RESEARCH ARTICLE

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

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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.

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

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, tree growth, tropical forest, water relations

1 | INTRODUCTION

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

Tropical forest response to climate extremes is the compounded outcome of individual tree responses, which may depend on local biotic interactions, such as interactions between neighbouring trees. While crowding by neighbours generally reduces tropical tree growth (Dawkins, 1959; Fortunel et al., 2018; Gourlet-Fleury & Houllier, 2000; Uriarte et al., 2004, 2010), the net effects of neighbourhood interactions may change from negative to positive under specific environmental conditions (Fichtner et al., 2020; Grossiord, 2020) such as with water levels (Aakala et al., 2018) and

disturbance history. For instance, competition for water may accentuate the negative effects of water limitations on tree growth, as shown in temperate and Mediterranean forests (Astigarraga et al., 2020; Bottero et al., 2017; Gómez-Aparicio et al., 2011). Conversely, species interactions can alter the depth of soil water uptake (Grossiord, Gessler, Granier, Berger, et al., 2014) or transpiration response to increasing drought stress (Grossiord, Gessler, Granier, Pollastrini, et al., 2014; Haberstroh & Werner, 2022). Yet, the effects of climate on tree growth have rarely been evaluated together with the effects of neighbourhood crowding in tropical forests (but see: Uriarte, Lasky, et al., 2016), and we still know little about the extent to which the interaction between climate extremes and neighbourhood interactions can attenuate or exacerbate their separate effects on tree growth, especially in tropical forests with different disturbance histories.

More than half of the world's tropical forests are designated production forests (Blaser et al., 2011), and forest management such as selective logging and thinning has long-lasting effects on forest composition, diversity and structure (Cannon et al., 1994; Clark & Covey, 2012; Finegan & Camacho, 1999; Mirabel et al., 2021; Osazuwa-Peters et al., 2015), which may alter forest resistance and resilience to extreme climate events (Hiltner et al., 2021). Specifically, disturbed forests host more light-demanding tree species than old-growth forests (Baraloto et al., 2012; Carreño-Rocabado et al., 2012; Kuusipalo et al., 1996; Mirabel et al., 2020, 2021; Whitmore, 1989), and these fast-growing species may be more sensitive to climate extremes (Bauman, Fortunel, Cernusak, et al., 2022; Uriarte, Schwartz, et al., 2016) and neighbourhood

crowding (Fortunel et al., 2016). Moreover, selective logging and thinning creates gaps, thereby increasing the openness of forest canopies and changing micro-climatic conditions (Ghuman & Lal, 1987; Peña-Claros et al., 2008). These logging gaps influence tree growth rates (Baraloto et al., 2005; Finegan et al., 1999; Hérault et al., 2010; Peña-Claros et al., 2008; Silva et al., 1995), but it remains unclear how disturbance history may influence tree growth responses to climate and neighbours.

Species differences in growth sensitivity to climate and neighbours likely depend on their functional strategies. While commonly measured traits pertaining to light capture, nutrient and carbon use such as specific leaf area and wood density can capture species differences in tree growth response to neighbourhood crowding (Fortunel et al., 2016; Kunstler et al., 2016), they are not always good proxies of species sensitivity to drought (Anderegg et al., 2018; Powell et al., 2017; Powers et al., 2020; Wagner, Rossi, Baraloto, et al., 2014, but see: Greenwood et al., 2017, Serra-Maluquer et al., 2022, Uriarte, Lasky, et al., 2016). A promising way forward is to integrate leaf traits that directly link to plant carbon-water relations or physiological responses to heat and water stress (Anderegg et al., 2018; Barros et al., 2019; McGregor et al., 2021; Powell et al., 2017; Powers et al., 2020; Rowland et al., 2021; Serra-Maluquer et al., 2022; see Table 1). For instance, stomatal density (Drake et al., 2013; Machado et al., 2021) and oxygen and carbon isotope composition (Farquhar et al., 1989, 2007; Moreno-Gutiérrez et al., 2012) can determine trade-offs between carbon assimilation and water loss at the leaf level under water-limited conditions (Guerrieri et al., 2019; Prieto et al., 2018; Scheidegger et al., 2000; Wang & Wen, 2022b). Leaf water potential at turgor loss point is linked to species abilities to maintain key plant functions and growth during drought (Bartlett et al., 2016; Bartlett, Scoffoni, & Sack, 2012; Maréchaux et al., 2018). Leaf minimum conductance (Blackman et al., 2019; Duursma et al., 2019; Machado et al., 2021) and leaf saturated water content (Blackman et al., 2019; Luo et al., 2021) may indicate species ability to resist or avoid heat- and drought-induced desiccation of plant tissue, and hence the potential for rapid post-drought growth. These leaf traits likely influence competition for water, but no study so far has evaluated their role in mediating tree growth response in the context of neighbourhood effects.

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

1. How do climate anomalies and neighbourhood crowding influence tree growth? We expect tree growth to decline with positive anomalies in maximum temperature (Tmax), atmospheric

evaporative demand (i.e. vapour pressure deficit, VPD) and climatic water deficit (CWD). As higher levels of solar radiation (SRad) lead to increased light availability, but also higher temperature and vapour pressure deficit, positive anomalies in SRad could either enhance or reduce tree growth. We further expect tree growth to decrease with higher neighbourhood crowding. Finally, we expect that climate anomalies and neighbourhood crowding can interact, thereby accentuating or attenuating their separate effects on tree growth.

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.

2 | MATERIALS AND METHODS

2.1 | Study site

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

2.2 | Tree growth and neighbourhood data

In each of the 15 forest plots, all trees ≥ 10 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 one or

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) and Machado et al. (2021)	87
Leaf	Chemistry	Bulk leaf oxygen stable isotope	$\delta^{18}O$ (‰)	Carbon-water use	Plants with high $\delta^{18}O$ have low stomatal conductance and transpiration rates and thus conserve water at the expense of carbon assimilation	Farquhar et al. (2007), Moreno-Gutiérrez et al. (2012) and Scheidegger et al. (2000)	81
Leaf	Chemistry	Bulk leaf carbon stable isotope	$\delta^{13}C$ (‰)	Carbon-water use	Plants with high $\delta^{13}C$ 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) and Scheidegger et al. (2000)	81
Leaf	Physiology	Water potential at turgor loss point	π_{tlp} (MPa)	Drought tolerance	Plants with low π_{tlp} maintain stomatal conductance, hydraulic conductance and photosynthetic gas exchange at lower soil water potential	Bartlett, Scoffoni, Ardy, et al. (2012) and Maréchaux 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) and 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) and 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	Osnas et al. (2013) and Wright et al. (2004)	101

TABLE 1 Continued

Organ	Trait type	Trait	Abbreviation (unit)	Function	Description	References	N
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) and 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) and Serra-Maluquer et al. (2022)	95

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

2-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 (Derroire et al., 2022a, 2022b, 2022c, 2022d, 2022e; Gourlet-Fleury et al., 2004). 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 year^{-1}) from DBH values between censuses t and $t-2$ as:

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

For each individual tree i, we thus calculated AGR for 15 2-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 (≤ -2 cm year^{-1}, resulting from a shift in the point of measurement, and ≥ 5 cm year^{-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 (DBH^2) 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, Lasky, et al., 2016), as:

$$NCI_{i,t-2} = \sum_{j \in N(i)} \frac{DBH_{j,t-2}^2}{d_{i,j}} \quad (2)$$

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, Lasky, et al., 2016), 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).

2.3 | Climate data

We considered four climate variables that have been previously shown to influence tropical tree 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, Fortunel, Cernusak, et al., 2022; Choat et al., 2018; Cunningham, 2005; Doughty & Goulden, 2008; Grossiord et al., 2020; Wagner et al., 2012). We extracted climate
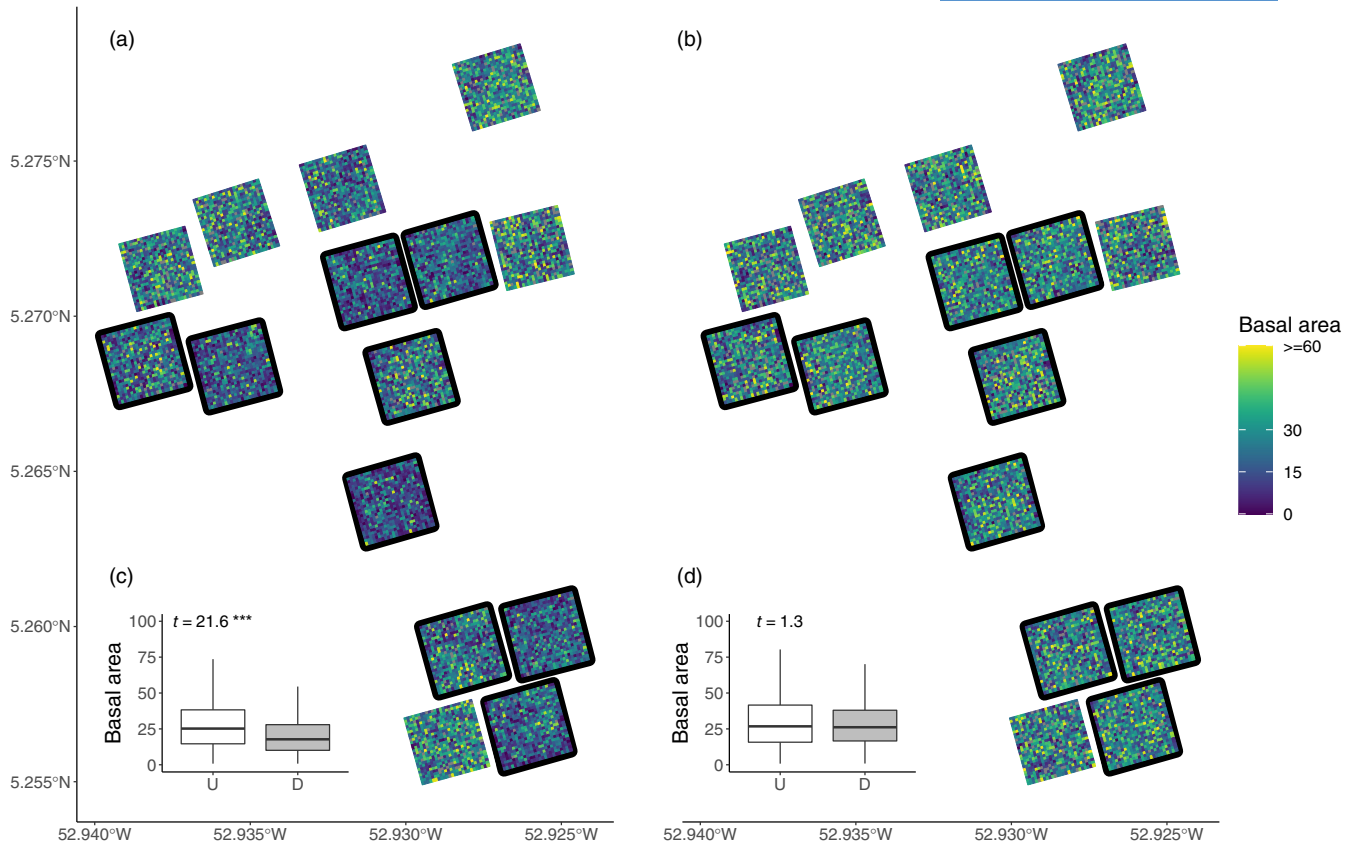
FIGURE 1 Spatial dimension of the 15 permanent forest plots and stand density in $10 \text{ m} \times 10 \text{ m}$ quadrats, given as basal area ($m^2 \text{ ha}^{-1}$), in (a) 1991 and (b) 2019. Disturbed plots are denoted by black contours. Box plots show differences in basal area between the 6 undisturbed (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.

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, expressed as the deviation of climate variables from their 30-year historical average, over each of the two-year census intervals. To this aim, we calculated the 30-year baseline (historical mean, $\mu_{m,baseline}$) and standard deviation ($\sigma_{m,baseline}$) for each month of the year (1–12) for the 1991–2021 period. We then calculated standardised anomalies for each month (1–12) m at time t as the deviation of the mean monthly climate variable $\mu_{m,t}$ from the long-term monthly baseline $\mu_{m,baseline}$ (Bauman, Fortunel, Cernusak, et al., 2022; Rifai et al., 2018). To investigate the effect of mean yearly anomalies on tree growth at 2-year census interval (CA_t), we averaged the standardised monthly anomalies over the $M = 24$ months prior to census t (July$_t$-July$_{t-2}$) as (Aubry-Kientz et al., 2015; Bauman, Fortunel, Cernusak, et al., 2022; Rifai et al., 2018):

$$CA_t = \frac{1}{M} \sum_{m=1}^{M} \frac{\mu_{m,t} - \mu_{m,baseline}}{\sigma_{m,baseline}} \qquad (3)$$

Using this approach, two-year periods with positive anomalies can directly be interpreted as periods in which trees experienced

higher solar radiation (SRad), heat (Tmax), atmospheric (VPD) or soil water (CWD) drought stress than usual (Figure 2).

2.4 | 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 represent 70% of all unique individual stems and 72% of all growth measurements at Paracou. We randomly selected 645 individuals located within the permanent 15 forest plots at Paracou, using the following criteria: (i) botanical identification at the species level, (ii) DBH within species-specific 10th and 90th percentile (to avoid sampling unusually small and large tree individuals), (iii) topographic position corresponding with the species topographic preference (i.e. individuals located at a certain topographic position (bottomland, slope, ridge) were only sampled if more than 10% of distinct stems of that species occur on the given topographic position). As the 102 target species include understory, mid-story and
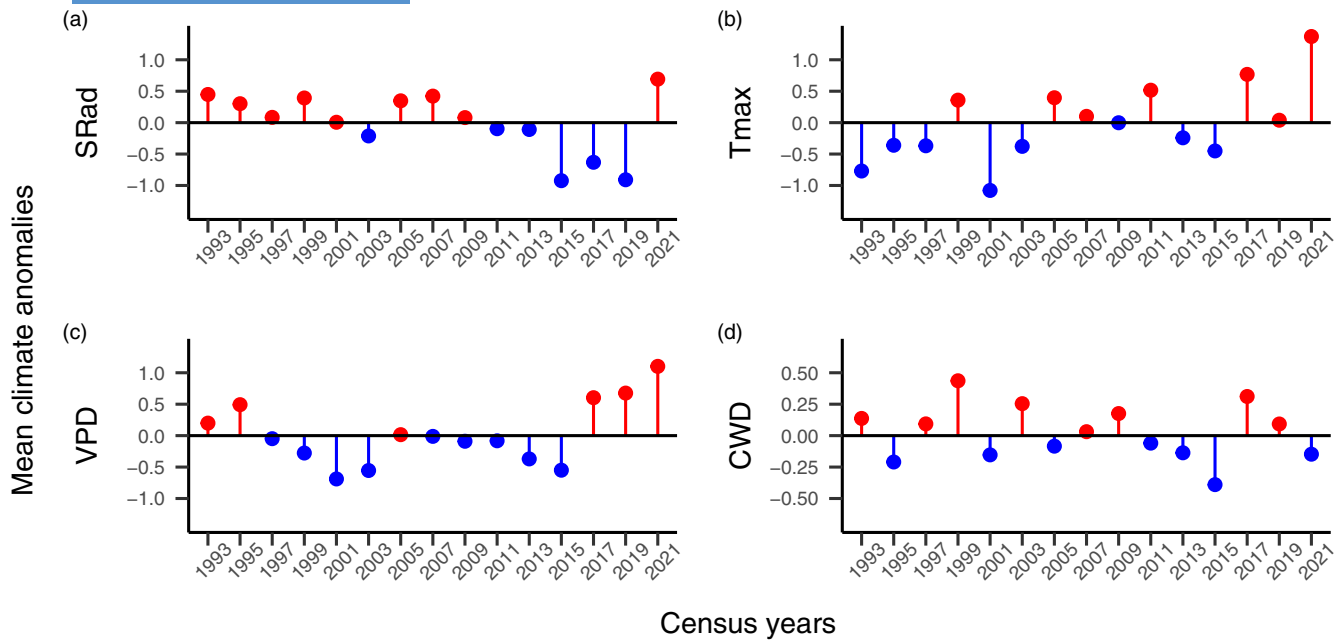
FIGURE 2 Mean standardised climate anomalies at Paracou for the 2-year census intervals over the study period for (a) solar radiation, (b) maximum temperature, (c) vapour pressure deficit and (d) climatic water deficit. Red and blue lines and circles represent positive and negative anomalies, respectively.

canopy species, we sampled only leaves from branches that were exposed to medium light conditions (Dawkins index: 3–4, Alder & Sunnott, 1992), thus excluding branches in full sun or shade. For each of the 645 individuals, we collected one fully expanded and healthy leaf from a healthy branch in the dry season in 2020–2021 for each leaf trait measurement. After harvest with a sling shot in the field, leaves were immediately put into ziplock bags with a moist paper towel and kept in the dark in a cooler to minimise transpiration during transport to the laboratory. No fieldwork permit was required.

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 the abaxial leaf surface at three positions of the widest part of the leaf blade, while avoiding major veins (Voleníková & Tichá, 2001). Imprints were mounted on microscope slides, and pictures were taken at a magnification of 300× using a light microscope (Keyence VHX 7000, Osaka, Japan). We took a minimum of three pictures, one per imprint when possible, for each sampled leaf. We used Fiji ImageJ (Schindelin et al., 2012) to count all complete stomata per image area. Imprint quality and resulting picture quality varied strongly between species and individuals, so we obtained stomata counts for 470 individuals and 87 species.

Leaf osmotic potential was measured using a vapour 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, Scoffoni, Ardy, et al. (2012) and Bartlett, Scoffoni and Sack (2012), 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 3–4 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 Toledo, Switzerland). We obtained saturated weights following the 'partial' rehydration protocol of Vendramini et al. (2002), which provides comparable measurements to the 'complete' rehydration protocol by Garnier et al. (2001) (Vaieretti et al., 2007). We wrapped fresh leaves into paper towels that were previously soaked with de-ionised water, and kept them for 24 h in the dark and at low temperature (4°C) for rehydration. Dry weights were measured after drying leaves for at least 72 h at 60°C (Sapes & Sala, 2021). We calculated LSWC from saturated and dry weights (Barrs & Weatherley, 1962).

Bulk leaf $\delta^{18}O$ and $\delta^{13}C$ were calculated from a composite sample of dried and coarsely chopped leaves, including those used for π_{tlp}, LSWC and g_{min} measurements. Samples were ground to fine powder using a ball mill (Retsch MM200, Hanau, Germany) for 5 min at maximum speed (100 rotations per minute) and further dried in a drying oven for 24 h at 85°C. Aliquots of 0.2 – 0.4 mg per sample were weighed into silver capsules and $\delta^{18}O$ signatures were measured with a high-temperature pyrolysis unit (TCEA) coupled to a Delta V isotope ratio mass spectrometer instrument (Thermo Scientific, Vienna, Austria). Aliquots of 1 – 2 mg per sample were weighed into tin capsules and $\delta^{13}C$ signatures were subsequently determined using an elemental analyser (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 conducted at Paracou (Levionnois et al., 2021; Maréchaux et al., 2015, 2019; Ziegler et al., 2019). We further compiled trait data for the 102 focal tree species for six leaf and wood traits that relate to light capture and carbon use from previous work conducted in French Guiana (Baraloto et al., 2010; Fortunel et al., 2012; Vleminckx et al., 2021). We included leaf area (LA), specific leaf area (SLA), leaf thickness (L_{thick}), leaf toughness (L_{though}), bark thickness ($Bark_{thick}$) and wood specific gravity (WSG, hereafter referred to as wood density; see Table 1). For all subsequent analyses including trait values, we considered species means.

2.5 | 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 modelled 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, Fortunel, Cernusak, et al., 2022; 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, Fortunel, Cernusak, et al., 2022).

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

We modelled 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 ($CA_t \times NCI_{t-2}$) (Bauman, Fortunel, Cernusak, et al., 2022, 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 co-variates, except for climate anomalies (Bauman, Fortunel, Cernusak, et al., 2022), were standardised to mean zero and unit standard deviation (Bauman, Fortunel, Cernusak, et al., 2022; Fortunel et al., 2018; McElreath, 2020; Uriarte, Lasky, et al., 2016). As we assumed tree growth to have a nonlinear, multiplicative relationship with DBH and NCI (Canham et al., 2004; Fortunel et al., 2016; Uriarte et al., 2010), we log-transformed DBH and NCI prior to standardisation to achieve an additive and linear relationship (Fortunel et al., 2018; Kunstler et al., 2016; Uriarte, Lasky, et al., 2016). As species strongly varied in their mean tree size, we standardised DBH to mean zero and unit standard deviation within species, to prevent confounding species differences in growth response to tree size with interspecific variation in mean DBH (Fortunel et al., 2018; Uriarte, Lasky, et al., 2016).

2.5.1 | M1: "No trait models"

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

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

$$\mu_{i,s,t,p} = \alpha_s + \beta_{1s} \times \log(DBH_{i,t-2}) + \beta_{2s} \times CA_t + \beta_{3s} \times \log(NCI_{i,t-2}) \\ + \beta_{4s} \times CA_t \times \log(NCI_{i,t-2}) + \gamma_p + \epsilon_i \tag{4b}$$

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

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

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

using the following weakly informative priors:

$$\gamma_p \sim \mathcal{N}(0,\sigma_\gamma)$$
$$\epsilon_i \sim \mathcal{N}(0,\sigma_\epsilon)$$
$$\alpha_0, \beta_{1-4,0} \sim \mathcal{N}(0,0.5) \quad (4f)$$
$$\sigma_{\alpha_s}, \sigma_{\beta_{1-4s}}, \sigma_\gamma, \sigma_\epsilon, \sigma \sim \exp(1)$$
$$R \sim \text{LKJcorr}(2)$$

where α_s represents the species-level intrinsic growth and $\beta_{1s}, \beta_{2s}, \beta_{3s}$ 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 (Equation 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 modelled as in Equation 4c, where α_0 represents the community-level intrinsic growth rate and $\beta_{1-4,0}$ the overall effect of covariates on growth across all species. To assess correlations (ρ) among species-level intrinsic growth α_s and growth response to model covariates β_{1-4s}, we fitted a matrix of correlation coefficients among all pairs of species-level parameters. In addition, modelling all species-level parameters as a multivariate normal distribution (Equation 4c) allows to share information across species, thus improving the fit for poorly represented species, while preventing overfitting (Bauman, Fortunel, Cernusak, et al., 2022; McElreath, 2020). The variance–covariance matrix S was constructed as shown in Equation 4d, where R is the correlation matrix of species-level parameters (Equation 4e). Varying intercepts for the p plots γ_p and the i individuals ϵ_i were modelled as given in Equation 4f with a mean centred on 0 (i.e. mean intercept across all plots and individuals, respectively). We specified weakly informative priors which are given in Equation 4f.

2.5.2 | 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 (Equations 4a, 4b and 4d–4f), all species-level parameters, except species-level growth response to tree size β_{1s}, were modelled in species-level regressions to capture species-specific differences, while simultaneously evaluating the effect of species-mean functional traits within these responses (Equation 5; Bauman, Fortunel, Cernusak, et al., 2022; Fortunel et al., 2018; Uriarte, Lasky, et al., 2016). More specifically, species-level parameters were modelled as:

$$\begin{pmatrix} \alpha_s \\ \beta_{1s} \\ \beta_{2s} \\ \beta_{3s} \\ \beta_{4s} \end{pmatrix} \sim \text{MV}\mathcal{N} \left[\begin{pmatrix} \alpha_0 + \alpha_1 \times \text{Trait}_s \\ \beta_{1,0} \\ \beta_{2,0} + \beta_{2,1} \times \text{Trait}_s \\ \beta_{3,0} + \beta_{3,1} \times \text{Trait}_s \\ \beta_{4,0} + \beta_{4,1} \times \text{Trait}_s \end{pmatrix}, S \right] \quad (5)$$

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

2.5.3 | Model fitting

All models were fitted in R environment (R Core Team, 2021; RStudio Team, 2020), on the Meso@LR HPC cluster using the package brms (Bürkner, 2017). Bayesian updating of parameters was performed via the No-U-Turn Sampler (NUTS) in Stan (Carpenter et al., 2017) using CmdStanR (Stan Development Team, 2022), which allows intra-chain parallelisation in the backend. We used four chains and 4000

iterations (2000 warm up) per chain. Chains of all models mixed well and generally converged within 2000 iterations (Rhat between 1 and 1.05). Model parameter posteriors were summarised through their median and 90% highest posterior density interval (HPDI) using the packages tidyverse (Wickham et al., 2019) and tidybayes (Kay, 2022). Model covariates were considered to have a clear effect when their slope coefficients 90%-HPDIs did not encompass zero. To assess the model goodness-of-fit, we calculated conditional and marginal $R2$ using the bayes_R2() function of the brms package (Bürkner, 2017), which calculates a Bayesian version of $R2$ for regression models (Gelman et al., 2019). M1- and M2-models had high explanatory power, with a mean conditional $R2$ of 0.62 and 0.64, respectively. For more detailed information on conditional and marginal $R2$ for each model fit, see Table S1.

3 | RESULTS

3.1 | Tree growth sensitivity to climate anomalies and neighbourhood crowding

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

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

Overall, individual-level tree growth response to the interaction between climate anomalies and neighbourhood crowding was weakly related to species identity. Yet, species showed a consistent
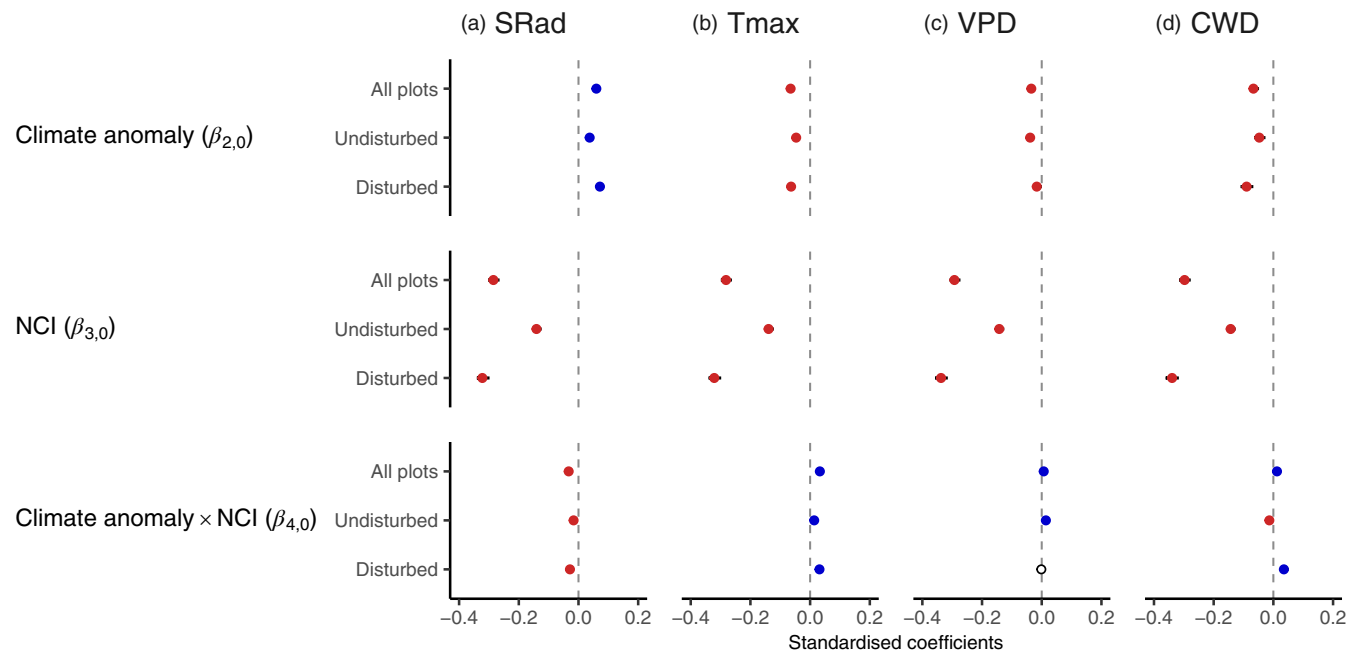

FIGURE 3 Community-level effects of climate anomaly ($\beta_{2,0}$), neighbourhood crowding (NCI, $\beta_{3,0}$), and their interaction (Climate anomaly × NCI, $\beta_{4,0}$) on tree growth (M1-models). Standardised coefficients from (a) SRad, (b) Tmax, (c) VPD and (d) CWD models are shown for all 15 plots combined, the 6 undisturbed plots and the nine disturbed plots respectively. Circles show posterior medians of standardised coefficients (community level responses, see: $\beta_{2-4,0}$ in Equation 4c), and lines indicate 90% highest posterior density intervals [HPDI]. Coloured 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 Figure S1A.

directional response (i.e. no species showed an opposite effect) to the interactive effects of neighbourhood crowding and anomalies (β_{4s}) in SRad, Tmax and CWD, but less in VPD. Specifically, neighbourhood crowding clearly attenuated positive effects (negative β_{4s}) of SRad anomalies in 18%, and negative effects (positive β_{4s}) of Tmax and CWD anomalies in 27% and 8% of all species. Neighbourhood crowding modulated negative effects of VPD anomalies in 7% of all species, either attenuating (81% of positive β_{4s}) or reinforcing (19% of negative β_{4s}) these effects. For details, see Table S3.

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

3.2 | Variation in tree growth response to climate and neighbours with forest 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 (Figure 3).

Although species intrinsic growth rates varied slightly between undisturbed and disturbed plots (Figure 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 (Figure 4a,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 (Figure 4c). For details on correlations of species-level parameters, see Table S4.

3.3 | Trait effects on tree growth response to climate anomalies and neighbourhood crowding

Parameter estimates of community-level tree growth regressions were consistent between the M1-models (310 focal species) and M2-models (subset of species with available trait information, Tables S2 and 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 (Figure S1B 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; Figure 5).

Species with lower LSWC and SLA, but higher δ^{13}C, L_{thick} and Bark$_{thick}$ grew faster with increasing SRad anomalies (Figure 5a). Species with lower SD, but higher δ^{18}O, L_{though} and WSG were less sensitive to anomalies in Tmax and VPD (Figure 5b,c). Additionally, species with higher δ^{13}C, g_{min}, LA and L_{thick} showed lower sensitivities to VPD anomalies (Figure 5c). Species with lower π_{tlp} but higher WSG were less sensitive to CWD anomalies. (Figure 5d). Species with lower SD, but higher δ^{18}O, L_{though} and WSG were less sensitive to neighbourhood crowding (Figure 5a–d). Finally, species with lower δ^{13}C but higher SLA benefited more from SRad anomalies when found in crowded environments (Figure 5a). Species with higher WSG profited less from the mitigating effects of neighbours against Tmax anomalies (Figure 5b), while species with higher SD and SLA, but lower LA, L_{thick}, L_{though} were less buffered against VPD anomalies by their neighbours (Figure 5c). Species traits did not mediate the interactive effects of CWD anomalies and neighbourhood crowding (Figure 5d).

4 | 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.

4.1 | Climate anomalies and neighbourhood crowding reduce tropical tree growth

High temperatures (Tmax) were associated with tree growth decline in half of the 300 species at Paracou (β_{2s}; Table S3), indicating that in years without strong positive anomalies, some species at the site may already operate near their temperature optimum. Indeed, higher Tmax (and minimum night time temperatures) can increase
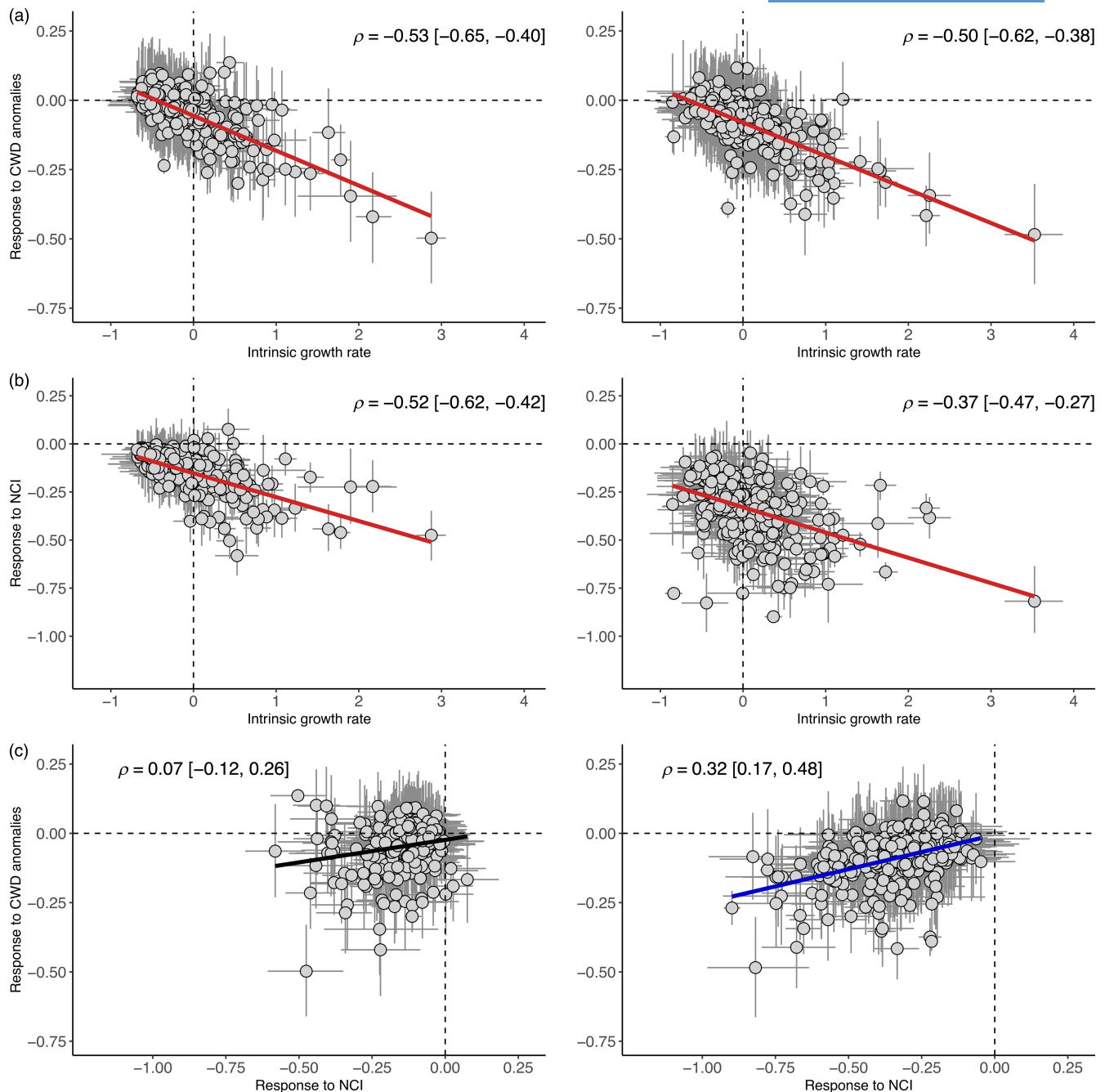
FIGURE 4 Correlations between (a) species intrinsic growth rates α_s and species-level growth response to CWD anomalies (β_{2s}), (b) species intrinsic growth rates α_s and species-level growth response to neighbourhood crowding (NCI, β_{3s}) and (c) species-level growth response to NCI (β_{3s}) and CWD anomalies (β_{2s}), estimated by the CWD M1-models for undisturbed (left) and disturbed (right) plots, respectively (Equation 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: Equation 4e). Median, lower and upper 90%-HPDI are given in the upper right-hand or left-hand corner of the figures.

respiration but decrease stomatal conductance and photosynthesis, thus reducing carbon assimilation (Anderegg et al., 2015; Doughty & Goulden, 2008) and gross primary production (Aguilos et al., 2018; Crous et al., 2022), which can lead to inter-annual declines in tropical woody productivity (Sullivan et al., 2020; Way & Oren, 2010) and carbon sinks (i.e. net ecosystem exchange; Anderegg et al., 2015). As

global temperatures are predicted to increase in the tropics with on-going climate change (Shukla et al., 2022), this thermal sensitivity of tropical species may lead to important reductions in tree growth in the future, which may alter long-term forest dynamics (Aubry-Kientz et al., 2019; Sullivan et al., 2020). Although Tmax directly influences VPD (Table S6 and Figure S2), VPD was a less important driver of
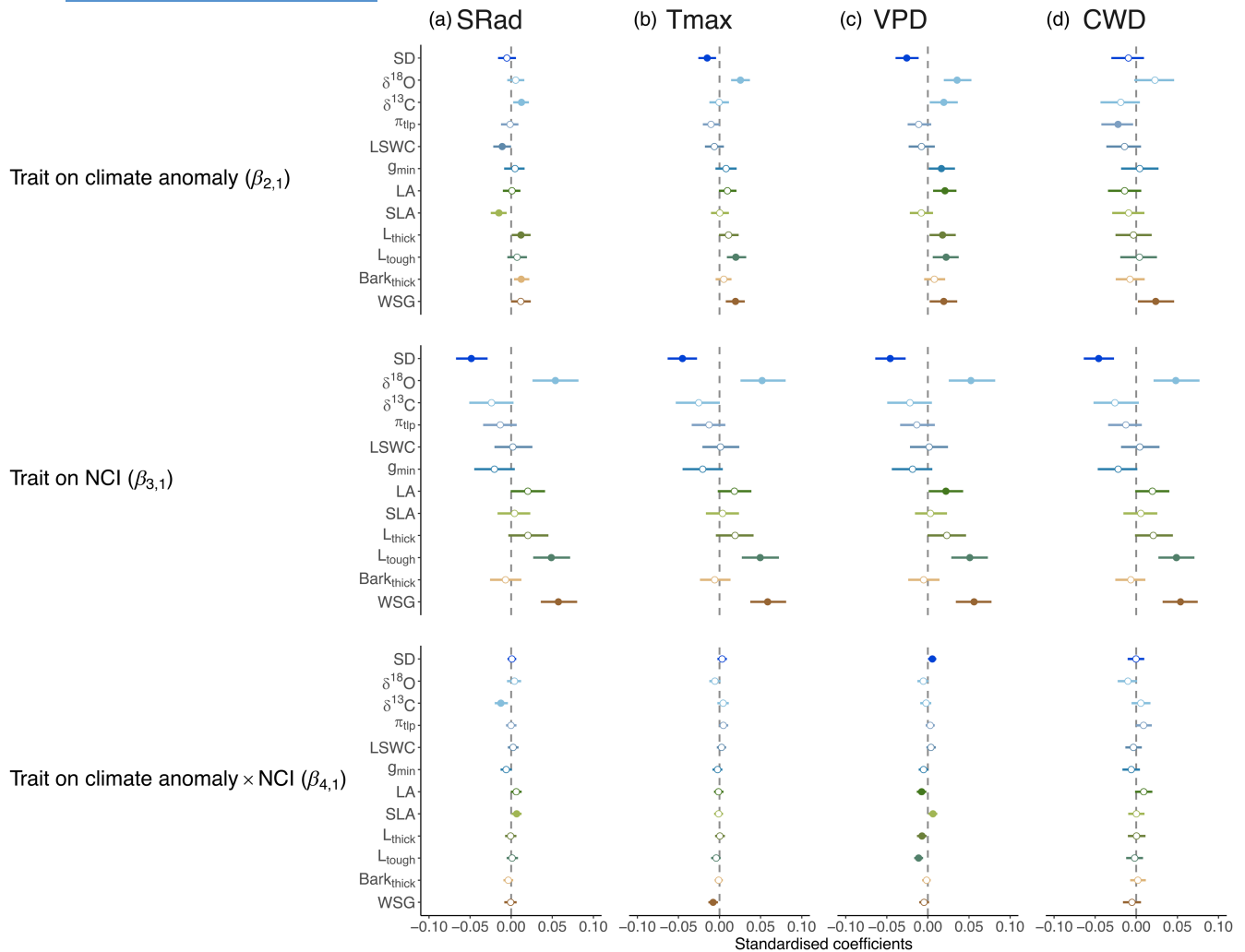
FIGURE 5 M2-models: trait effects on tree growth response to climate anomalies $\beta_{2,1}$, neighbourhood crowding $\beta_{3,1}$ and the climate anomaly-crowding interaction $\beta_{4,1}$ (see: Equation 5). Standardised coefficients from (a) SRad, (b) Tmax, (c) VPD and (d) CWD models are shown for 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).

tree growth at Paracou. While positive VPD anomalies likely reduce tree growth by reducing stomatal conductance and thereby carbon assimilation (Grossiord et al., 2020; Sanginés de Cárcer et al., 2018), it does not affect respiration. Conversely, positive anomalies in CWD strongly reduced tree growth at Paracou (Aubry-Kientz et al., 2015; Wagner et al., 2012), in contrast to previous work in the Australian wet tropics indicating that VPD may limit tree growth before soil water becomes scarce (Bauman, Fortunel, Cernusak, et al., 2022; Choat et al., 2012; Rifai et al., 2018). Our results suggest that trees at Paracou may be more sensitive to soil water stress than to atmospheric water stress. Alternatively, atmospheric water stress may not be severe enough at Paracou to lead to important growth reductions. In addition, trees allocated more to diameter growth with higher anomalies in solar radiation (SRad), which contrasts with recent work

showing negative effects of light anomalies on tropical tree growth in Australia's wet tropics (Bauman, Fortunel, Cernusak, et al., 2022). Light availability is an important driver of tree growth and primary production at Paracou (Aguilos et al., 2018; Wagner et al., 2012; Wagner, Rossi, Aubry-Kientz, et al., 2014), a typical light-limited tropical forest (Guan et al., 2015; Wagner et al., 2016). Furthermore, years with positive anomalies in SRad, did not necessarily translate into years with increased heat stress and atmospheric drought stress (Table S6 and Figure S2), therefore reducing confounding and opposing effects of light availability and heat or atmospheric drought stress on tree growth. We explored the effects of different climate drivers separately, but there could be interactive effects between climate factors because they are causally linked. Future studies could further improve our understanding of tropical forest

sensitivity to climate by embedding the causal associations among climate variables into the model structure, and by explicitly modelling their interactive effects (Allen et al., 2010, 2015; Hammond et al., 2022; Zuidema et al., 2022). Neighbourhood crowding was the strongest driver of tree growth at Paracou, confirming the importance of neighbourhood interactions for tropical forest dynamics (Canham et al., 2004; Dawkins, 1959; Fortunel et al., 2018; Uriarte, Lasky, et al., 2016; Zambrano et al., 2017).

Neighbourhood crowding overall reduced tree growth across the 300 focal species, in line with previous work across forest systems (Kunstler et al., 2016). Importantly, we provide first evidence that climate anomalies can interact with neighbourhood crowding to shape tropical tree growth, thereby attenuating their respective separate effects. In particular, the negative (Tmax, VPD, CWD) and positive (SRad) effects of climate anomalies on tree growth were attenuated in more crowded neighbourhoods. Denser neighbourhoods may result into higher levels of canopy closure, decreasing light availability (Gaudio et al., 2017; Ghuman & Lal, 1987), but simultaneously providing thermal insulation (Fetcher et al., 1985; Gaudio et al., 2017; Ghuman & Lal, 1987), thereby sustaining a more favourable micro-climate during extreme macro-climatic events (De Frenne et al., 2013, 2019). Contrary to our expectation, more crowded trees were also less sensitive to CWD anomalies, indicating that buffering effects might out-weigh increased competition for soil water during drought. During periods of lower soil water content, more crowded trees may have benefited from complementary neighbourhood water uptake, hydraulic redistribution or improved water retention through higher root densities (Grossiord, 2020; Grossiord, Gessler, Granier, Pollastrini, et al., 2014; Grossiord, Granier, Ratcliffe, Bouriaud, et al., 2014; Hafner et al., 2021). Previous studies have also shown mitigating effects of neighbourhood diversity or species richness on tree growth response to drought across forest biomes (Fichtner et al., 2020; Gillerot et al., 2021; Grossiord, Gessler, Granier, Berger, et al., 2014; O'Brien et al., 2017; Pardos et al., 2021), in contrast with findings showing exacerbating effects of stand or neighbourhood densities on tree demographic response to climatic stresses in temperate (Bottero et al., 2017) and Mediterranean (Astigarraga et al., 2020; Gómez-Aparicio et al., 2011) forests. Our results suggest that accounting for the interactive effects of climate and neighbours offers a promising way towards an improved understanding of tropical forest resistance and resilience to climate change.

4.2 | Disturbance increases tropical forest sensitivity to climate anomalies and neighbourhood crowding

As expected, disturbed plots were more sensitive (i.e. showed greater tree growth reductions) to separate and joint effects of climate anomalies and neighbourhood crowding than undisturbed plots at Paracou (Figure 3a–d), highlighting the lasting impact of human activities such as logging and thinning on tropical forest dynamics

(Fargeon et al., 2016; Hérault et al., 2010; Hérault & Piponiot, 2018; Hiltner et al., 2021; Piponiot et al., 2016). Differences between disturbed and undisturbed plots in effect sizes of climate anomalies and neighbourhood crowding may originate from differences in tree community composition. Indeed, disturbed plots at Paracou harbour more fast-growing species (Mirabel et al., 2020, 2021), which tend to be more sensitive to climate anomalies, as shown in other tropical forests (Bauman, Fortunel, Cernusak, et al., 2022; Esquivel-Muelbert et al., 2020). The higher abundance of fast-growing species and individuals on disturbed plots was also reflected in the higher community-level intrinsic growth rate (α_0) of disturbed plots (Figure S1 and Table S2). While higher sensitivity of disturbed communities to environmental drivers is consistent with expectations from the 'fast-slow' spectrum (Reich, 2014), we show that this trend extends to increased susceptibility to biotic stressors such as neighbourhood crowding (Figure 4a,b, Table S4). In addition, greater canopy openness in disturbed plots may lead to more severe climate effects through tighter coupling of micro- and macro-climatic conditions (De Frenne et al., 2013, 2019; Ghuman & Lal, 1987; Von Arx et al., 2012).

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

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

and the resistance and resilience of tropical forests to future climate change (Hiltner et al., 2021).

4.3 | Traits mediate tree growth response to climate anomalies and neighbourhood crowding

In line with expectations from the 'fast-slow' economic spectrum (Reich, 2014), high species intrinsic growth rates were related to acquisitive strategies for carbon and water (Figure S1B). Fast growing species had high SD and low $\delta^{18}O$, highlighting the key role of stomatal conductance and transpiration rates for efficient carbon assimilation (Drake et al., 2013; Hepworth et al., 2015; Jarvis, 1981; Poorter & Bongers, 2006; Wong et al., 1979). Fast-growing species also exhibited leaf and wood traits pertaining to acquisitive strategies such as lower L_{thick}, L_{though}, and WSG, supporting previous findings that a species investment into tissue longevity comes at higher construction costs (Hérault et al., 2011; Philipson et al., 2014; Poorter et al., 2008, 2010; Reich, 2014; Wright et al., 2010).

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

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, Scoffoni, & Sack, 2012), 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 (Blackman et al., 2016; Duursma et al., 2019), we found they were less vulnerable to atmospheric drought stress. As elevated VPD leads to stomatal closure (Grossiord et al., 2020), residual water loss could maintain evaporative cooling (given nonlimiting soil water conditions), which potentially prevents irreversible leaf tissue damage through overheating (Drake et al., 2018). The maintainance of evaporative cooling could

thus allow species to quickly resume carbon assimilation after atmospheric drought stress, while simultaneously reducing post-drought respiration rates linked to tissue repair (Drake et al., 2018; Powell et al., 2017).

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

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

However, species traits poorly captured the interactive effects of climate anomalies and neighbourhood crowding on tree growth at Paracou (Figure 5a–d). Trait differences between neighbouring trees rather than the traits of the focal tree alone may be playing a key role in driving the interactive effects of climate anomalies and neighbourhood crowding on tree growth, in particular as trait differences can reflect niche partitioning and competitive hierarchies between neighbouring individuals (Fortunel et al., 2016; Kunstler et al., 2016). To clarify this, future work could explore the relative contribution of focal tree traits and trait differences in mediating tree growth response to the interaction between climate extremes and neighbourhood crowding.

5 | CONCLUSION

Tropical trees are particularly sensitive to climate stress and interactions with neighbours, suggesting that ongoing climate change and associated changes in forest composition and structure may result in a long-term slowdown of carbon sequestration in tropical forests. Our study shows that climate anomalies and neighbourhood crowding can interact positively in shaping tropical tree growth, suggesting that trees growing in more crowded neighbourhood may be less sensitive to climate extremes. Logged forests suffered considerably

stronger growth reductions in response to water stress, suggesting lower resistance of managed tropical forests to climate change. Our findings reveal that functional traits, in particular related to water relations, can capture differences in species sensitivities to atmospheric and soil water stress and neighbourhood crowding (though not their interactive effects), that can be implemented in models to improve predictions of the future of these highly diverse ecosystems.

AUTHOR CONTRIBUTIONS

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FUNDING INFORMATION

CONFLICT OF INTEREST STATEMENT

PEER REVIEW

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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

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

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

Supplementary Methods S1. Corrections of tree inventory data.

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

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

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

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.

Table S6. Pearson's correlation coefficients among mean anomalies of the four climate variables.