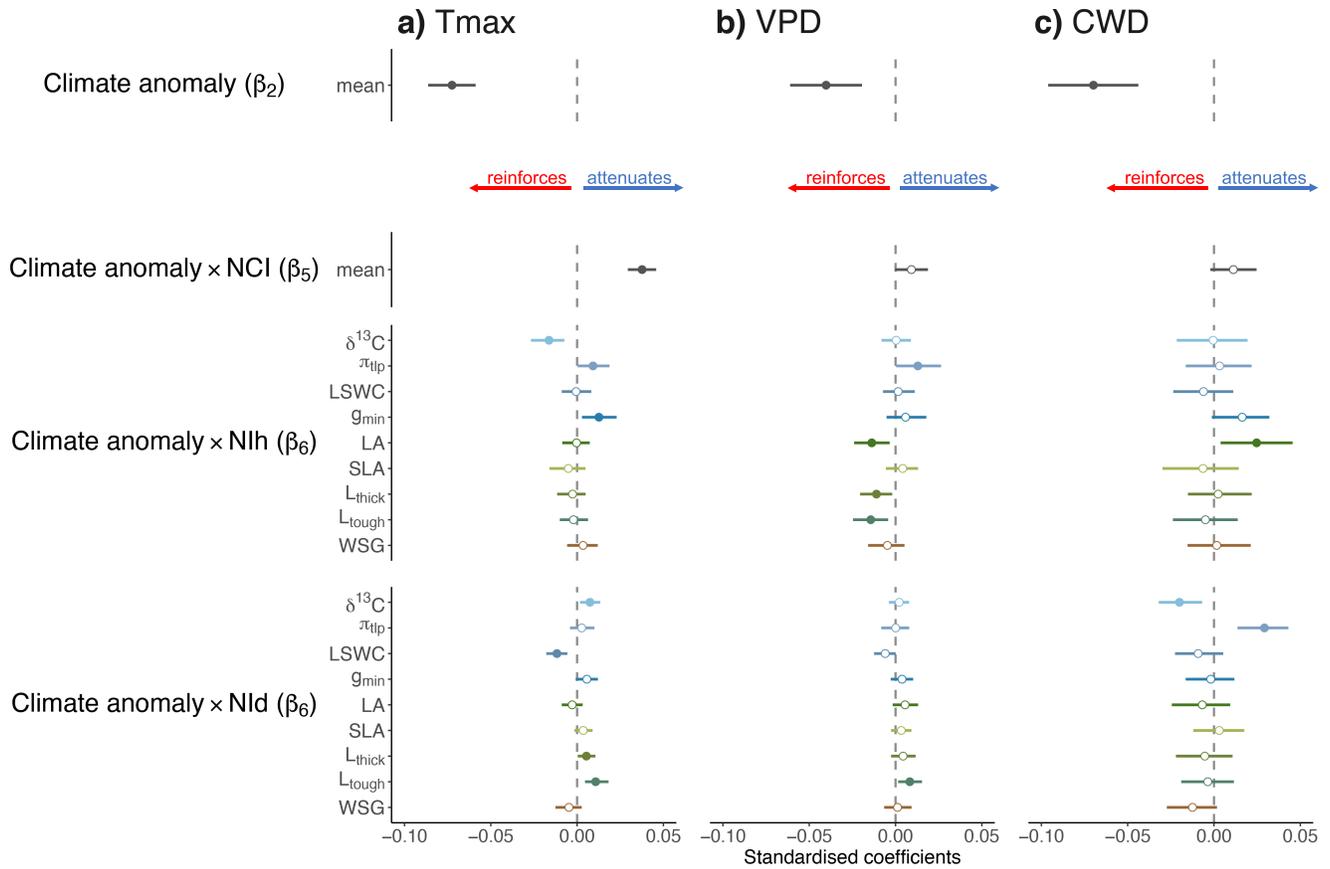


Figure 3. Community-level effects of climate anomaly (β_2), and the interactions between climate anomaly and neutral neighbourhood crowding (Climate anomaly \times NCI, β_5), hierarchical (Climate anomaly \times NIh, β_6) and dissimilarity (Climate anomaly \times NId, β_6) neighbourhood index on tree 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 ($\delta^{13}\text{C}$) 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_{tough}) 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).

258 Discussion

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

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

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

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

290 a higher water use efficiency (higher $\delta^{13}\text{C}$), a greater ability to maintain physiological function-
291 ing under decreasing water availability (more negative π_{tlp}) and conserve water under drought
292 stress (lower g_{min}) than its neighbours may provide a competitive advantage, as reflected by faster
293 growth. Contrasting to our findings for water-related traits and previous research (Fortunel *et al.*,
294 2016; Kunstler *et al.*, 2016), greater conservatism in carbon use relative to neighbours (lower SLA
295 and greater L_{thick} , L_{tough} and WSG) was consistently associated to reduced tree growth. This high-
296 lights that greater resource conservatism in comparison to neighbours does not always result in
297 a competitive advantage in tropical forests. Having more conservative carbon-use strategies than
298 one's neighbours implies being surrounded by more resource acquisitive neighbours that may faster
299 deplete common resources (Garbowski *et al.*, 2020; Goldberg, 1990). Specifically, faster growth at
300 the expense of less mechanically resistant leaf and wood tissue (Chave *et al.*, 2009; Reich, 2014)
301 promotes fast colonisation of forest gaps both vertically and horizontally (Westoby *et al.*, 2002),
302 which constitutes a strong competitive advantage in disturbed plots making up 51% of growth
303 observations at Paracou.

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

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

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

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

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

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380 **List of Supporting Information**

381 In file SupportingInformation_1.pdf

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

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

386 **Figure S3.** Standardised regression coefficients of community level parameter estimates from NIid
387 models.

388 **Methods S1.** Corrections of tree inventory data.

389 **Methods S2.** Gapfilling of missing species information.

390 **Methods S3.** Calculation of climate anomalies.

391 **Methods S4.** Additional information on neighbourhood indices.

392 **Methods S5.** Transformation of response variable and model covariates.

393 **Methods S6.** Full model equation.

394 **Methods S7.** Information on model stability.

395

396 In file SupportingInformation_2.xlsx

397 **Table S1.** Conditional and marginal R² estimates models.

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

400 **Table S3.** Pairwise Pearson correlation coefficients between neighbourhood indices.

401

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