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1 **Climate anomalies and neighbourhood crowding interact**
2 **in shaping tree growth in old-growth and**
3 **selectively-logged tropical forests**

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28 **Abstract**

29 1. Climate extremes and biotic interactions at the neighbourhood scale affect tropical forest dy-
30 namics with long-term consequences for biodiversity, global carbon cycling and climate change
31 mitigation. However, forest disturbance may change crowding intensity, and thus the relative con-
32 tribution of climate extremes and neighbourhood interactions on tree growth, thereby influencing
33 tropical forest resistance and resilience to climate change. Here, we aim to evaluate the sepa-
34 rate and interactive effects of climate and neighbours on tree growth in old-growth and disturbed
35 tropical forests.

36 2. We used 30 years of growth measurements for over 300 tropical tree species from 15 forest
37 plots in French Guiana to investigate the separate and interactive effects of climate anomalies
38 (in solar radiation, maximum temperature, vapor pressure deficit and climatic water deficit) and
39 neighbourhood crowding on individual tree growth. Contrasting old-growth and selectively-logged
40 forests, we also examined how disturbance history affects tree growth sensitivity to climate and
41 neighbours. Finally, for the most abundant 100 species, we evaluated the role of 12 functional
42 traits pertaining to water relations, light and carbon use in mediating tree growth sensitivity to
43 climate anomalies, neighbourhood crowding, and their interactions.

44 3. Climate anomalies tied to heat and drought stress and neighbourhood crowding independently
45 reduced tree growth, and showed positive interactive effects which attenuated their separate effects
46 on tree growth. Their separate and interactive effects were stronger in disturbed than undisturbed
47 forests. Fast-growing species (i.e. higher intrinsic growth rates) were more abundant in disturbed
48 forests and more sensitive to climate anomalies and neighbourhood crowding. Traits related to
49 water relations, light and carbon use captured species sensitivities to different climate anomalies
50 and neighbourhood crowding levels, but were weak predictors of their interactions.

51 4. **Synthesis:** Our results demonstrate that climate anomalies and neighbourhood crowding can
52 interact to shape tropical tree growth, suggesting that considering the biotic context may improve
53 predictions of tropical forest dynamics facing altered climate regimes. Furthermore, species traits
54 can capture tree growth sensitivity to the separate effects of climate and neighbours, suggesting

55 that better representing leading functional dimensions in tropical tree strategies offers a promising
56 way towards a better understanding of the underlying ecological mechanisms that govern tropical
57 forest dynamics.

58 **Keywords:** climate change, drought stress, functional traits, tropical forest, tree growth, water
59 relations

60 **Résumé**

61 1. Les extrêmes climatiques ainsi que les interactions biotiques à l'échelle du voisinage, affectent
62 la dynamique des forêts tropicales, avec des conséquences à long terme pour la biodiversité, le
63 cycle global du carbone et l'atténuation du changement climatique. Cependant, les perturbations
64 forestières peuvent faire varier localement les voisinages, et ainsi modifier la contribution relative
65 des extrêmes climatiques et des interactions de voisinage sur la croissance des arbres, ce qui peut
66 impacter la résistance et la résilience des forêts tropicales au changement climatique. Nos travaux
67 visent à évaluer les effets individuels et interactifs du climat et des voisins sur la croissance des
68 arbres dans les forêts tropicales non-perturbées et perturbées.

69 2. Nous avons utilisé 30 ans de mesures de croissance pour plus de 300 espèces d'arbres tropicaux
70 provenant de 15 parcelles forestières en Guyane française pour étudier les effets individuels et
71 interactifs des anomalies climatiques (en termes de rayonnement solaire, de température maximale,
72 de déficit de pression de vapeur, et de déficit hydrique climatique) et des interactions de voisinage
73 sur la croissance individuelle des arbres. En comparant les forêts exploitées sélectivement aux
74 forêts non-perturbées, nous avons également examiné comment l'historique des perturbations peut
75 influencer la sensibilité de la croissance des arbres au climat et aux voisins. Enfin, pour les 100
76 espèces les plus abondantes, nous avons évalué le rôle de 12 traits fonctionnels reflétant les relations
77 hydriques, l'utilisation de la lumière et du carbone sur la réponse de la croissance des arbres aux
78 anomalies climatiques, aux interactions de voisinage et à leurs interactions.

79 3. Les anomalies climatiques liées aux stress thermique et hydrique, ainsi que les interactions
80 de voisinage, réduisent la croissance des arbres. De plus, elles peuvent interagir positivement,
81 ce qui atténue leurs effets individuels sur la croissance des arbres. Leurs effets individuels et
82 interactifs sont plus forts dans les forêts perturbées que dans les forêts non-perturbées. Les espèces
83 à croissance rapide (c'est-à-dire à taux de croissance intrinsèque plus élevé) sont plus abondantes
84 dans les forêts perturbées, et aussi plus sensibles aux anomalies climatiques et aux interactions
85 de voisinage. Les traits liés aux relations hydriques, à la lumière et à l'utilisation du carbone
86 captent la sensibilité des espèces aux différentes anomalies climatiques et aux différents niveaux

87 d'interactions de voisinage, mais ne prédisent pas leurs interactions.

88 **4. Synthèse:** Nos résultats montrent que les anomalies climatiques et les interactions de voisinage
89 peuvent interagir pour façonner la croissance des arbres tropicaux, ce qui suggère que prendre en
90 compte le contexte biotique peut améliorer les prévisions de la dynamique des forêts tropicales
91 face aux changements climatiques. En outre, les traits des espèces peuvent capter la sensibilité de
92 la croissance des arbres aux effets individuels du climat et des voisins, ce qui suggère que mieux
93 représenter les principales dimensions des stratégies fonctionnelles des arbres tropicaux ouvre sur
94 une meilleure compréhension des mécanismes écologiques qui régissent la dynamique des forêts
95 tropicales.

96 **Mots-clés :** changement climatique, stress hydrique, traits fonctionnels, forêt tropicale, crois-
97 sance des arbres, relations hydriques

98 **Introduction**

99 Tropical forests are biodiversity hotspots ([Gatti et al. 2022](#), [Pillay et al. 2022](#)) and major contrib-
100 utors to global carbon and water cycles ([Needham et al. 2018](#), [Pan et al. 2011](#)), but the services
101 they provide to human populations are threatened by climate change and anthropogenic distur-
102 bance ([Brodrigg et al. 2020](#), [Malhi et al. 2008](#), [Nunes et al. 2022](#), [Vancutsem et al. 2021](#)). In
103 particular, extreme droughts are linked to higher solar radiation, maximum temperatures, atmo-
104 spheric evaporative demands and lower soil water availability, which have been shown to negatively
105 impact tropical forest dynamics by reducing tree growth and increasing tree mortality ([Bauman
106 et al. 2022b,a](#), [Rifai et al. 2018](#)). As climate change is predicted to result in higher frequencies,
107 intensities, and duration of extreme droughts in the tropics ([Shukla et al. 2022](#)), this may have
108 important long-term implications for tropical tree dynamics and diversity, and therefore global
109 carbon sequestration and residence time ([Sullivan et al. 2020](#)).

110 Tropical forest response to climate extremes is the compounded outcome of individual tree re-
111 sponses, which may depend on local biotic interactions, such as interactions between neighbour-
112 ing trees. While crowding by neighbours generally reduces tropical tree growth ([Dawkins 1959](#),
113 [Gourlet-Fleury and Houllier 2000](#), [Fortunel et al. 2018](#), [Uriarte et al. 2004, 2010](#)), the net effects
114 of neighbourhood interactions may change from negative to positive under specific environmental
115 conditions ([Grossiord 2020](#), [Fichtner et al. 2020](#)) such as with water levels ([Aakala et al. 2018](#)) and
116 disturbance history. For instance, competition for water may accentuate the negative effects of
117 water limitations on tree growth, as shown in temperate and Mediterranean forests ([Bottero et al.
118 2017](#), [Gómez-Aparicio et al. 2011](#), [Astigarraga et al. 2020](#)). Conversely, species interactions can
119 alter the depth of soil water uptake ([Grossiord et al. 2014a](#)) or transpiration response to increasing
120 drought stress ([Grossiord et al. 2014b](#), [Haberstroh and Werner 2022](#)). Yet, the effects of climate
121 on tree growth have rarely been evaluated together with the effects of neighbourhood crowding in
122 tropical forests (but see: [Uriarte et al. 2016a](#)), and we still know little about the extent to which
123 the interaction between climate extremes and neighbourhood interactions can attenuate or exac-
124 erbate their separate effects on tree growth, especially in tropical forests with different disturbance

125 histories.

126 More than half of the world's tropical forests are designated production forests (Blaser et al.
127 2011), and forest management such as selective logging and thinning has long-lasting effects on
128 forest composition, diversity and structure (Clark and Covey 2012, Cannon et al. 1994, Finegan
129 and Camacho 1999, Mirabel et al. 2021, Osazuwa-Peters et al. 2015), which may alter forest
130 resistance and resilience to extreme climate events (Hiltner et al. 2021). Specifically, disturbed
131 forests host more light-demanding tree species than old-growth forests (Carreño-Rocabado et al.
132 2012, Baraloto et al. 2012, Kuusipalo et al. 1996, Mirabel et al. 2020, 2021, Whitmore 1989),
133 and these fast-growing species may be more sensitive to climate extremes (Bauman et al. 2022a,
134 Uriarte et al. 2016b) and neighbourhood crowding (Fortunel et al. 2016). Moreover, selective
135 logging and thinning creates gaps, thereby increasing the openness of forest canopies and changing
136 micro-climatic conditions (Ghuman and Lal 1987, Peña-Claros et al. 2008). These logging gaps
137 influence tree growth rates (Baraloto et al. 2005, Hérault et al. 2010, Peña-Claros et al. 2008, Silva
138 et al. 1995, Finegan et al. 1999), but it remains unclear how disturbance history may influence
139 tree growth responses to climate and neighbours.

140 Species differences in growth sensitivity to climate and neighbours likely depend on their functional
141 strategies. While commonly measured traits pertaining to light capture, nutrient and carbon use
142 such as specific leaf area and wood density can capture species differences in tree growth response
143 to neighbourhood crowding (Fortunel et al. 2016, Kunstler et al. 2016), they are not always good
144 proxies of species sensitivity to drought (Anderegg et al. 2018, Powell et al. 2017, Powers et al.
145 2020, Wagner et al. 2014b, but see: Uriarte et al. 2016a, Greenwood et al. 2017, Serra-Maluquer
146 et al. 2022). A promising way forward is to integrate leaf traits that directly link to plant carbon-
147 water relations or physiological responses to heat and water stress (Anderegg et al. 2018, Barros
148 et al. 2019, McGregor et al. 2021, Powell et al. 2017, Powers et al. 2020, Rowland et al. 2021,
149 Serra-Maluquer et al. 2022) (see: Table 1). For instance, stomatal density (Drake et al. 2013,
150 Machado et al. 2021) and oxygen and carbon isotope composition (Farquhar et al. 1989, 2007,
151 Moreno-Gutiérrez et al. 2012) can determine trade-offs between carbon assimilation and water loss
152 at the leaf level under water-limited conditions (Guerrieri et al. 2019, Prieto et al. 2018, Scheidegger

153 [et al. 2000](#), [Wang and Wen 2022b](#)). Leaf water potential at turgor loss point is linked to species
154 abilities to maintain key plant functions and growth during drought ([Bartlett et al. 2012b](#), [2016](#),
155 [Maréchaux et al. 2018](#)). Leaf minimum conductance ([Blackman et al. 2019](#), [Duursma et al. 2019](#),
156 [Machado et al. 2021](#)) and leaf saturated water content ([Blackman et al. 2019](#), [Luo et al. 2021](#)) may
157 indicate species ability to resist or avoid heat- and drought-induced desiccation of plant tissue, and
158 hence the potential for rapid post-drought growth. These leaf traits likely influence competition
159 for water, but no study so far has evaluated their role in mediating tree growth response in the
160 context of neighbourhood effects.

161 Here, we tested the separate and interactive effects of climate and neighbours by leveraging 30 years
162 of individual tree diameter growth data for more than 300 tropical tree species from 15 tropical
163 forest plots, including six old-growth forest plots and nine post-logging forest plots, located at the
164 CIRAD (Centre de coopération Internationale en Recherche Agronomique pour le Développement)
165 experimental site of Paracou in French Guiana ([Gourlet-Fleury et al. 2004](#)). For the most abundant
166 species (ca. 100), we collected 12 traits pertaining to water relations, light capture and carbon
167 use (Table 1) to examine their role in mediating tree growth response to climate anomalies and
168 neighbourhood crowding. Specifically we asked:

169 1) How do climate anomalies and neighbourhood crowding influence tree growth? We expect
170 tree growth to decline with positive anomalies in maximum temperature (T_{max}), atmospheric
171 evaporative demand (i.e. vapor pressure deficit, VPD) and climatic water deficit (CWD). As higher
172 levels of solar radiation (SRad) lead to increased light availability, but also higher temperature and
173 vapour pressure deficit, positive anomalies in SRad could either enhance or reduce tree growth.
174 We further expect tree growth to decrease with higher neighbourhood crowding. Finally, we
175 expect that climate anomalies and neighbourhood crowding can interact, thereby accentuating or
176 attenuating their separate effects on tree growth.

177 2) Does tree growth response to climate and neighbours vary with forest disturbance history? We
178 expect stronger climate-induced growth declines in disturbed forests as a more open canopy offers
179 less buffer against climate anomalies. We also expect stronger sensitivity to climate anomalies and

180 neighbourhood crowding in disturbed forests as they host more fast-growing species that may be
181 more vulnerable to both abiotic and biotic stressors.

182 3) Do leaf water-related traits and commonly-measured leaf and stem traits pertaining to light
183 and carbon use capture species differences in tree growth response to climate anomalies and neigh-
184 bourhood crowding? We expect greater tree growth sensitivity to heat and drought stress and
185 neighbourhood crowding in fast-growing, light-demanding, water-spender or drought intolerant
186 species.

187 **Materials and Methods**

188 **Study site**

189 Our analyses used the permanent forest plot system of the CIRAD experimental site at the Paracou
190 Tropical Forest Research Station (5°18'N, 52°53'W) in French Guiana. Mean annual precipitation
191 at Paracou is 3041 mm yr⁻¹, with a pronounced dry season (< 100 mm month⁻¹) from August
192 through November. Paracou is characterised as a tropical lowland forest site consisting of old-
193 growth terra firme forest. Fifteen permanent forest plots of 6.25 ha each were established from
194 1984 to 1990, of which nine plots were subjected to different types (selective logging and thinning)
195 and intensities of silvicultural treatments (Fig. 1), resulting in above-ground biomass (AGB) loss
196 (12–33% AGB loss in the three plots subjected to selective logging and 33–56% AGB loss in the six
197 plots that were subjected to selective logging and thinning) (Gourlet-Fleury et al. 2004, Hérault
198 and Piconiot 2018) and differences in species composition (Mirabel et al. 2020, 2021). In the 2021
199 inventory, there were 70,238 trees belonging to 591 species (including subspecies), 227 genera and
200 63 families.

201 **Tree growth and neighbourhood data**

202 In each of the 15 forest plots, all trees ≥ 10 cm DBH (diameter at breast height, i.e. 1.3 m) were
203 mapped to a precision of 0.5 m and were botanically identified. Tree inventories took place at

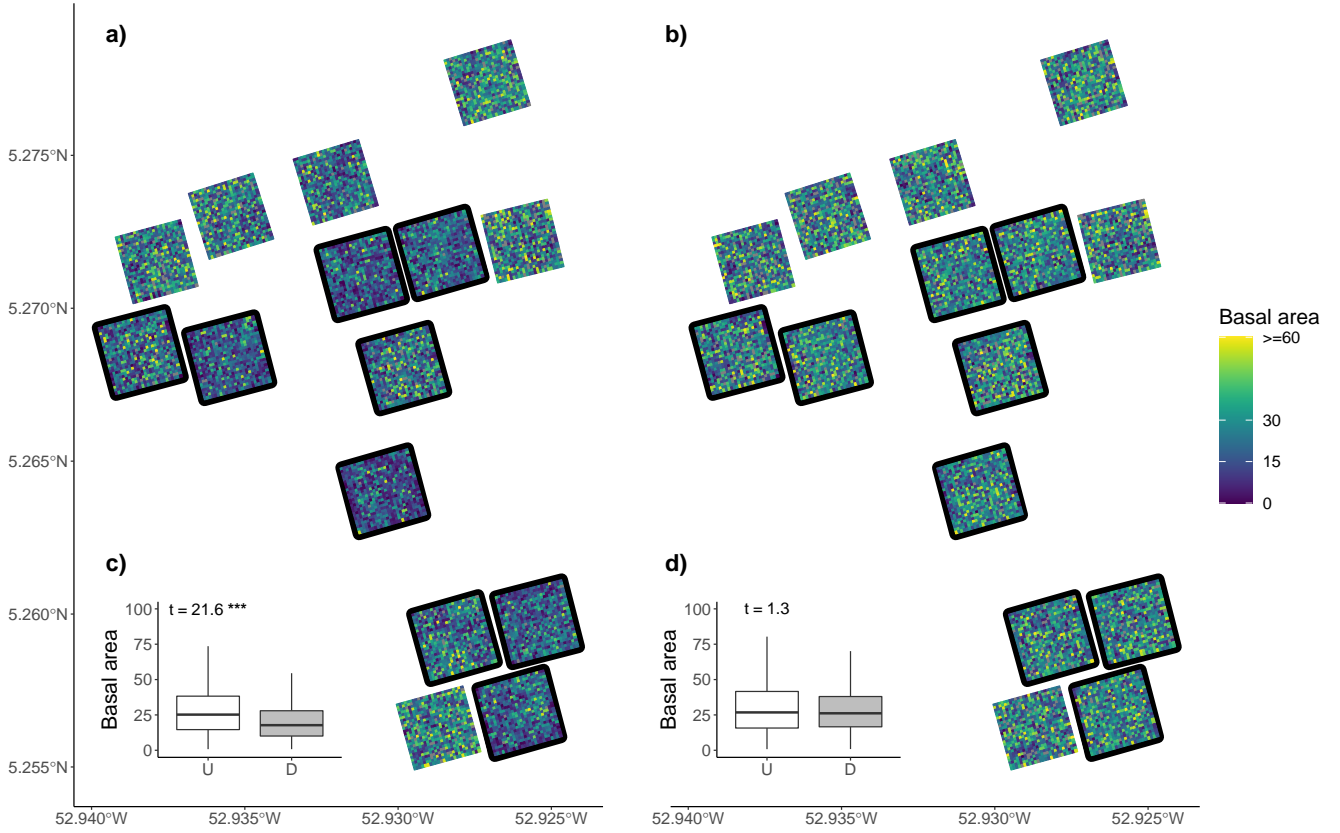


Figure 1. Spatial dimension of the 15 permanent forest plots and stand density in $10\text{ m} \times 10\text{ m}$ quadrats, given as basal area ($\text{m}^2\text{ ha}^{-1}$), in a) 1991 and b) 2019. Disturbed plots are denoted by black contours. Box plots show differences in basal area between the 6 undisturbed (U) and the 9 disturbed (D) forest plots in c) 1991 and d) 2019. t value of Welch's two sample t -test, performed on log transformed basal area, and significance level (***) = $p < 0.001$ are given in the left hand corner of the box plots.

204 one or two year intervals during which the status (alive/dead) and circumference to a precision of
 205 0.5 cm of every tree were recorded, from which we calculated DBH. New recruits (trees reaching
 206 the threshold DBH of 10 cm) were mapped and identified at each census (Gourlet-Fleury et al.
 207 2004, Derroire et al. 2022a,b,c,d,e). To reduce noise in annual growth data (potentially caused
 208 by measurement/rounding errors), for each individual i of species s , we calculated the annualised
 209 absolute diameter growth rate (AGR, cm yr^{-1}) from DBH values between censuses t and $t - 2$ as:

$$\text{AGR}_{i,s,t} = \frac{\text{DBH}_{i,s,t} - \text{DBH}_{i,s,t-2}}{t - (t - 2)} \quad (\text{eqn 1})$$

210 For each individual tree i , we thus calculated AGR for 15 two-year census intervals between 1991
211 and 2021. We excluded the following stems from the focal tree data: (a) Palm species due to their
212 lack of secondary growth, (b) individuals with human-induced damage (e.g. through logging or
213 thinning treatments), (c) missing or uncertain botanical determination, (d) with estimated cir-
214 cumference (e.g. due to buttresses), and (e) abnormal tree growth values ($\leq -2 \text{ cm yr}^{-1}$, resulting
215 from a shift in the point of measurement, and $\geq 5 \text{ cm yr}^{-1}$). The upper and lower thresholds for
216 abnormal growth values were based on expert knowledge for Paracou site.

217 The growth of an individual tree i can be influenced by its $N(i)$ neighbours within a given radius
218 via their size (DBH^2) and the inverse of their distance to the focal tree (d) (Canham et al. 2004,
219 Fortunel et al. 2016, Uriarte et al. 2010). For each focal tree individual i at the start of the growth
220 census interval $t - 2$, we calculated its neighbourhood crowding index ($\text{NCI}_{i,t-2}$) as the weighted
221 sum of all neighbours $N(i)$ within a 10 m radius of individual i (Fortunel et al. 2018, Lasky et al.
222 2014, Uriarte et al. 2016a), as:

$$\text{NCI}_{i,t-2} = \sum_{j \in N(i)} \frac{\text{DBH}_{j,t-2}^2}{d_{i,j}} \quad (\text{eqn 2})$$

223 We chose a 10 m radius to be able to compare with previous studies conducted in tropical forests
224 (Fortunel et al. 2018, Lasky et al. 2014, Uriarte et al. 2016a), and well capture neighbourhood effects
225 while keeping edge effects low (Zambrano et al. 2020). To avoid incomplete neighbourhoods, all
226 focal tree individuals closer than 10 m to the plot edge were excluded. We kept as neighbours
227 individuals with human-induced damage, missing or uncertain botanical determination, estimated
228 circumferences, and corrected abnormal diameter increments (see: Supplementary Methods S1 for
229 details).

230 Climate data

231 We considered four climate variables that have been previously shown to influence tropical tree
232 growth: solar radiation (SRad) representing light availability, maximum temperature (Tmax) cap-

233 turing heat stress, vapour pressure deficit (VPD) relating to atmospheric evaporative demands and
 234 climatic water deficit (CWD) capturing soil water availability by relating precipitation to evapo-
 235 transpiration (Bauman et al. 2022a, Choat et al. 2018, Cunningham 2005, Doughty and Goulden
 236 2008, Grossiord et al. 2020, Wagner et al. 2012). We extracted climate variables from TerraCli-
 237 mate, a high-resolution global data set of monthly climate variables and climatic water balance
 238 (Abatzoglou et al. 2018).

239 We identified anomalous years over the study period by calculating mean climate anomalies, ex-
 240 pressed as the deviation of climate variables from their 30-year historical average, over each of
 241 the two-year census intervals. To this aim, we calculated the 30-year baseline (historical mean,
 242 $\mu_{m,\text{baseline}}$) and standard deviation ($\sigma_{m,\text{baseline}}$) for each month of the year (1-12) for the 1991-2021
 243 period. We then calculated standardised anomalies for each month (1-12) m at time t as the de-
 244 viation of the mean monthly climate variable $\mu_{m,t}$ from the long-term monthly baseline $\mu_{m,\text{baseline}}$
 245 (Bauman et al. 2022a, Rifai et al. 2018). To investigate the effect of mean yearly anomalies on
 246 tree growth at two-year census interval (CA_t), we averaged the standardised monthly anomalies
 247 over the $M = 24$ months prior to census t (July $_t$ -July $_{t-2}$) as (Aubry-Kientz et al. 2015, Bauman
 248 et al. 2022a, Rifai et al. 2018):

$$\text{CA}_t = \frac{1}{M} \sum_{m=1}^M \frac{\mu_{m,t} - \mu_{m,\text{baseline}}}{\sigma_{m,\text{baseline}}} \quad (\text{eqn 3})$$

249 Using this approach, two-year periods with positive anomalies can directly be interpreted as periods
 250 in which trees experienced higher solar radiation (SRad), heat (Tmax), atmospheric (VPD) or soil
 251 water (CWD) drought stress than usual.

252 **Functional trait data**

253 We determined six leaf traits pertaining to water relations (Table 1): stomatal density (SD),
 254 oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) stable isotope composition, water potential at turgor loss point
 255 (π_{tlp}), minimum conductance (g_{min}) and saturated water content (LSWC). We sampled 645 trees
 256 belonging to 102 of the most abundant species (from 76 genera and 34 families) that together

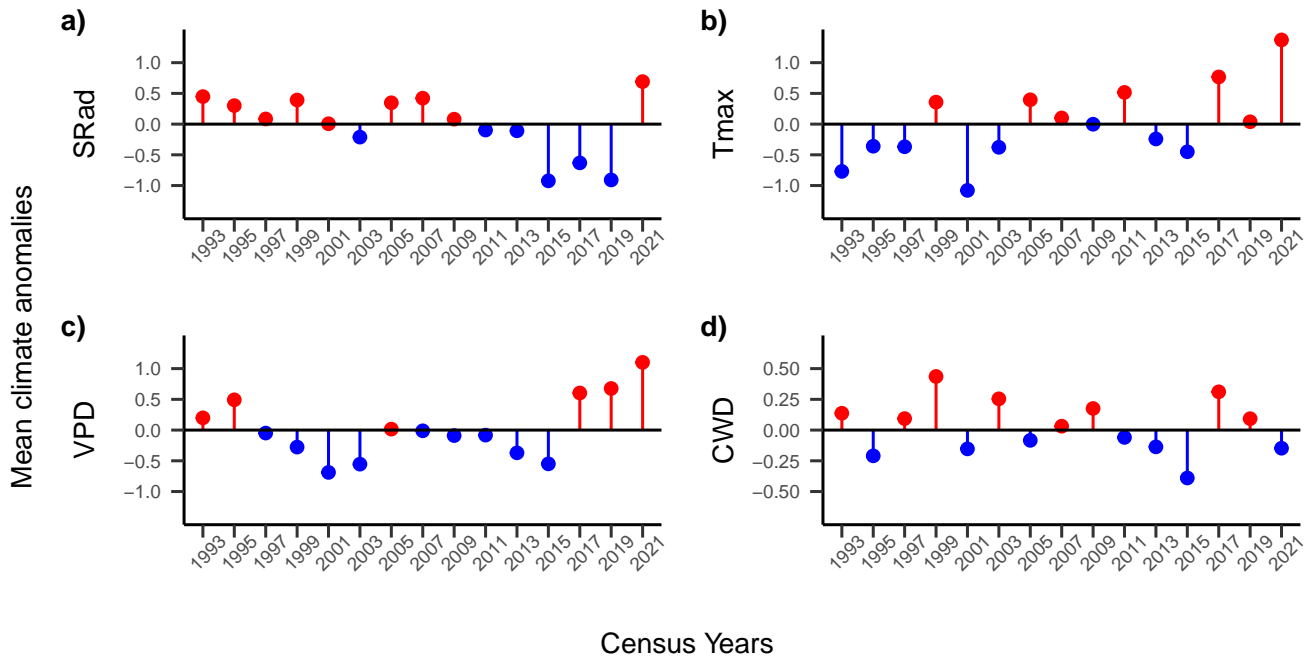


Figure 2. Mean standardised climate anomalies at Paracou for the two-year census intervals over the study period for a) solar radiation, b) maximum temperature, c) vapour pressure deficit and d) climatic water deficit. Red and blue lines and circles represent positive and negative anomalies respectively.

257 represent 70% of all unique individual stems and 72% of all growth measurements at Paracou. We
 258 randomly-selected 645 individuals located within the permanent 15 forest plots at Paracou, using
 259 the following criteria: (i) botanical identification at the species level, (ii) DBH within species-
 260 specific 10th and 90th percentile (to avoid sampling unusually small and large tree individuals),
 261 (iii) topographic position corresponding with the species topographic preference (i.e. individuals
 262 located at a certain topographic position (bottomland, slope, ridge) were only sampled if more than
 263 10% of distinct stems of that species occur on the given topographic position). As the 102 target
 264 species include understory, mid-story and canopy species, we sampled only leaves from branches
 265 that were exposed to medium light conditions (Dawkins index: 3-4, Alder and Sunnott 1992), thus
 266 excluding branches in full sun or shade. For each of the 645 individuals, we collected one fully
 267 expanded and healthy leaf from a healthy branch in the dry season in 2020-2021 for each leaf trait
 268 measurement. After harvest with a sling shot in the field, leaves were immediately put into ziplock
 269 bags with a moist paper towel and kept in the dark in a cooler to minimize transpiration during
 270 transport to the lab. No fieldwork permit was required.

271 To measure leaf SD, we used nail polish or silicon-based dental paste (Speedex Universal Silicon

272 Activator and Speedex Light Body, Coltène/Whaledent AG, Switzerland) to take imprints from
273 the abaxial leaf surface at three positions of the widest part of the leaf blade, while avoiding major
274 veins (Voleníková and Tichá 2001). Imprints were mounted on microscope slides, and pictures were
275 taken at a magnification of 300x using a light microscope (Keyence VHX 7000, Osaka, Japan). We
276 took a minimum of 3 pictures, 1 per imprint when possible, for each sampled leaf. We used Fiji
277 ImageJ (Schindelin et al. 2012) to count all complete stomata per image area. Imprint quality and
278 resulting picture quality varied strongly between species and individuals, so we obtained stomata
279 counts for 470 individuals and 87 species.

280 Leaf osmotic potential was measured using a vapor pressure osmometer (VAPRO 5520, Wescor,
281 Logan, UT, USA). Leaf water potential at turgor loss point (π_{tlp}) was linearly estimated from
282 osmotic potential at full hydration, following the standard protocol of Bartlett et al. (2012b,a),
283 which has been validated for species in French Guiana (Maréchaux et al. 2016).

284 Leaf g_{min} was estimated from leaf drying curves. We monitored leaf weight loss over time, following
285 the protocol of Sack et al. (2003). Time intervals for weight measurements were set to 30 min.
286 Leaves of tropical species lose water very rapidly, so that consecutive measurements over 3 to 4 h
287 were sufficient to assess minimum conductance.

288 We measured leaf saturated and dry weights with a digital scale at a 0.0001 g precision (Mettler
289 Toledo, Switzerland). We obtained saturated weights following the ‘partial’ rehydration protocol of
290 Vendramini et al. (2002), which provides comparable measurements to the ‘complete’ rehydration
291 protocol by Garnier et al. (2001) (Vaieretti et al. 2007). We wrapped fresh leaves into paper towels
292 that were previously soaked with de-ionised water, and kept them for 24 hours in the dark and at
293 low temperature (4 °C) for rehydration. Dry weights were measured after drying leaves for at least
294 72 hours at 60 °C (Sapes and Sala 2021). We calculated LSWC from saturated and dry weights
295 (Barrs and Weatherley 1962).

296 Bulk leaf $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ were calculated from a composite sample of dried and coarsely chopped
297 leaves, including those used for π_{tlp} , LSWC and g_{min} measurements. Samples were ground to
298 fine powder using a ball mill (Retsch MM200, Hanau, Germany) for five minutes at maximum

299 speed (100 rotations per minute) and further dried in a drying oven for 24 h at 85 °C. Aliquots of
300 0.2 – 0.4 mg per sample were weighed into silver capsules and $\delta^{18}\text{O}$ signatures were measured with
301 a high temperature pyrolysis unit (TCEA) coupled to a Delta V isotope ratio mass spectrometer
302 instrument (Thermo Scientific, Vienna, Austria). Aliquots of 1 – 2 mg per sample were weighed
303 into tin capsules and $\delta^{13}\text{C}$ signatures were subsequently determined using an elemental analyser
304 (Flash EA), linked by a Conflo IV Universal Interface to a Delta V isotope ratio mass spectrometer.

305 We combined our measurements for the six leaf traits with data from previous field campaigns
306 conducted at Paracou ([Levionnois et al. 2021](#), [Maréchaux et al. 2015, 2019](#), [Ziegler et al. 2019](#)).
307 We further compiled trait data for the 102 focal tree species for six leaf and wood traits that relate
308 to light capture and carbon use from previous work conducted in French Guiana ([Baraloto et al.](#)
309 [2010](#), [Fortunel et al. 2012](#), [Vleminckx et al. 2021](#)). We included leaf area (LA), specific leaf area
310 (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}), bark thickness ($\text{Bark}_{\text{thick}}$) and wood specific
311 gravity (WSG, hereafter referred to as wood density) (see: Table 1). For all subsequent analyses
312 including trait values, we considered species means.

Table 1. Functional traits for the most abundant 100 species at Paracou, French Guiana

Organ	Trait type	Trait	Abbreviation (Unit)	Function	Description	References	N
Leaf	Anatomy	Stomata density	SD (n mm ⁻²)	Gas exchange	SD relates to potential maximum stomatal conductance, promoting gas exchange and evaporative cooling, but increasing water loss through transpiration.	Bertolino et al. 2019, Drake et al. 2013, Machado et al. 2021	87
Leaf	Chemistry	Bulk leaf oxygen stable isotope	$\delta^{18}\text{O}$ (‰)	Carbon-water use	Plants with high $\delta^{18}\text{O}$ have low stomatal conductance and transpiration rates and thus conserve water at the expense of carbon assimilation.	Farquhar et al. 2007, Moreno-Gutierrez et al. 2012, Scheidegger et al. 2000	81
Leaf	Chemistry	Bulk leaf carbon stable isotope	$\delta^{13}\text{C}$ (‰)	Carbon-water use	Plants with high $\delta^{13}\text{C}$ have high intrinsic water-use efficiency (high photosynthetic rates relative to stomatal conductance) and thus conserve water at the expense of carbon assimilation.	Farquhar et al. 1989, Cernusak et al. 2013, Scheidegger et al. 2000	81
Leaf	Physiology	Water potential at turgor loss point	π_{tip} (MPa)	Drought tolerance	Plants with low π_{tip} maintain stomatal conductance, hydraulic conductance and photosynthetic gas exchange at lower soil water potential.	Bartlett et al. 2012, Marechaux et al. 2018	100
Leaf	Physiology	Minimum conductance	g_{min} (mmol m ⁻² s ⁻¹)	Water conservation	Low g_{min} limits residual water loss after stomatal closure through leaf cuticle and incompletely closed stomata, thereby increasing dry-down time.	Blackman et al. 2019, Duursma et al. 2019, Machado et al. 2021	102
Leaf	Physiology	Leaf saturated water content	LSWC (%)	Water storage	LSWC translates into water reserves that may allow maintenance of leaf water potential when water supply becomes limiting.	Blackman et al. 2019, Gleason et al. 2014, Luo et al. 2021	100
Leaf	Structure	Leaf area	LA (cm ²)	Light capture	Large leaves intercept more light, have thick leaf boundary layer that limits heat exchange with surrounding air, but are at risk of heat damage when stomatal closure prevents transpirational cooling.	Wright et al. 2017	101
Leaf	Structure	Specific leaf area	SLA (m ² kg ⁻¹)	Light capture and carbon use	High SLA reflects greater allocation of dry mass/carbon to light interception than physical resistance, and is associated with resource acquisitive strategies along the leaf economic spectrum.	Osnes et al. 2013, Wright et al. 2004	101
Leaf	Structure	Leaf thickness	L _{thick} (mm)	Carbon use	L _{thick} relates to structural support, physical resistance and leaf lifespan.	Vile et al. 2005	100
Leaf	Structure	Leaf toughness	L _{tough} (N)	Carbon use	L _{tough} relates to structural support, physical resistance and leaf lifespan.	Kitajima and Poorter 2010	100
Wood	Structure	Stem bark thickness	Bark _{thick} (mm)	Mechanical support, water transport and storage capacity	Plants with thick bark have low respiration rates, but high mechanical strength, resistance to abiotic and biotic threats, and stem water storage.	Loram-Lourenço et al. 2022, Poorter et al. 2014, Rosell et al. 2014	100
Wood	Structure	Stem wood specific gravity	WSG	Mechanical support, water transport and storage capacity	Dense wood increases mechanical strength and resistance to abiotic and biotic threats, and is related to high embolism resistance, but is more costly to produce per volume.	Chave et al. 2009, Poorter et al. 2010, Serra-Maluquer et al. 2022	95

Note: For a given trait N indicates the number of species for which we had available trait information.

313 Models

314 We used Bayesian hierarchical models to evaluate the separate and interactive effects of climate
315 anomalies and neighbourhood crowding on individual absolute growth rates (AGR). We modeled
316 the natural logarithm of absolute growth rates ($\log(\text{AGR})$) because of the high heteroscedasticity
317 within the growth data set and to reduce the influence of outliers (Bauman et al. 2022a, Fortunel
318 et al. 2018, Hérault et al. 2011). To deal with negative and zero growth before taking the logarithm,
319 we added to each observed growth value the constant $1.1|\text{AGR}_{\min}|$, where $|\text{AGR}_{\min}|$ is the absolute
320 minimum value of observed growth of the dataset (Bauman et al. 2022a).

321 The hierarchies of the models consist of modelling individual-level growth rates to simultaneously
322 fit a community-level regression and a species-level regression. The community level modelled AGR
323 responses to covariates via hyperparameters (i.e. statistical distributions from which species-level
324 intercepts and slope coefficients arose), while the species level captured species-specific AGR sensi-
325 tivities to covariates (i.e. slope parameters) and species-level intercepts (hereafter intrinsic AGR)
326 - i.e. species-level deviations from the community average parameters. While the community-level
327 regression (eqn 4a) was kept the same across all models, the species-level regressions (capturing
328 species-specific differences in intrinsic growth rates and growth responses to model covariates)
329 only depend on species identity in M1-models (eqn 4c), while species parameters are a function of
330 species traits in M2-models (eqn 5). The models further include a covariance matrix (eqn 4e) to
331 estimate correlations ρ among species-level parameters. To capture part of the unexplained growth
332 variation related to individuals and plots we allowed intercepts to vary by plots γ_p and individuals
333 ϵ_i (eqn 4f) (Bauman et al. 2022a, Fortunel et al. 2018).

334 We modeled individual $\log(\text{AGR}_t)$ as a linear function of (i) tree size at the beginning of the census
335 interval (DBH_{t-2}), (ii) monthly climate anomalies averaged over the census interval (CA_t), (iii)
336 neighbourhood crowding at the beginning of the census interval (NCI_{t-2}) and (iv) the interaction
337 between climate anomalies and neighbourhood crowding ($\text{CA}_t \times \text{NCI}_{t-2}$) (Bauman et al. 2022a,
338 Fortunel et al. 2018). To allow direct comparison between covariates and ease assignment of
339 plausible weakly-informative prior to the parameters, $\log(\text{AGR}_t)$ and all covariates, except for

340 climate anomalies (Bauman et al. 2022a), were standardised to mean zero and unit standard
 341 deviation (Bauman et al. 2022a, Fortunel et al. 2018, McElreath 2020, Uriarte et al. 2016a). As we
 342 assumed tree growth to have a non-linear, multiplicative relationship with DBH and NCI (Canham
 343 et al. 2004, Fortunel et al. 2016, Uriarte et al. 2010), we log transformed DBH and NCI prior to
 344 standardisation to achieve an additive and linear relationship (Kunstler et al. 2016, Uriarte et al.
 345 2016a, Fortunel et al. 2018). As species strongly varied in their mean tree size, we standardised
 346 DBH to mean zero and unit standard deviation within species, to prevent confounding species
 347 differences in growth response to tree size with interspecific variation in mean DBH (Fortunel
 348 et al. 2018, Uriarte et al. 2016a).

349 **M1: "no trait models"**

350 To manage model complexity in assessing tree growth response to the separate and interactive
 351 effects of climate anomalies and neighbourhood crowding and examine the influence of forest
 352 disturbance history, we fitted models separately for each of the four climate variables (SRad,
 353 Tmax, VPD and CWD) and for (i) all 15 plots combined, (ii) the six undisturbed plots and (iii)
 354 the nine disturbed plots, resulting in a total of 12 M1-models. To ensure sufficient statistical power,
 355 M1-models were run on observed growth for all species with at least 100 growth measurements.
 356 M1-models were therefore based on 48,203, 20,688 and 27,515 individuals, belonging to 310, 306
 357 and 307 species, respectively. To allow for direct comparison of parameter estimates between
 358 control and disturbed forest, we standardised and centered growth and all model covariates before
 359 splitting the data set (Ren et al. 2021). For each individual i of species s between censuses $t - 2$
 360 and t , we modeled tree growth as:

$$\log(\text{AGR}_{i,s,t,p}) \sim \mathcal{N}(\mu_{i,s,t,p}, \sigma) \quad (\text{eqn 4a})$$

361

$$\begin{aligned} \mu_{i,s,t,p} = & \alpha_s + \beta_{1s} \times \log(\text{DBH}_{i,t-2}) + \beta_{2s} \times \text{CA}_t + \beta_{3s} \times \log(\text{NCI}_{i,t-2}) \\ & + \beta_{4s} \times \text{CA}_t \times \log(\text{NCI}_{i,t-2}) + \gamma_p + \epsilon_i \end{aligned} \quad (\text{eqn 4b})$$

362

$$\begin{pmatrix} \alpha_s \\ \beta_{1s} \\ \beta_{2s} \\ \beta_{3s} \\ \beta_{4s} \end{pmatrix} \sim MVNormal \left[\begin{pmatrix} \alpha_0 \\ \beta_{1,0} \\ \beta_{2,0} \\ \beta_{3,0} \\ \beta_{4,0} \end{pmatrix}, S \right] \quad (\text{eqn 4c})$$

363

$$S = \begin{pmatrix} \sigma_{\alpha_s} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{\beta_{2s}} & 0 & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{3s}} & 0 \\ 0 & 0 & 0 & 0 & \sigma_{\beta_{4s}} \end{pmatrix} \times R \times \begin{pmatrix} \sigma_{\alpha_s} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{\beta_{2s}} & 0 & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{3s}} & 0 \\ 0 & 0 & 0 & 0 & \sigma_{\beta_{4s}} \end{pmatrix} \quad (\text{eqn 4d})$$

364

$$R = \begin{pmatrix} 1 & \rho_{\alpha_s, \beta_{1s}} & \rho_{\alpha_s, \beta_{2s}} & \rho_{\alpha_s, \beta_{3s}} & \rho_{\alpha_s, \beta_{4s}} \\ \rho_{\alpha_s, \beta_{1s}} & 1 & \rho_{\beta_{1s}, \beta_{2s}} & \rho_{\beta_{1s}, \beta_{3s}} & \rho_{\beta_{1s}, \beta_{4s}} \\ \rho_{\alpha_s, \beta_{2s}} & \rho_{\beta_{1s}, \beta_{2s}} & 1 & \rho_{\beta_{2s}, \beta_{3s}} & \rho_{\beta_{2s}, \beta_{4s}} \\ \rho_{\alpha_s, \beta_{3s}} & \rho_{\beta_{1s}, \beta_{3s}} & \rho_{\beta_{2s}, \beta_{3s}} & 1 & \rho_{\beta_{3s}, \beta_{4s}} \\ \rho_{\alpha_s, \beta_{4s}} & \rho_{\beta_{1s}, \beta_{4s}} & \rho_{\beta_{2s}, \beta_{4s}} & \rho_{\beta_{3s}, \beta_{4s}} & 1 \end{pmatrix} \quad (\text{eqn 4e})$$

365 using the following weakly informative priors:

$$\gamma_p \sim \mathcal{N}(0, \sigma_\gamma)$$

$$\epsilon_i \sim \mathcal{N}(0, \sigma_\epsilon)$$

$$\alpha_0, \beta_{1-4,0} \sim \mathcal{N}(0, 0.5) \quad (\text{eqn 4f})$$

$$\sigma_{\alpha_s}, \sigma_{\beta_{1-4s}}, \sigma_\gamma, \sigma_\epsilon, \sigma \sim \exp(1)$$

$$R \sim LKJcorr(2)$$

366 where α_s represents the species-level intrinsic growth and β_{1s} , β_{2s} , β_{3s} and β_{4s} represent species-level
 367 growth responses to tree size (DBH), climate anomalies (CA), neighbourhood crowding (NCI) and
 368 the interactive effect of climate anomalies and neighbourhood crowding (eqn 4a). Negative values
 369 of α_s indicate species whose growth is lower and positive values indicate species whose growth

370 is higher than the average AGR across all species. Negative values of β_{1-3s} indicate decreases
371 in growth with increasing model covariate. The interpretation of β_{4s} depends on the respective
372 directions of β_{2s} and β_{3s} . If the sign of β_{4s} is the same as the signs of β_{2s} and β_{3s} , the interaction
373 between neighbourhood crowding and climate can accentuate their separate effects. Conversely, if
374 the sign of β_{4s} is opposite from both signs of β_{2s} and β_{3s} , the interaction between climate anomalies
375 and neighbourhood crowding can attenuate their separate effects. The strength and implications
376 of the interactions usually require a visual exploration to provide a full interpretation.

377 Species intrinsic growth α_s and growth response to covariates β_{1-4s} for the s species were modeled
378 as in [eqn 4c](#), where α_0 represents the community-level intrinsic growth rate and $\beta_{1-4,0}$ the overall
379 effect of covariates on growth across all species. To assess correlations (ρ) among species-level in-
380 trinsic growth α_s and growth response to model covariates β_{1-4s} , we fitted a matrix of correlation
381 coefficients among all pairs of species-level parameters. In addition, modeling all species-level pa-
382 rameters as a multivariate normal distribution ([eqn 4c](#)) allows to share information across species,
383 thus improving the fit for poorly represented species, while preventing overfitting ([Bauman et al.](#)
384 [2022a](#), [McElreath 2020](#)). The variance-covariance matrix S was constructed as shown in [eqn 4d](#),
385 where R is the correlation matrix of species-level parameters ([eqn 4e](#)). Varying intercepts for the
386 p plots γ_p and the i individuals ϵ_i were modeled as given in [eqn 4f](#) with a mean centered on 0
387 (i.e. mean intercept across all plots and individuals respectively). We specified weakly informative
388 priors which are given in [eqn 4f](#).

389 **M2: "trait models"**

390 To assess the effect of traits on species intrinsic growth α_s , and growth response to climate anoma-
391 lies β_{2s} , neighbourhood crowding β_{3s} and their joint effects β_{4s} , we fitted M2-models for a subset
392 of 81-102 tree species (representing over 40,000 trees), for which we had available trait data (Table
393 [1](#)). To manage model complexity, M2-models were fitted separately for each of the four climate
394 variables (SRad, Tmax, VPD and CWD) and for each of the 12 functional traits, resulting in a
395 total of 48 M2-models. While the hierarchical structure, variance-covariance matrix and equation
396 of the community level hierarchy of the M2-models is identical to M1-models ([eqn 4a-eqn 4b](#); [eqn](#)

397 4d-eqn 4f), all species-level parameters, except species-level growth response to tree size β_{1s} , were
 398 modeled in species-level regressions to capture species-specific differences, while simultaneously
 399 evaluating the effect of species-mean functional traits within these responses (eqn 5) (Fortunel
 400 et al. 2018, Uriarte et al. 2016a, Bauman et al. 2022a). More specifically, species-level parameters
 401 were modelled as:

$$\begin{pmatrix} \alpha_s \\ \beta_{1s} \\ \beta_{2s} \\ \beta_{3s} \\ \beta_{4s} \end{pmatrix} \sim MVN \left[\begin{pmatrix} \alpha_0 + \alpha_1 \times Trait_s \\ \beta_{1,0} \\ \beta_{2,0} + \beta_{2,1} \times Trait_s \\ \beta_{3,0} + \beta_{3,1} \times Trait_s \\ \beta_{4,0} + \beta_{4,1} \times Trait_s \end{pmatrix}, S \right] \quad (\text{eqn 5})$$

402 where α_0 represents the community-level intrinsic growth (i.e. grand intercept) and $\beta_{2-4,0}$ the
 403 community-level response to model covariates (i.e grand slopes) whose posterior distributions rep-
 404 resent the effect of covariates on AGR across all species. α_1 and $\beta_{2-4,1}$ represent the departure from
 405 the community level AGR and community level response to model covariates with one standard
 406 deviation change in the value of $Trait_s$ of species s . Traits were standardised to mean zero and
 407 unit standard deviation across species, thus implying that parameter β_{2-4s} equals $\beta_{2-4,0}$ for the
 408 mean trait value of the data set. Given their skewed distributions, we log transformed values of
 409 stomatal density (SD), leaf saturated water content (LSWC), minimum conductance (g_{\min}), leaf
 410 area (LA), leaf thickness (L_{thick}), leaf toughness (L_{though}) and bark thickness ($Bark_{\text{thick}}$), prior to
 411 standardisation, to prevent the tail of the distribution from dominating the model fit (Fortunel
 412 et al. 2018). Species AGR responses to model covariates can thus be accentuated (i.e. the sign of
 413 the trait effect $\beta_{2-4,1}$ is the same as that of the corresponding community level response $\beta_{2-4,0}$)
 414 or attenuated (i.e. the sign of the trait effect $\beta_{2-4,1}$ is the opposite of that of the corresponding
 415 community level response $\beta_{2-4,0}$) with increasing values of $Trait_s$ (Bauman et al. 2022a, Fortunel
 416 et al. 2018, Uriarte et al. 2016a).

417 **Model fitting**

418 All models were fitted in R environment (R Core Team 2021, RStudio Team 2020), on the
419 Meso@LR HPC cluster using the package brms (Bürkner 2017). Bayesian updating of param-
420 eters was performed via the No-U-Turn Sampler (NUTS) in Stan (Carpenter et al. 2017) using
421 CmdStanR (Stan Development Team 2022), which allows intra-chain parallelisation in the back-
422 end. We used four chains and 4000 iterations (2000 warm up) per chain. Chains of all models mixed
423 well and generally converged within 2000 iterations (Rhat between 1 and 1.05). Model parame-
424 ter posteriors were summarised through their median and 90%-highest posterior density interval
425 (HPDI) using the packages tidyverse (Wickham et al. 2019) and tidybayes (Kay 2022). Model
426 covariates were considered to have a clear effect when their slope coefficients 90%-HPDIs did not
427 encompass zero. To assess the model goodness of fit, we calculated conditional and marginal R2
428 using the bayes_R2() function of the brms package (Bürkner 2017), which calculates a Bayesian
429 version of R2 for regression models (Gelman et al. 2019). M1- and M2-models had high explanatory
430 power, with a mean conditional R2 of 0.62 and 0.64, respectively. For more detailed information
431 on conditional and marginal R2 for each model fit see Table S1.

432 **Results**

433 **Tree growth sensitivity to climate anomalies and neighbourhood crowd-** 434 **ing**

435 Across the 15 plots, anomalies in all four climate variables influenced tree growth at Paracou
436 (Fig. 3). Positive anomalies in solar radiation (SRad) enhanced tree growth, whereas positive
437 anomalies in maximum temperature (Tmax), vapour pressure deficit (VPD) and climatic water
438 deficit (CWD) reduced tree growth. Neighbourhood crowding reduced tree growth, and this effect
439 was stronger than that of any of the climate anomalies. Moreover, neighbourhood crowding showed
440 positive interactive effects with climate anomalies linked to heat and drought stress (Tmax, VPD
441 and CWD) on tree growth, but negative interactive effects with anomalies in SRad on tree growth.
442 More crowded trees suffered less from negative effects of Tmax, VPD and CWD anomalies, while

443 also benefiting less from the positive effects of SRad anomalies.

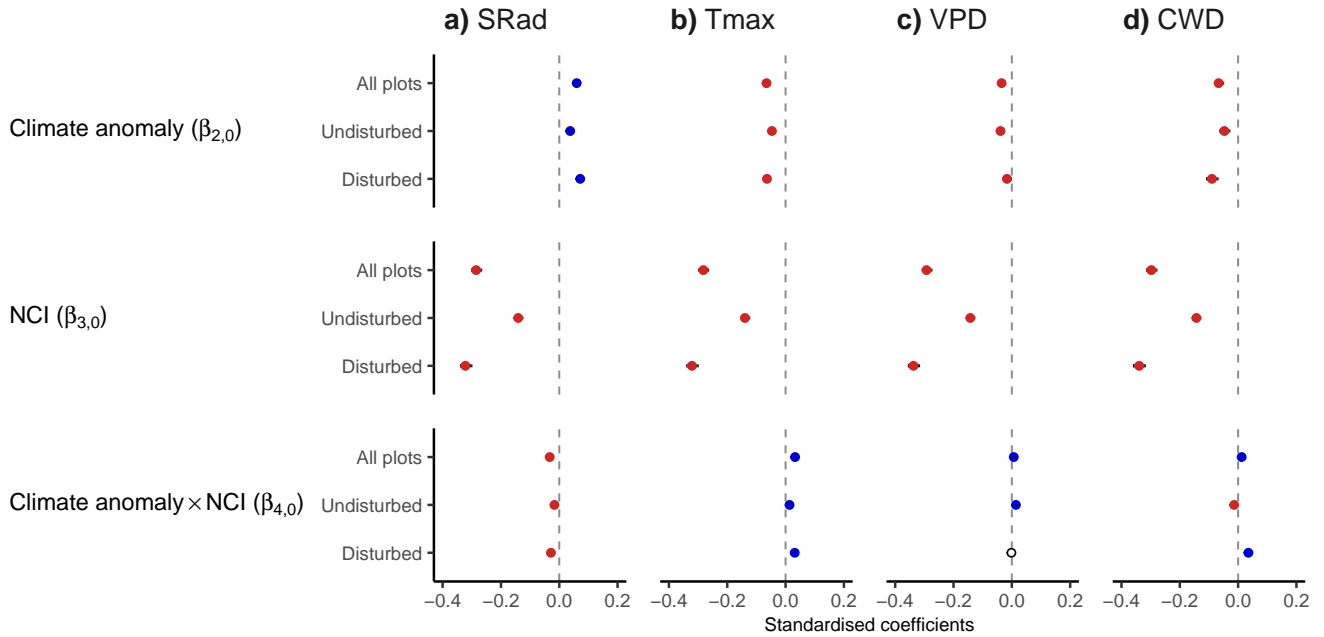


Figure 3. Community-level effects of climate anomaly ($\beta_{2,0}$), neighbourhood crowding (NCI, $\beta_{3,0}$), and their interaction (Climate anomaly \times NCI, $\beta_{4,0}$) on tree growth (M1-models). Standardised coefficients from a) SRad, b) Tmax, c) VPD and d) CWD models are shown for all 15 plots combined, the 6 undisturbed plots and the 9 disturbed plots respectively. Circles show posterior medians of standardised coefficients (community level responses, see: $\beta_{2-4,0}$ in eqn 4c), and lines indicate 90% highest posterior density intervals [HPDI]. Colored circles indicate clear negative (red) and positive (blue) effects (i.e. slope coefficient 90%-HPDIs not encompassing zero), while white circles indicate no effects. Positive $\beta_{2-3,0}$ values indicate faster growth, while negative $\beta_{2-3,0}$ values indicate slower growth with increasing model covariate (details in Table S2). The interpretation of $\beta_{4,0}$ depends on the direction of the climate effect $\beta_{2,0}$. If the sign of $\beta_{4,0}$ is the same as the sign of $\beta_{2,0}$, neighbourhood crowding accentuates the effect of climate, inversely if the sign of $\beta_{4,0}$ is in the opposite of the sign of $\beta_{2,0}$, neighbourhood crowding attenuates the effect of climate. Community-level intercepts (α_0) and tree size effects (DBH, $\beta_{1,0}$) are shown in Fig. S1 A.

444 Tree growth sensitivity to climate anomalies ($\beta_{2,s}$) and neighbourhood crowding ($\beta_{3,s}$) varied among
 445 the focal 310 species: 39% showed clear responses to SRad anomalies (of which 98% showed positive
 446 and only 2% negative responses). Moreover, 45% responded to Tmax anomalies (of which 99%
 447 responded negatively and only 1% positively) and 21% responded to VPD anomalies (of which
 448 86% responded negatively and 14% positively). Finally, 21% responded to anomalies in CWD (of
 449 which 94% responded negatively and 6% positively). On average across the four climate models,
 450 88% of all species showed marked responses to NCI, all of them suppressed by higher crowding
 451 intensities.

452 Overall, individual-level tree growth response to the interaction between climate anomalies and
453 neighbourhood crowding was weakly related to species identity. Yet, species showed a consistent
454 directional response (i.e. no species showed an opposite effect) to the interactive effects of neigh-
455 bourhood crowding and anomalies (β_{4s}) in SRad, Tmax and CWD, but less in VPD. Specifically,
456 neighbourhood crowding clearly attenuated positive effects (negative β_{4s}) of SRad anomalies in
457 18%, and negative effects (positive β_{4s}) of Tmax and CWD anomalies in 27% and 8% of all species.
458 Neighbourhood crowding modulated negative effects of VPD anomalies in 7% of all species, either
459 attenuating (81% of positive β_{4s}) or reinforcing (19% of negative β_{4s}) these effects. For details see
460 Table S3.

461 Species-level intrinsic AGR (M1, α_s) were negatively associated with AGR response to anomalies
462 (M1, β_{2s}), as shown by the median $\tilde{\rho}$, lower 5% quantile $q_5(\rho)$ and upper 5% quantile $q_{95}(\rho)$ of the
463 highest posterior density, in SRad ($\tilde{\rho} = -0.20$, $q_5(\rho) = -0.32$, $q_{95}(\rho) = -0.09$), Tmax ($\tilde{\rho} = -0.69$,
464 $q_5(\rho) = -0.76$, $q_{95}(\rho) = -0.62$), VPD ($\tilde{\rho} = -0.59$, $q_5(\rho) = -0.66$, $q_{95}(\rho) = -0.52$) and CWD
465 ($\tilde{\rho} = -0.55$, $q_5(\rho) = -0.65$, $q_{95} = -0.46$) as well as neighbourhood crowding ($\tilde{\rho} = -0.43$, $q_5(\rho) =$
466 -0.51 , $q_{95}(\rho) = -0.33$, mean across climate models). Tree growth sensitivity to neighbourhood
467 crowding (M1, β_{3s}) was negatively associated with the response to SRad anomalies ($\tilde{\rho} = -0.17$,
468 $q_5(\rho) = -0.30$, $q_{95}(\rho) = -0.04$) and positively with the response to anomalies in Tmax ($\tilde{\rho} = 0.26$,
469 $q_5(\rho) = 0.13$, $q_{95}(\rho) = 0.37$) and CWD ($\tilde{\rho} = 0.28$, $q_5(\rho) = 0.15$, $q_{95}(\rho) = 0.41$) For details see Table
470 S4: All plots).

471 **Variation in tree growth response to climate and neighbours with forest** 472 **disturbance history**

473 The effects of climate anomalies (M1, $\beta_{2,0}$) and neighbourhood crowding (M1, $\beta_{3,0}$) were consistent
474 between the six undisturbed and nine disturbed plots, but were usually stronger in disturbed plots
475 (except for VPD anomalies). In particular, tree growth sensitivity to neighbourhood crowding
476 was twice as strong in disturbed plots than undisturbed plots. In addition, the interactive effects
477 between climate anomalies and neighbourhood crowding were usually greater in disturbed plots,
478 further attenuating their separate effects in these forests. More crowded trees in disturbed plots

479 were more buffered against climate anomalies (except for the VPD anomalies:NCI interaction).
480 However, while negative effects of CWD anomalies on growth were mitigated by neighbourhood
481 crowding in disturbed plots, they were reinforced in undisturbed plots (Fig. 3).

482 Although species intrinsic growth rates varied slightly between undisturbed and disturbed plots
483 (Fig. S2), correlations between species intrinsic growth rates (M1, intercept α_s) and their growth
484 response to climate anomalies (M1, β_{2s}) and neighbourhood crowding (M1, β_{3s}) were overall con-
485 sistent between undisturbed and disturbed plots (Fig. 4 a-b). However, while species that suffered
486 stronger growth declines due to neighbourhood crowding (M1, β_{3s}) were also more sensitive to pos-
487 itive CWD anomalies (M1, β_{2s}) in disturbed plots, we found no clear relationship in undisturbed
488 plots (Fig. 4 c). For details on correlations of species-level parameters see: Table S4.

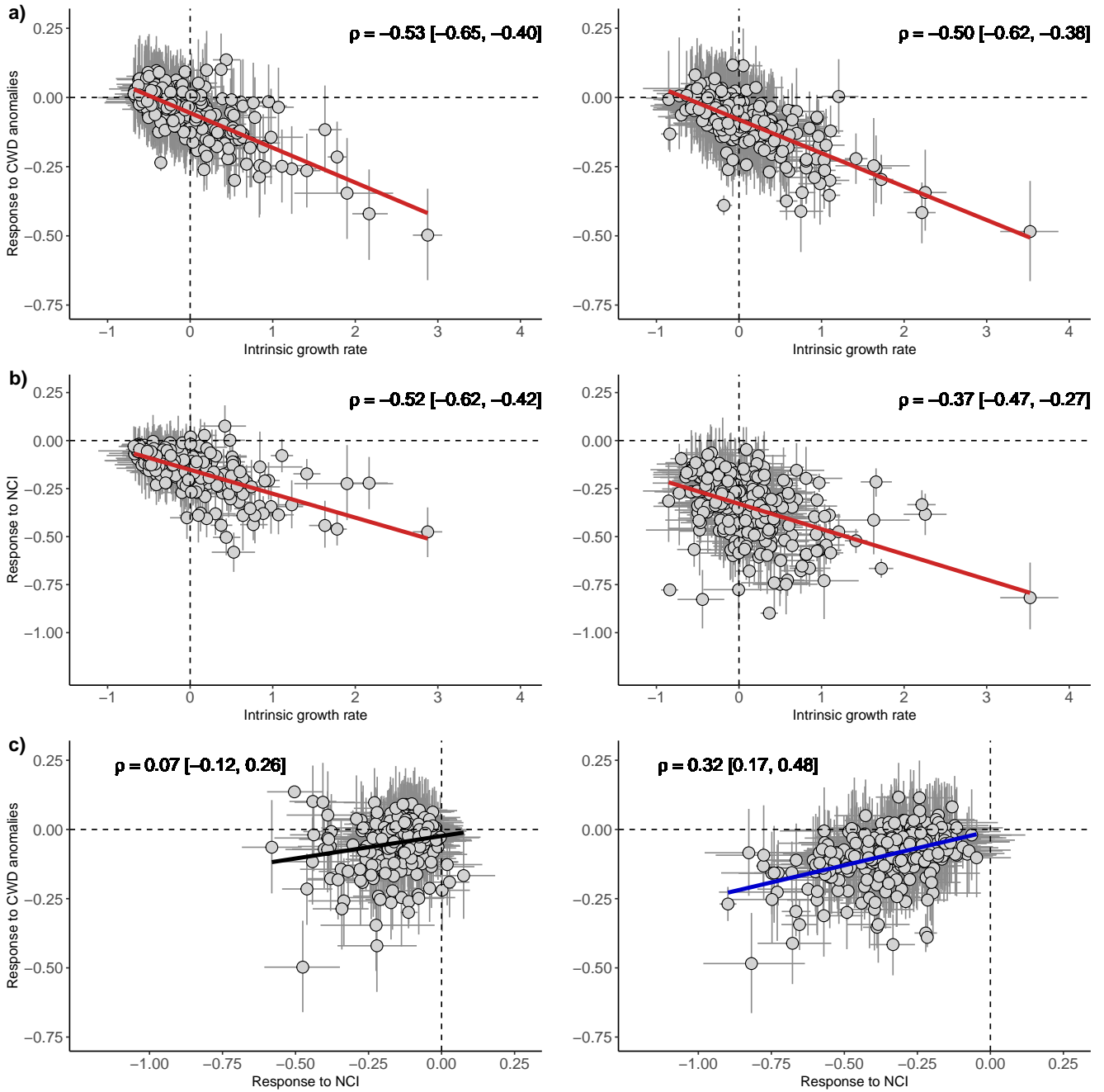


Figure 4. Correlations between a) species intrinsic growth rates α_s and species-level growth response to CWD anomalies (β_{2s}), b) species intrinsic growth rates α_s and species-level growth response to neighbourhood crowding (NCI, β_{3s}) and c) species-level growth response to NCI (β_{3s}) and CWD anomalies (β_{2s}), estimated by the CWD M1-models for undisturbed (left) and disturbed (right) plots, respectively (eqn 4c). Circles represent species coefficients (i.e. species median posteriors). Vertical and horizontal lines represent coefficients 90%-highest posterior density intervals (HPDI). Blue and red regression lines indicate positive and negative correlations, respectively. ρ values were obtained from the variance-covariance matrix (see: eqn 4e). Median, lower and upper 90%-HPDI are given in the upper right-hand or left-hand corner of the figures.

489 Trait effects on tree growth response to climate anomalies and neigh- 490 bourhood crowding

491 Parameter estimates of community-level tree growth regressions were consistent between the M1-
492 models (310 focal species) and M2-models (subset of species with available trait information, Table
493 S2 and Table S5). Fast-growing tree species (i.e. with high intrinsic growth rates, α_s) had higher
494 SD, but lower $\delta^{18}\text{O}$, LA, L_{thick} , L_{through} and WSG (Fig. S1 B and Table S5). Species traits influenced
495 tree growth response to climate anomalies, neighbourhood crowding and their interaction, either
496 reinforcing (values of $\beta_{2-4,1}$ moved β_{2-4s} further away from zero with increasing trait value) or
497 attenuating them (values of $\beta_{2-4,1}$ moved β_{2-4s} closer to zero with increasing trait value) (Fig. 5).

498 Species with lower LSWC and SLA, but higher $\delta^{13}\text{C}$, L_{thick} and $\text{Bark}_{\text{thick}}$ grew faster with increasing
499 SRad anomalies (Fig. 5 a). Species with lower SD, but higher $\delta^{18}\text{O}$, L_{through} and WSG were less
500 sensitive to anomalies in Tmax and VPD (Fig. 5 b-c). Additionally, species with higher $\delta^{13}\text{C}$,
501 g_{min} , LA and L_{thick} showed lower sensitivities to VPD anomalies (Fig. 5 c). Species with lower
502 π_{tlp} but higher WSG were less sensitive to CWD anomalies. (Fig. 5 d). Species with lower SD,
503 but higher $\delta^{18}\text{O}$, L_{through} and WSG were less sensitive to neighbourhood crowding (Fig. 5 a-d).
504 Finally, species with lower $\delta^{13}\text{C}$ but higher SLA benefited more from SRad anomalies when found
505 in crowded environments (Fig. 5 a). Species with higher WSG profited less from the mitigating
506 effects of neighbours against Tmax anomalies (Fig. 5 b), while species with higher SD and SLA,
507 but lower LA, L_{thick} , L_{through} were less buffered against VPD anomalies by their neighbours (Fig.
508 5 c). Species traits did not mediate the interactive effects of CWD anomalies and neighbourhood
509 crowding (Fig. 5 d).

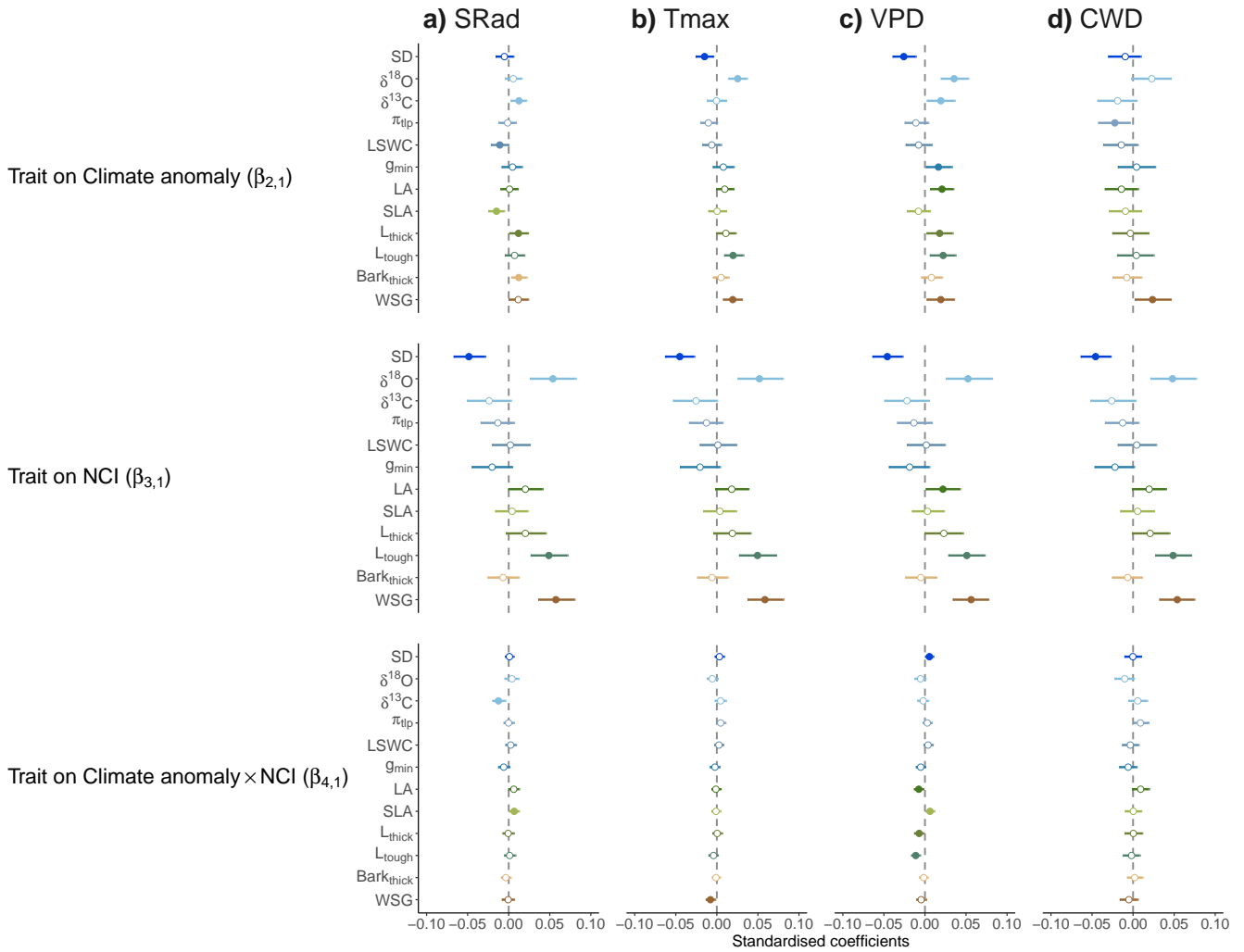


Figure 5. M2-models: trait effects on tree growth response to climate anomalies $\beta_{2,1}$, neighbourhood crowding $\beta_{3,1}$ and the climate anomaly-crowding interaction $\beta_{4,1}$ (see: eqn 5). Standardised coefficients from a) SRad, b) Tmax, c) VPD and d) CWD models are shown for each of the 12 trait models: stomatal density (SD), leaf oxygen ($\delta^{18}\text{O}$) and carbon ($\delta^{13}\text{C}$) isotope composition, water potential at turgor loss point (π_{tip}), leaf saturated water content (LSWC), minimum conductance (g_{min}), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{tough}), bark thickness ($\text{Bark}_{\text{thick}}$) and wood specific gravity (WSG). Circles show posterior medians of standardised coefficients, and lines indicate 90% HPDIs. Filled circles indicate negative and positive effects (i.e. slope coefficient 90%-HPDI not encompassing zero) and empty circles indicate no clear effects. Positive $\beta_{2-4,1}$ values indicate faster growth with increasing trait values, while negative $\beta_{2-4,1}$ values indicate slower growth with increasing trait values (details in Table S5).

510 Discussion

511 In this study, we examined the separate and interactive effects of climate anomalies and neighbours
 512 on tree growth, combining 30 years of climate and tree growth data for over 300 species from 15

513 permanent forest plots, with contrasting disturbance histories. For the most abundant species (ca.
514 100), we further evaluated the effect of 12 traits pertaining to water relations, light capture and
515 carbon use (Table 1), in mediating tree growth response to climate and neighbours.

516 **Climate anomalies and neighbourhood crowding reduce tropical tree** 517 **growth**

518 High temperatures (Tmax) were associated with tree growth decline in half of the 300 species at
519 Paracou (β_{2s} ; Table S3), indicating that in years without strong positive anomalies, some species
520 at the site may already operate near their temperature optimum. Indeed, higher Tmax (and
521 minimum night time temperatures) can increase respiration but decrease stomatal conductance and
522 photosynthesis, thus reducing carbon assimilation (Anderegg et al. 2015, Doughty and Goulden
523 2008) and gross primary production (Aguilos et al. 2018, Crous et al. 2022), which can lead to
524 inter-annual declines in tropical woody productivity (Sullivan et al. 2020, Way and Oren 2010)
525 and carbon sinks (i.e. net ecosystem exchange) (Anderegg et al. 2015). As global temperatures
526 are predicted to increase in the tropics with ongoing climate change (Shukla et al. 2022), this
527 thermal sensitivity of tropical species may lead to important reductions in tree growth in the
528 future, which may alter long-term forest dynamics (Aubry-Kientz et al. 2019, Sullivan et al. 2020).
529 Although Tmax directly influences VPD (Table S6 and Fig. S2), VPD was a less important
530 driver of tree growth at Paracou. While positive VPD anomalies likely reduce tree growth by
531 reducing stomatal conductance and thereby carbon assimilation (Grossiord et al. 2020, Sanginés de
532 Cárcer et al. 2018), it does not affect respiration. Conversely, positive anomalies in CWD strongly
533 reduced tree growth at Paracou (Wagner et al. 2012, Aubry-Kientz et al. 2015), in contrast to
534 previous work in the Australian wet tropics indicating that VPD may limit tree growth before
535 soil water becomes scarce (Bauman et al. 2022a, Choat et al. 2012, Rifai et al. 2018). Our results
536 suggest that trees at Paracou may be more sensitive to soil water stress than to atmospheric water
537 stress. Alternatively, atmospheric water stress may not be severe enough at Paracou to lead to
538 important growth reductions. In addition, trees allocated more to diameter growth with higher
539 anomalies in solar radiation (SRad), which contrasts with recent work showing negative effects of

540 light anomalies on tropical tree growth in Australia’s wet tropics ([Bauman et al. 2022a](#)). Light
541 availability is an important driver of tree growth and primary production at Paracou ([Aguilos](#)
542 [et al. 2018](#), [Wagner et al. 2012, 2014a](#)), a typical light-limited tropical forest ([Guan et al. 2015](#),
543 [Wagner et al. 2016](#)). Furthermore, years with positive anomalies in SRad, did not necessarily
544 translate into years with increased heat stress and atmospheric drought stress (Table [S6](#) and
545 Fig. [S2](#)), therefore reducing confounding and opposing effects of light availability and heat or
546 atmospheric drought stress on tree growth. We explored the effects of different climate drivers
547 separately, but there could be interactive effects between climate factors because they are causally
548 linked. Future studies could further improve our understanding of tropical forest sensitivity to
549 climate by embedding the causal associations among climate variables into the model structure,
550 and by explicitly modelling their interactive effects ([Allen et al. 2010, 2015](#), [Hammond et al. 2022](#),
551 [Zuidema et al. 2022](#)). Neighbourhood crowding was the strongest driver of tree growth at Paracou,
552 confirming the importance of neighbourhood interactions for tropical forest dynamics ([Dawkins](#)
553 [1959](#), [Canham et al. 2004](#), [Fortunel et al. 2018](#), [Uriarte et al. 2016a](#), [Zambrano et al. 2017](#)).

554 Neighbourhood crowding overall reduced tree growth across the 300 focal species, in line with
555 previous work across forest systems ([Kunstler et al. 2016](#)). Importantly, we provide first evidence
556 that climate anomalies can interact with neighbourhood crowding to shape tropical tree growth,
557 thereby attenuating their respective separate effects. In particular, the negative (Tmax, VPD,
558 CWD) and positive (SRad) effects of climate anomalies on tree growth were attenuated in more
559 crowded neighbourhoods. Denser neighbourhoods may result into higher levels of canopy closure,
560 decreasing light availability ([Gaudio et al. 2017](#), [Ghuman and Lal 1987](#)), but simultaneously pro-
561 viding thermal insulation ([Fetcher et al. 1985](#), [Gaudio et al. 2017](#), [Ghuman and Lal 1987](#)), thereby
562 sustaining a more favourable micro-climate during extreme macro-climatic events ([De Frenne et al.](#)
563 [2013, 2019](#)). Contrary to our expectation, more crowded trees were also less sensitive to CWD
564 anomalies, indicating that buffering effects might out-weigh increased competition for soil water
565 during drought. During periods of lower soil water content, more crowded trees may have benefited
566 from complementary neighbourhood water uptake, hydraulic redistribution or improved water re-
567 tention through higher root densities ([Grossiord et al. 2014c,b](#), [Grossiord 2020](#), [Hafner et al. 2021](#)).

568 Previous studies have also shown mitigating effects of neighbourhood diversity or species richness
569 on tree growth response to drought across forest biomes (Fichtner et al. 2020, Gillerot et al. 2021,
570 Grossiord et al. 2014a, O'Brien et al. 2017, Pardos et al. 2021), in contrast with findings showing
571 exacerbating effects of stand or neighbourhood densities on tree demographic response to climatic
572 stresses in temperate (Bottero et al. 2017) and Mediterranean (Astigarraga et al. 2020, Gómez-
573 Aparicio et al. 2011) forests. Our results suggest that accounting for the interactive effects of
574 climate and neighbours offers a promising way towards an improved understanding of tropical
575 forest resistance and resilience to climate change.

576 **Disturbance increases tropical forest sensitivity to climate anomalies** 577 **and neighbourhood crowding**

578 As expected, disturbed plots were more sensitive (i.e. showed greater tree growth reductions)
579 to separate and joint effects of climate anomalies and neighbourhood crowding than undisturbed
580 plots at Paracou (Fig. 3 a-d), highlighting the lasting impact of human activities such as log-
581 ging and thinning on tropical forest dynamics (Hérault et al. 2010, Hérault and Piponiot 2018,
582 Hiltner et al. 2021, Fargeon et al. 2016, Piponiot et al. 2016). Differences between disturbed and
583 undisturbed plots in effect sizes of climate anomalies and neighbourhood crowding may originate
584 from differences in tree community composition. Indeed, disturbed plots at Paracou harbor more
585 fast-growing species (Mirabel et al. 2020, 2021), which tend to be more sensitive to climate anoma-
586 lies, as shown in other tropical forests (Bauman et al. 2022a, Esquivel-Muelbert et al. 2020). The
587 higher abundance of fast growing species and individuals on disturbed plots was also reflected
588 in the higher community-level intrinsic growth rate (α_0) of disturbed plots (Fig. S1 and Table
589 S2). While higher sensitivity of disturbed communities to environmental drivers is consistent with
590 expectations from the 'fast-slow' spectrum (Reich 2014), we show that this trend extends to in-
591 creased susceptibility to biotic stressors such as neighbourhood crowding (Fig. 4 a-b, Table S4).
592 In addition, greater canopy openness in disturbed plots may lead to more severe climate effects
593 through tighter coupling of micro- and macro-climatic conditions (De Frenne et al. 2013, 2019,
594 Ghuman and Lal 1987, Von Arx et al. 2012).

595 We further demonstrate that interactive effects of climate and neighbours (i.e. $\beta_{4,0}$) can shift from
596 negative to positive depending on forest disturbance history at Paracou. In particular, denser
597 neighbourhoods reinforced soil water stress in undisturbed plots, while they acted as a buffer
598 against soil water stress in disturbed plots. This suggests that in disturbed plots, positive biotic
599 interactions (e.g. complementary resource use between neighbours and direct or indirect facilita-
600 tive effects of neighbouring trees) can mitigate competitive effects for soil water during drought.
601 Disturbed plots typically have more and larger canopy gaps than undisturbed plots, and soil drying
602 (and thus water availability) is controlled by evaporation from the soil surface in large forest gaps,
603 but by root water extraction in the dense understory and small forest gaps (Marthews et al. 2008).
604 In line with the stress gradient hypothesis, our results suggest that positive biotic interactions may
605 become more important under more stressful environmental conditions at Paracou (Bertness and
606 Callaway 1994, Brooker et al. 2007, Callaway 1995, Callaway and Walker 1997, Isbell et al. 2015).

607 Neutral crowding indices have recently been suggested to quantify silvicultural treatments (Yue
608 et al. 2022), but in this study they were insufficient to capture all dimensions in disturbance history.
609 Logging effects on forest communities involve not only alterations in forest structure, but also in
610 forest composition. In addition, previous work in temperate and Mediterranean forests suggested
611 that forest management via thinning may help to alleviate the negative impact of climate change
612 on forest dynamics (Astigarraga et al. 2020, Gómez-Aparicio et al. 2011), but our study provides
613 a more nuanced perspective in tropical forests where the interactive effects of neighbourhoods
614 and climate may change from negative to positive depending on the specific climatic variable.
615 Given that more than half of the world’s tropical forests are designated production forests (Blaser
616 et al. 2011), our results warrant closer examination of how logging and land use practices affect
617 neighbourhood interactions and the resistance and resilience of tropical forests to future climate
618 change (Hiltner et al. 2021)

619 **Traits mediate tree growth response to climate anomalies and neigh-** 620 **bourhood crowding**

621 In line with expectations from the 'fast-slow' economic spectrum (Reich 2014), high species in-
622 trinsic growth rates were related to acquisitive strategies for carbon and water (Fig. S1 B). Fast
623 growing species had high SD and low $\delta^{18}\text{O}$, highlighting the key role of stomatal conductance and
624 transpiration rates for efficient carbon assimilation (Drake et al. 2013, Hepworth et al. 2015, Jarvis
625 1981, Poorter and Bongers 2006, Wong et al. 1979). Fast-growing species also exhibited leaf and
626 wood traits pertaining to acquisitive strategies such as lower L_{thick} , L_{though} , and WSG, supporting
627 previous findings that a species investment into tissue longevity comes at higher construction costs
628 (Hérault et al. 2011, Philipson et al. 2014, Poorter et al. 2008, 2010, Reich 2014, Wright et al.
629 2010).

630 Focusing on ca. 100 species that make up >70% of total stems and basal area at Paracou, our
631 study showed that the effects of climate on tree growth were mediated by different traits depending
632 on the climate variable (Fig. 5 b-c). Leaf water-related traits overall mediated the negative effects
633 of climate anomalies related to heat and drought stress. More specifically, species that prioritise
634 water-conservation over carbon gain (e.g. low SD and high $\delta^{18}\text{O}$) were less sensitive to heat and
635 atmospheric drought stress. These functional strategies reduced species' potential for fast growth,
636 but may allow species to maintain photosynthesis and CO_2 assimilation during periods of elevated
637 temperature and atmospheric evaporative demands (Caine et al. 2019, Hepworth et al. 2015, Reich
638 2014, Wang and Wen 2022a).

639 The mitigating effects of traits linked to carbon-water relations were less clear for tree growth
640 response to soil water stress (CWD), potentially because individual topographic position may lead
641 to a decoupling between growth sensitivity to soil water stress and water conservation capacity
642 (Esteban et al. 2021, Hammond et al. 2022). Still, the growth of species with more negative π_{tlp}
643 was less impacted by soil drought stress. Lower π_{tlp} (Table 1) captures species' drought-related
644 mortality risks (Powell et al. 2017) and distribution along aridity gradients (Bartlett et al. 2012b),
645 but previous work from different biomes found mixed evidence for species drought-related growth

646 reductions (McGregor et al. 2021, Smith-Martin et al. 2023, Song et al. 2022).

647 While we predicted species with higher g_{\min} would suffer stronger drought-related growth declines
648 (Blackman et al. 2016, Duursma et al. 2019), we found they were less vulnerable to atmospheric
649 drought stress. As elevated VPD leads to stomatal closure (Grossiord et al. 2020), residual water
650 loss could maintain evaporative cooling (given non limiting soil water conditions), which potentially
651 prevents irreversible leaf tissue damage through overheating (Drake et al. 2018). The maintenance
652 of evaporative cooling could thus allow species to quickly resume carbon assimilation after atmo-
653 spheric drought stress, while simultaneously reducing post-drought respiration rates linked to tissue
654 repair (Drake et al. 2018, Powell et al. 2017).

655 Leaf and wood morphological traits also captured tree growth response to climate anomalies at
656 Paracou. Species with conservative tissues (i.e. lower SLA, higher L_{thick} and $\text{Bark}_{\text{thick}}$) grew faster
657 at higher solar radiation (Fig. 5 a). During atmospheric drought and heat stress, species with
658 thicker and tougher leaves may experience less tissue damage through desiccation, thus reducing
659 post-drought costs for tissue repair (Poorter et al. 2010, Nardini 2022), while species with larger
660 leaves have higher evaporative cooling through transpiration (Gates 2003, Schuepp 1993, Wright
661 et al. 2017), leading to less growth reductions. Moreover, species with high WSG were less vulner-
662 able to heat stress, atmospheric and soil drought stress at Paracou, confirming previous findings
663 (Greenwood et al. 2017, Wagner et al. 2014b).

664 Slow-growing, resource-conservative species tend to be more tolerant to competition at Paracou.
665 In particular, species conservative for carbon (with higher L_{though} and WSG) were less sensitive to
666 neighbourhood crowding, as found in previous studies across forest biomes (Fortunel et al. 2016,
667 Kunstler et al. 2016). In addition, species conservative for water (with lower SD, stomatal conduc-
668 tance and transpiration rates) were also less sensitive to neighbourhood crowding, highlighting the
669 role of water limitation in these tropical wet forests. This is a similar suite of traits that mediated
670 growth response to heat stress, suggesting that species suffering most from T_{\max} anomalies are
671 also experiencing stronger neighbourhood effects (Table S4).

672 However, species traits poorly captured the interactive effects of climate anomalies and neighbour-

673 hood crowding on tree growth at Paracou (Fig. 5 a-d). Trait differences between neighbouring
674 trees rather than the traits of the focal tree alone may be playing a key role in driving the inter-
675 active effects of climate anomalies and neighbourhood crowding on tree growth, in particular as
676 trait differences can reflect niche partitioning and competitive hierarchies between neighbouring
677 individuals (Fortunel et al. 2016, Kunstler et al. 2016). To clarify this, future work could explore
678 the relative contribution of focal tree traits and trait differences in mediating tree growth response
679 to the interaction between climate extremes and neighbourhood crowding.

680 **Conclusion**

681 Tropical trees are particularly sensitive to climate stress and interactions with neighbours, sug-
682 gesting that ongoing climate change and associated changes in forest composition and structure
683 may result in a long-term slowdown of carbon sequestration in tropical forests. Our study shows
684 that climate anomalies and neighbourhood crowding can interact positively in shaping tropical
685 tree growth, suggesting that trees growing in more crowded neighbourhood may be less sensitive
686 to climate extremes. Logged forests suffered considerably stronger growth reductions in response
687 to water stress, suggesting lower resistance of managed tropical forests to climate change. Our
688 findings reveal that functional traits, in particular related to water relations, can capture differ-
689 ences in species sensitivities to atmospheric and soil water stress and neighbourhood crowding
690 (though not their interactive effects), that can be implemented in models to improve predictions
691 of the future of these highly diverse ecosystems.

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713 **Author Contributions**

714 Daniela Nemetschek, Claire Fortunel and Géraldine Derroire designed the study. Daniela Nemetschek,
715 Marion Boisseaux, Johanna Auer, Vinciane Badouard, Christopher Baraloto, Quentin Le Blaye,

716 Damien Bonal, Sabrina Coste, Elia Dardevet, Claire Fortunel, Patrick Heuret, Sébastien Levion-
717 nois, Isabelle Maréchaux, Clément Stahl, Jason Vleminckx, Wolfgang Wanek and Camille Ziegler
718 collected or contributed trait data. Daniela Nemetschek formatted and vetted the plot census,
719 climate and functional trait data, with help from Claire Fortunel, Géraldine Derroire, Eric Marcon
720 and Marion Boisseaux. Daniela Nemetschek, Claire Fortunel and Géraldine Derroire designed the
721 tree growth models, with input from Eric Marcon, David Bauman, Sean M. McMahon and Mélaine
722 Aubry-Kientz. Daniela Nemetschek performed the analyses, with help from Claire Fortunel, Géral-
723 dine Derroire and Eric Marcon. Daniela Nemetschek and Claire Fortunel led the interpretation
724 of the results and the writing of the first draft, with frequent input from Géraldine Derroire. All
725 authors contributed to revisions and gave final approval for publication.

726 **Data Availability Statement**

727 Plot census data was extracted from the Paracou Station database, for which access is available at
728 <https://dataverse.cirad.fr/dataverse/paracou>, with corresponding DOIs: [10.18167/DVN1/NSCWF0](https://doi.org/10.18167/DVN1/NSCWF0);
729 [10.18167/DVN1/Q8V2YI](https://doi.org/10.18167/DVN1/Q8V2YI); [10.18167/DVN1/LIVCEK](https://doi.org/10.18167/DVN1/LIVCEK); [10.18167/DVN1/HWTD4U](https://doi.org/10.18167/DVN1/HWTD4U);
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732 **Conflict of interest**

733 The authors declare there are no competing interests.

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1469 **List of Supporting Information**

1470 See PDF file SupportingInformation_1.pdf

1471 **Figure S1.** M1-model standardised regression coefficients of community level intercepts, effect of
1472 DBH and M2-model trait effects on intercepts

1473 **Figure S2.** M1-CWD model standardised regression coefficients of species-level intercepts in
1474 undisturbed and disturbed plots.

1475 **Figure S3.** Bi-plot of principal component analysis (PCA) on climate variables.

1476 **Supplementary Methods S1.** Corrections of tree inventory data.

1477 **Supplementary Methods S2.** R code for M1- and M2-models.

1478

1479 See Excel file SupportingInformation_2.xlsx

1480 **Table S1.** Conditional and marginal R2 estimates for M1- and M2-models

1481 **Table S2.** Standardised regression coefficients of community level parameters and group-level
1482 sigmas for M1-models.

1483 **Table S3.** Summarised species-level responses to model covariates for M1-models.

1484 **Table S4.** Estimates of correlations (ρ) between species-level parameters for M1-models.

1485 **Table S5.** Standardised regression coefficients of community level parameters and group-level
1486 sigmas for M2-models.

1487 **Table S6.** Pearson correlation coefficients among mean anomalies of the 4 climate variables.