

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

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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

1. Climate extremes and biotic interactions at the neighbourhood scale affect tropical forest dynamics with long-term consequences for biodiversity, global carbon cycling and climate change mitigation. However, forest disturbance may change crowding intensity, and thus the relative contribution of climate extremes and neighbourhood interactions on tree growth, thereby influencing tropical forest resistance and resilience to climate change. Here, we aim to evaluate the separate and interactive effects of climate and neighbours on tree growth in old-growth and disturbed tropical forests.

We used 30 years of growth measurements for over 300 tropical tree species from 15 forest 2.36 plots in French Guiana to investigate the separate and interactive effects of climate anomalies 37 (in solar radiation, maximum temperature, vapor pressure deficit and climatic water deficit) and 38 neighbourhood crowding on individual tree growth. Contrasting old-growth and selectively-logged 39 forests, we also examined how disturbance history affects tree growth sensitivity to climate and 40 neighbours. Finally, for the most abundant 100 species, we evaluated the role of 12 functional 41 traits pertaining to water relations, light and carbon use in mediating tree growth sensitivity to 42 climate anomalies, neighbourhood crowding, and their interactions. 43

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

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

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

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

60 Résumé

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

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

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

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

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

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

98 Introduction

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

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

125 histories.

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

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

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

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

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

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

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

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

¹⁸⁷ Materials and Methods

188 Study site

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

²⁰¹ Tree growth and neighbourhood data

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

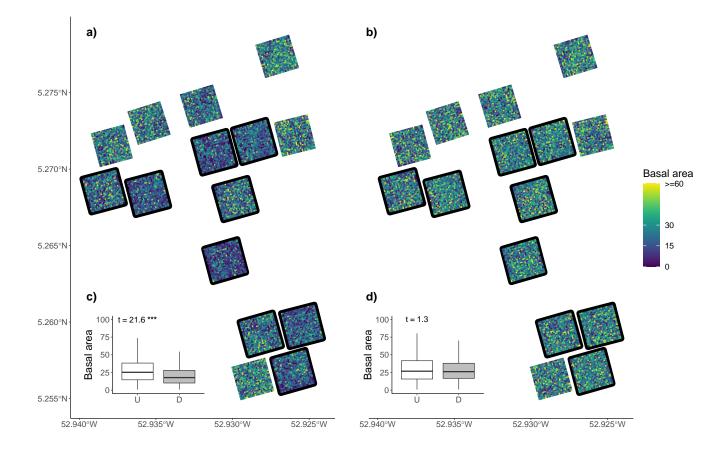


Figure 1. Spatial dimension of the 15 permanent forest plots and stand density in $10 \text{ m} \times 10 \text{ m}$ quadrats, given as basal area (m² ha⁻¹), in a) 1991 and b) 2019. Disturbed plots are denoted by black contours. Box plots show differences in basal area between the 6 undisturbed (U) and 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.

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

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

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

The growth of an individual tree *i* can be influenced by its N(i) neighbours within a given radius via their size (DBH²) and the inverse of their distance to the focal tree (*d*) (Canham et al. 2004, Fortunel et al. 2016, Uriarte et al. 2010). For each focal tree individual *i* at the start of the growth census interval t - 2, we calculated its neighbourhood crowding index (NCI_{*i*,*t*-2}) as the weighted sum of all neighbours N(i) within a 10 m radius of individual *i* (Fortunel et al. 2018, Lasky et al. 2014, Uriarte et al. 2016a), as:

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

We chose a 10 m radius to be able to compare with previous studies conducted in tropical forests (Fortunel et al. 2018, Lasky et al. 2014, Uriarte et al. 2016a), and well capture neighbourhood effects while keeping edge effects low (Zambrano et al. 2020). To avoid incomplete neighbourhoods, all focal tree individuals closer than 10 m to the plot edge were excluded. We kept as neighbours individuals with human-induced damage, missing or uncertain botanical determination, estimated circumferences, and corrected abnormal diameter increments (see: Supplementary Methods S1 for 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) capturing heat stress, vapour pressure deficit (VPD) relating to atmospheric evaporative demands and
climatic water deficit (CWD) capturing soil water availability by relating precipitation to evapotranspiration (Bauman et al. 2022a, Choat et al. 2018, Cunningham 2005, Doughty and Goulden
2008, Grossiord et al. 2020, Wagner et al. 2012). We extracted climate variables from TerraClimate, a high-resolution global data set of monthly climate variables and climatic water balance
(Abatzoglou et al. 2018).

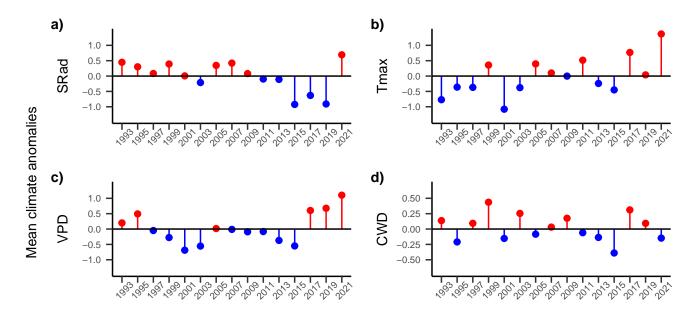
We identified anomalous years over the study period by calculating mean climate anomalies, ex-239 pressed as the deviation of climate variables from their 30-year historical average, over each of 240 the two-year census intervals. To this aim, we calculated the 30-year baseline (historical mean, 241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

$$CA_t = \frac{1}{M} \sum_{m=1}^{M} \frac{\mu_{m,t} - \mu_{m,\text{baseline}}}{\sigma_{m,\text{baseline}}}$$
(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

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



Census Years

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.

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

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

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

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

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

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

²⁹⁶ Bulk leaf δ^{18} O and δ^{13} 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 δ^{18} 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 δ^{13} 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.

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

Organ	Trait type	Trait	Abbreviation (Unit)	Function	Description	References	z
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	δ ¹⁸ Ο (‰)	Carbon-water use	Plants with high δ^{18} 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	δ ¹³ C (‰)	Carbon-water use	Plants with high δ^{13} 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	πtlp (MPa)	Drought tolerance	Plants with low $\pi_{t D}$ 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	gmin (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 (cm²)	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.	Osnas et al. 2013, Wright et al. 2004	101
Leaf	Structure	Leaf thickness	Lthick (mm)	Carbon use	L _{thick} relates to structural support, physical resistance and leaf lifespan.	Vile et al. 2005	100
Leaf	Structure	Leaf toughness	Ltough (N)	Carbon use	L _{tough} relates to structural support, physical resistance and leaf lifespan.	Kitajima and Poorter 2010	100
Mood	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	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

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

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

storage capacity

313 Models

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

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

We modeled individual log(AGR_t) as a linear function of (i) tree size at the beginning of the census interval (DBH_{t-2}), (ii) monthly climate anomalies averaged over the census interval (CA_t), (iii) neighbourhood crowding at the beginning of the census interval (NCI_{t-2}) and (iv) the interaction between climate anomalies and neighbourhood crowding (CA_t × NCI_{t-2}) (Bauman et al. 2022a, Fortunel et al. 2018). To allow direct comparison between covariates and ease assignment of plausible weakly-informative prior to the parameters, log(AGR_t) and all covariates, except for

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

349 M1: "no trait models"

To manage model complexity in assessing tree growth response to the separate and interactive 350 effects of climate anomalies and neighbourhood crowding and examine the influence of forest 351 disturbance history, we fitted models separately for each of the four climate variables (SRad, 352 Tmax, VPD and CWD) and for (i) all 15 plots combined, (ii) the six undisturbed plots and (iii) 353 the nine disturbed plots, resulting in a total of 12 M1-models. To ensure sufficient statistical power, 354 M1-models were run on observed growth for all species with at least 100 growth measurements. 355 M1-models were therefore based on 48,203, 20,688 and 27,515 individuals, belonging to 310, 306 356 and 307 species, respectively. To allow for direct comparison of parameter estimates between 357 control and disturbed forest, we standardised and centered growth and all model covariates before 358 splitting the data set (Ren et al. 2021). For each individual i of species s between censuses t-2359 and t, we modeled tree growth as: 360

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

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

361

$$= \begin{pmatrix} \alpha_{s} \\ \beta_{1s} \\ \beta_{2s} \\ \beta_{3s} \\ \beta_{4s} \end{pmatrix} \sim MVNormal \begin{bmatrix} \alpha_{0} \\ \beta_{1,0} \\ \beta_{2,0} \\ \beta_{3,0} \\ \beta_{4,0} \end{pmatrix}, S$$
 (eqn 4c)
$$= \begin{pmatrix} \sigma_{\alpha_{s}} & 0 & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & \sigma_{\beta_{1s}} & 0 & 0 & 0 \\ 0 & 0 & \sigma_{\beta_{2s}} & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{2s}} & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{2s}} & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{2s}} & 0 \\ 0 & 0 & 0 & \sigma_{\beta_{2s}} & 0$$

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

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

using the following weakly informative priors:

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

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

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

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

$$R \sim LKJcorr(2)$$

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

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

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

389 M2: "trait models"

To assess the effect of traits on species intrinsic growth α_s , and growth response to climate anomalies β_{2s} , neighbourhood crowding β_{3s} and their joint effects β_{4s} , we fitted M2-models for a subset of 81-102 tree species (representing over 40,000 trees), for which we had available trait data (Table 1). To manage model complexity, M2-models were fitted separately for each of the four climate variables (SRad, Tmax, VPD and CWD) and for each of the 12 functional traits, resulting in a total of 48 M2-models. While the hierarchical structure, variance-covariance matrix and equation 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:

$$\begin{pmatrix} \alpha_s \\ \beta_{1s} \\ \beta_{2s} \\ \beta_{3s} \\ \beta_{4s} \end{pmatrix} \sim MV\mathcal{N} \begin{bmatrix} \alpha_0 + \alpha_1 \times Trait_s \\ \beta_{1,0} \\ \beta_{2,0} + \beta_{2,1} \times Trait_s \\ \beta_{3,0} + \beta_{3,1} \times Trait_s \\ \beta_{4,0} + \beta_{4,1} \times Trait_s \end{bmatrix}, S$$
 (eqn 5)

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

417 Model fitting

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

432 **Results**

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

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

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

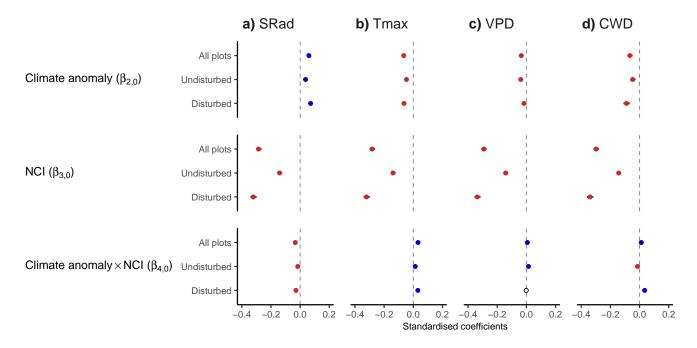


Figure 3. Community-level effects of climate anomaly ($\beta_{2,0}$), neighbourhood crowding (NCI, $\beta_{3,0}$), and their interaction (Climate anomaly×NCI, $\beta_{4,0}$) on tree growth (M1-models). Standardised coefficients from a) SRad, b) Tmax, c) VPD and d) CWD models are shown for all 15 plots 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 β_{4s} 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.

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

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

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

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

The effects of climate anomalies (M1, $\beta_{2,0}$) and neighbourhood crowding (M1, $\beta_{3,0}$) were consistent between the six undisturbed and nine disturbed plots, but were usually stronger in disturbed plots (except for VPD anomalies). In particular, tree growth sensitivity to neighbourhood crowding was twice as strong in disturbed plots than undisturbed plots. In addition, the interactive effects between climate anomalies and neighbourhood crowding were usually greater in disturbed plots, further attenuating their separate effects in these forests. More crowded trees in disturbed plots were more buffered against climate anomalies (except for the VPD anomalies:NCI interaction).
However, while negative effects of CWD anomalies on growth were mitigated by neighbourhood
crowding in disturbed plots, they were reinforced in undisturbed plots (Fig. 3).

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

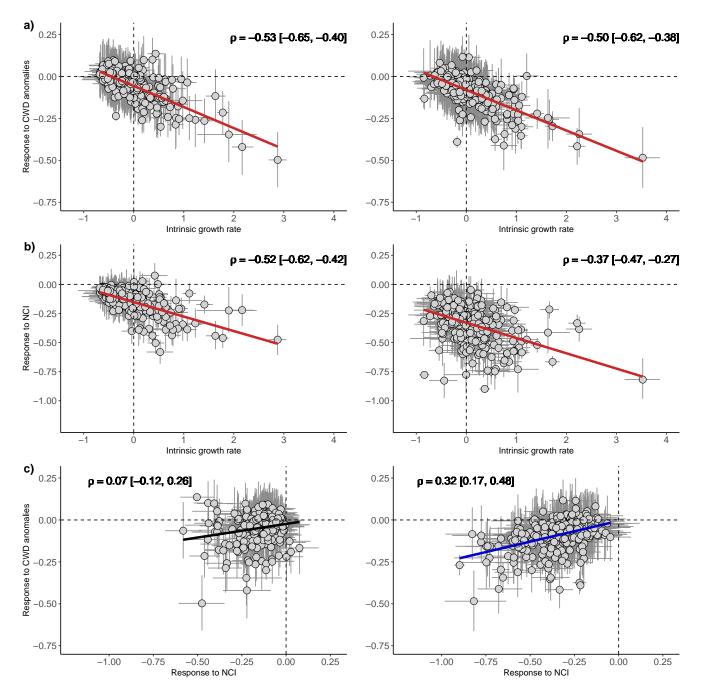


Figure 4. Correlations between a) species intrinsic growth rates α_s and species-level growth response to CWD anomalies (β_{2s}), b) species intrinsic growth rates α_s and species-level growth response to neighbourhood crowding (NCI, β_{3s}) and c) species-level growth response to NCI (β_{3s}) and CWD 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

Parameter estimates of community-level tree growth regressions were consistent between the M1models (310 focal species) and M2-models (subset of species with available trait information, Table S2 and Table S5). Fast-growing tree species (i.e. with high intrinsic growth rates, α_s) had higher SD, but lower δ^{18} O, LA, L_{thick}, L_{though} and WSG (Fig. S1 B and Table S5). Species traits influenced tree growth response to climate anomalies, neighbourhood crowding and their interaction, either reinforcing (values of $\beta_{2-4,1}$ moved β_{2-4s} further away from zero with increasing trait value) or attenuating them (values of $\beta_{2-4,1}$ moved β_{2-4s} closer to zero with increasing trait value) (Fig. 5).

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

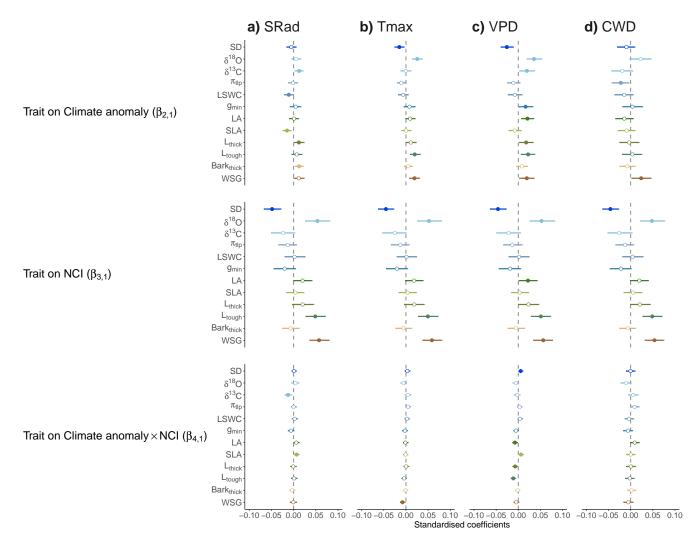


Figure 5. M2-models: trait effects on tree growth response to climate anomalies $\beta_{2,1}$, neighbourhood crowding $\beta_{3,1}$ and the climate anomaly-crowding interaction $\beta_{4,1}$ (see: eqn 5). Standardised coefficients from a) SRad, b) Tmax, c) VPD and d) CWD models are shown for each of the 12 trait models: stomatal density (SD), leaf oxygen (δ^{18} O) and carbon (δ^{13} C) isotope composition, water potential at turgor loss point (π_{tlp}), leaf saturated water content (LSWC), minimum conductance (g_{min}), leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}), bark thickness (Bark_{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

In this study, we examined the separate and interactive effects of climate anomalies and neighbours on tree growth, combining 30 years of climate and tree growth data for over 300 species from 15 permanent forest plots, with contrasting disturbance histories. For the most abundant species (ca. 100), we further evaluated the effect of 12 traits pertaining to water relations, light capture and carbon use (Table 1), in mediating tree growth response to climate and neighbours.

⁵¹⁶ Climate anomalies and neighbourhood crowding reduce tropical tree ⁵¹⁷ growth

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

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

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

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

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

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

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

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

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

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

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

The mitigating effects of traits linked to carbon-water relations were less clear for tree growth response to soil water stress (CWD), potentially because individual topographic position may lead to a decoupling between growth sensitivity to soil water stress and water conservation capacity (Esteban et al. 2021, Hammond et al. 2022). Still, the growth of species with more negative π_{tlp} was less impacted by soil drought stress. Lower π_{tlp} (Table 1) captures species' drought-related mortality risks (Powell et al. 2017) and distribution along aridity gradients (Bartlett et al. 2012b), but previous work from different biomes found mixed evidence for species drought-related growth reductions (McGregor et al. 2021, Smith-Martin et al. 2023, Song et al. 2022).

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

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

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

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

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

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713 Author Contributions

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

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

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;

⁷²⁹ 10.18167/DVN1/Q8V2YI; 10.18167/DVN1/LIVCEK; 10.18167/DVN1/HWTD4U;

10.18167/DVN1/HIGNWQ. Species mean values for the six leaf water-related traits are available
 at 10.5281/zenodo.10396927

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

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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.

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- ¹⁴⁷⁹ See Excel file SupportingInformation_2.xlsx
- ¹⁴⁸⁰ Table S1. Conditional and margignal R2 estimates for M1- and M2-models
- Table S2. Standardised regression coefficients of community level parameters and group-level
 sigmas for M1-models.
- ¹⁴⁸³ Table S3. Summarised species-level responses to model covariates for M1-models.
- Table S4. Estimates of correlations (ρ) between species-level parameters for M1-models.
- Table S5. Standardised regression coefficients of community level parameters and group-level
 sigmas for M2-models.
- ¹⁴⁸⁷ Table S6. Pearson correlation coefficients among mean anomalies of the 4 climate variables.