**Title:** Tropical tree drought sensitivity is jointly shaped by drought characteristics, species adaptations, and individual microenvironments

**Authors**

Krishna Anujan1,2\* ORCiD: 0000-0003-3604-5895  
Sean McMahon2,3 ORCiD: 0000-0001-8302-6908  
Sarayudh Bunyavejchewin4 ORCiD: 0000-0002-1976-5041  
Stuart J. Davies3 ORCiD: 0000-0002-8596-7522  
Helene C. Muller-Landau3 ORCiD : 0000-0002-3526-9021  
Nantachai Pongpattananurak5 ORCiD: 0000-0001-8687-6182  
Kristina Anderson-Teixeira1,3 ORCiD: 0000-0001-8461-9713

**Affiliations:**

1Smithsonian’s National Zoo and Conservation Biology Institute, Front Royal, VA, USA  
2Smithsonian Environmental Research Centre, Edgewater, MD, USA  
3Smithsonian Tropical Research Institute, Panama  
4National Park, Wildlife and Plant Conservation Department, Bangkok, Thailand  
5Kasetsart University, Chatuchak, Bangkok, Thailand

\*=corresponding author

**Running title:**

**Article Type:** Letter

**Number of Words in Abstract:**  
**Number of Words in Main Text:**  
**Number of References:**  
**Number of Figures:** 5  
**Number of Tables:** 1  
**Number of Text boxes:** 0

**Corresponding author address:** [anujank@si.edu](mailto:anujank@si.edu)

# Keywords

# Statement of Authorship

# Data Accessibility Statement

# Conflict of Interest

# Abstract (150 words)

The frequency and intensity of droughts are increasing across forests worldwide, altering tree demography and its contribution to the land carbon sink. In seasonally dry tropical forests, species adaptations to strong dry seasons might confer drought resistance, but this resistance may be variable with individual microenvironments and across drought events. We analysed a unique data record - manual dendrometer band measurements over 15 years on 1820 trees across 30 species in a seasonally dry tropical forest in Thailand, to assess the drought sensitivity of tree growth in two climatically distinct droughts. Species and individuals exhibited a wide range of drought sensitivities within a drought event, and inconsistent responses across these two droughts. Deciduous species were more sensitive than evergreen species in the wet-season drought, and this difference was amplified in wetter microclimates. Although exposed trees were more sensitive, access to water through larger size or topographic location buffered growth declines. Heterogeneous responses of species and individuals to droughts indicate potential spatiotemporal insurance effects in diverse forests in the face of increased climate anomalies.

# Introduction

In forests worldwide, intense drought is becoming more frequent, affecting forest demography, diversity, and C cycling (Intergovernmental Panel On Climate Change (Ipcc) 2023). Understanding these impacts is an important research priority, particularly for tropical forests, which are critical C sinks; tropical tree woody growth removes roughly 25 Gt CO2 annually offsetting ~20% of anthropogenic fossil fuel emissions (Anderson-Teixeira *et al.* 2016, 2021; Beer *et al.* 2010; Brando *et al.* 2019). Drought events can threaten this sink; the 2015-2016 ENSO drought in the Amazon temporarily shifted the region from a net sink to a net source of carbon (Brando *et al.* 2019). However, nuanced study of tropical tree woody growth responses to drought is inhibited by the fact that few tropical species form rings and long-term annual records are rare (Zuidema *et al.* 2022). Separate studies have shown that drought characteristics species traits, and microenvironment all affect tree growth responses (Bennett *et al.* 2015; McGregor *et al.* 2021), but we know little about their combined effects or potential interactions, which could fundamentally alter our understanding of forest responses to drought. Specifically, if drought tolerance is influenced independently by drought characteristics, species traits, and microenvironment, tree drought responses may be conserved, and therefore linearly predictable; i.e., a species with low sensitivity to past droughts would have low sensitivity in any microhabitat and through any drought. In contrast, if these factors interact, the species and individuals that exhibit resistance to one drought may prove much more vulnerable in a different drought. The resultant amplification of the complexity and diversity of drought responses may act as a mechanism for promoting species diversity and stabilizing ecosystem function as drought regimes intensify (Dahinden *et al.* 2017; Luo & Keenan 2022; Naumann *et al.* 2018).

Drought characteristics can influence climatic drivers of tree growth and their timing, and affect drought sensitivity of tropical trees. Droughts are notoriously hard to define and encompass a variety of types based on the meteorogical or climatic variables affected (Slette *et al.* 2019). Here we define drought as hot/dry conditions anomalously departing from their long-term means during any given time of year. Tree growth responses to drought timing can be pronounced in seasonally dry tropical forests because of strong seasonality in climate and consequently on photosynthesis, allocation and growth (including dry seasons unfavourable to growth) (García-Cervigón *et al.* 2020). (Here we distinguish dry season from drought; dry season represents hot/dry conditions that are periodic, annual and predictable, droughts are unpredictable eith anomalous hot, dry conditions relative to seasonal expectations.) Seasonally dry tropical forests are also at thermal and water stress tolerance thresholds for many species, making them more vulnerable to drought (Allen *et al.* 2017), and leading to stand-level patterns of drought-associated water stress (Aguirre-Gutiérrez *et al.* 2019; Bauman *et al.* 2022; Bennett *et al.* 2023). Analyses to date have found that the woody growth of tropical trees is particularly vulnerable to dry season precipitation(Clark *et al.* 2021; Clark *et al.* 2010; Zuidema *et al.* 2022); however, these analyses represent only a very limited set of tropical tree species and climates. Trees in seasonally dry tropical forests exhibit a mix of strategies - along a spectrum of conservative to acquisitive water-use - that support survival and growth despite strong seasonal hot/dry stress. These strategies might confer differential advantages under drought conditions.

Tree species in seasonally dry forests have diverse evolutionary strategies to maximise growth and survival under periodic hot/dry conditions. These strategies can range along a spectrum from hydraulic safety to efficiency leading to tolerance or avoidance of dry conditions(González-M. *et al.* 2021). Dry season deciduousness represents an extreme “avoidance” strategy along this continuum, where species lose leaves during the dry season to avoid water loss and have acquisitive strategies during leaf on periods (De Souza *et al.* 2020). Other strategies include deep roots (hydraulic safety, to access deeper water in the dry season), more negative leaf turgor loss point (hydraulic safety, to maintain gas exchange and photosynthesis under hot and dry conditions), large vessels (hydraulic efficiency) (Chitra-Tarak *et al.* 2021; González-M. *et al.* 2021). Under drought conditions, some of these strategies can lend drought resistance while others can amplify drought sensitivity especially under severe droughts (Chitra-Tarak *et al.* 2021; González-M. *et al.* 2021; Kunert *et al.* 2021). Moreover, besides being constant or adaptively conserved, these strategies can also have developmental or ecophysiological controls; e.g. some species regulate negative TLPs, leaf deciduousness and root depth, based on environmental cues leading to intraspecific or interannual variation potentially resulting in spatiotemporal variation in drought responses [Williams *et al.* (2008); REFS Lasky? Hulshof?].

Individual growth responses to drought can depend on the specific microenvironments that trees experience leading to varied atmospheric and hydrological stresses with distinct ecological consequences. Physiologically, trees experience drought stress as a combination of higher evaporative demand and higher thermal stress on leaves, and greater stress on roots because of low soil moisture. This results in greater stress on trees that have exposed crowns (Vinod *et al.* 2023), shallower roots or growing in drier microenvironments []. Consequently, larger trees, with more exposed crowns, suffer more growth declines during drought (Bennett *et al.* 2015). However, these responses can potentially be different across species or with drought severity. Trees with deeper roots that rely on regular access to deep water may be more vulnerable during severe droughts when those sources are depleted (Chitra-Tarak *et al.* 2021). Indeed, there is evidence that trees near streams undergo greater growth declines (McGregor *et al.* 2021) and increases in mortality (Zuleta *et al.* 2017) during drought. Finally, species strategies may constrain tree light and water microenvironments; e.g. evergreen species can covary with soil moisture (Kunert *et al.* 2021), shade tolerant and understory species may be rarely exposed to hot/dry air. Whether drought characteristics interfere positively or negatively with these evolutionary and physiological strategies and whether it leads to consistent or heterogenous sensitivities across drought events is as yet unknown.

We hypothesize that tropical tree drought sensitivity is jointly and interactively shaped by drought characteristics, species adaptations, and individual microenvironments. We test this by examining individual tree growth during two ENSO drought years within a 14-year record of dendrometer band measurements in a seasonally dry forest in Thailand. Specifically, we test predictions that i) both species and individuals respond differently to different droughts. ii) Deciduous species, which rely on wet seasons for growth, are particularly sensitive to wet season drought. iii) Exposed trees are more sensitive to drought, but water availability, either through larger size or topographic location, can buffer growth declines.

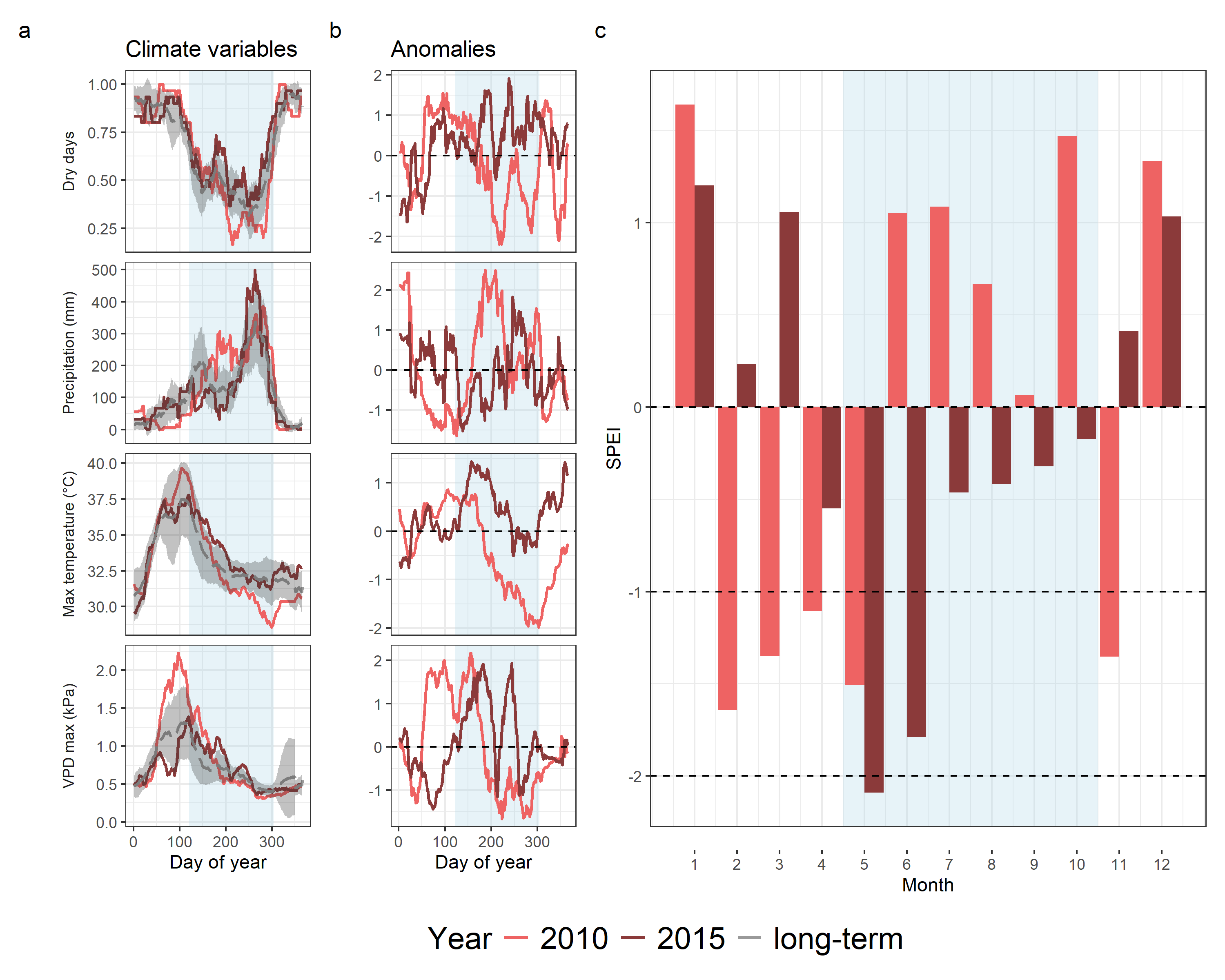
Table 1: Summary table of hypotheses tested, effects of variables on drought sensitivity and corresponding evidence

|  | 2010 | 2015 | evidence |
| --- | --- | --- | --- |
| **Drought characteristics** |  |  |  |
| Climate anomaly (SPEI, VPD etc.) | strong | moderate | Fig 1 |
| Timing | dry season | wet season | Fig 1 |
| **Species effects** |  |  |  |
| Deciduousness | no | - | Fig 3 |
| 2010 sensitivity |  | no | Fig S5 |
| **Microenvironment effects** |  |  |  |
| TWI | - | + | Fig 3, 4 |
| Deciduousness:TWI | no | - | Fig 3 |
| exposure | - | - | Fig 4, 5 |
| other size effects | + | - | Fig 4 |
| 2010 sensitivity |  | no | Fig S6 |

# Materials and Methods

***Sites and data***

We analysed data from manual dendrometer band censuses from 2008-2023 in the Huai Kha Khaeng ForestGEO plot (15.6324 N, 99.217 E), hereafter “HKK”, in the Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani, Thailand. This is a 50-hectare plot in mixed deciduous tropical forest, with a mean annual temperature of 1400 mm and a strong dry season from November to April (Anderson-Teixeira *et al.* 2015). The dominant canopy species are *Hopea odorata*, *Vatica harmandiana*, *Dipterocarpus alatus* and *Tetrameles nudiflora* and lower layers of the canopy are dominated by sub-canopy evergreen and deciduous species like *Miliusa horsfieldii* and *Polyalthia viridis*. Long-term analysis of tree-ring data shows that tree growth at Huai Kha Khaeng has been influenced by temperature and rainfall (Vlam *et al.* 2014).



***Figure 1. Climatic characteristics of drought years and average years*** in the Huai Kha Khaeng ForestGEO plot. For four daily climate variables dry days, precipitation, maximum temperature and VPD, panel a) represents rolling means for 30 days around the focal day for that year. Grey line represents the mean of this rolling mean from 2008 to 2019 and ribbons represent standard deviation around this mean. Panel b) represents anomalies of this rolling mean from the values across the timeseries. Values, therefore represents the number of standard deviations from the mean on a given day. c) shows Standardised Precipitation Evapotranspiration Index (SPEI) values for each month in 2010 and 2015. Across all panels, light blue background represents the average wet season, from May to October. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/10>

In the HKK plot, metal dendrometer bands were installed in 2008 on 2353 trees across 152 species following standard protocol (Muller-Landau 2008). Trees were selected were based on the relative abundance of species in the forest, with more individuals banded from the abundant species (ranging from 230 trees to 1 tree per species), and spanning the size and habitat distribution within the plot. On each tree, the dendrometer band was installed at 1.4 m from the ground, a height of 10 cm above the regular point of measure for the whole plot census (typically 1.3 m), except on irregular trunks or buttresses when they were shifted above. All dendrobands were censused two times a year - in the wet and dry season - typically in June and January. During the census, the size of the window opening along the band was measured using Mitutoyo digital callipers (least count = 0.01 mm) and the diameter of the tree at the dendrometer band was measured using standard DBH tape.

***Calculating annualised growth increments***

Using the late wet/early dry dendrometer band censuses, we calculated annualised growth for each year for each tree. We first removed measurements with likely data entry errors because of misplaced decimals, potential misidentified bands (old band numbers that restarted after stopping) or misidentified individuals (individuals with conflicting metadata across censuses). We used the raw window size measurements combined with the diameter measurement at installation to calculate diameter at each dendroband census using standard equations that uses the chord across the measurement window to estimate the arc, assuming a circular cross section[condit]. We used a direct measurement of at the time of installation if it was available. If the tape measurement at the first window size measurement was not available for any band, we excluded window size measurements until the first available diameter measurement. We then calculated annualised diameter increments for each individual for each year by finding the difference in diameter from the previous year () and adjusting for the number of days between measurements ().

To ensure that the data did not smooth over multiple years, we excluded increment measures with missing values for and then excluded large measurement outliers (> 3 standard deviations from the mean across all observations). Tape measurements themselves are not precise enough for calculating drought sensitivity; error for each tape measure is 1mm, error for growth is at least 2mm. In comparison, median annual growth across trees in HKK is ~1.4 mm and calculating deviation from annual growth needs sub-mm precision. However, tape measurements can be used to check for consistency in trends or identify outliers. We calculated increments from annual tape measurements made on each dendrobanded tree at each census and removed dendroband measurements that had low agreement with these annualised increments calculated from tape measurements. Finally, we excluded trees with negative increments over the whole timeseries, and included only species that had at least 10 individuals, resulting in a final dataset of 1820 individuals across 30 species.



***Figure 2: Growth increment timeseries and drought sensitivity*** across trees and species in the Huai Kha Khaeng ForestGEO plot. a) Median of annualised growth increments across species (colours) and the whole plot (black) from 2009 - 2022 from late wet/early dry season dendroband measurements. 2010 and 2015 were moderate and very strong ENSO events respectively. b) Distribution of drought sensitivity of tree growth across all individuals in the two drought years. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/11>

***Drought years and characteristics***

We identified drought years of interest in the dendroband timeseries - 2010 and 2015 - by examining two drought indices and corroborating with plot-level ecological responses and expert information. Within the dendroband timeseries, two ENSO events had occurred; 2010 was a moderate ENSO event while 2015 was a very strong ENSO event [REF]. We also used the SPEIbase dataset (Vicente-Serrano *et al.* 2010) to calculate the Standardised Precipitation-Evapotranspiration Index, a drought severity index, calculated at the monthly scale. Defining drought as periods with two or more consecutive months with SPEI < -1 also resulted in 2010 and 2015 as drought events. These years also corresponded with expert knowledge of major droughts that affected the region as well as with plot-level growth declines in the timeseries. We also note that we chose not to include 2020 in our analysis despite low growth, because a) declines in growth can occur due to various reasons which could have distinct ecological responses in species and individuals b) 2020 did not emerge as a drought year either in the examination of drought indicators or from expert knowledge.

To characterise these two droughts, we used climate data from a weather station near the plot and publicly available climate data for the region. We used daily weather data collected from 2001 to 2019 at the Forest Fire Research Station [CHECK WHERE], located ~20 km from the ForestGEO plot. We first calculated daily values of Vapour Pressure Deficit (VPD) using the equation

We then calculated rolling means of precipitation, number of dry days (precipitation = 0), VPD and maximum temperature over 15 day periods across the whole year for each year. Finally, we calculated daily rolling anomalies for each variable for 2010 and 2015 from the long-term daily expectation as

***Variables for analysis***

For the two drought years, 2010 and 2015, we calculated growth sensitivity for each tree to each drought as a growth anomaly from its mean annual increment from calculated from dendrometer band window size.

We first calculated the mean annual increment for each tree as the mean of the annualised increments across the whole timeseries. We then calculated sensitivity for each tree for each drought as

By scaling the difference in increment to the mean annual growth of each tree, this metric allows us to compare across slow and fast growing individuals and species.

To account for potential biases in dendrometer band increments from water-related growth or shrinkage, we also calculated growth occurrence using a zero-growth assumption (Zweifel *et al.* 2016). Timing of measurement and seasonal dynamics in tree hydration and bark dynamics could contribute to negative values in dendrometer band increments, unlike woody growth from tree ring datasets (Chitra-Tarak *et al.* 2015). Using a zero-growth model, we calculated growth occurrence as 1 under positive diameter change and any change <=0 as 0. To account for biases introduced by timing of measurements and seasonal dynamics, we used this simplifying assumption to corroborate the patterns observed with the sensitivity metric.

Across all individuals in the plot, we calculated topographic wetness index for an expectation of the water availability across space based on the concavity/convexity of a location. We used a Digital Elevation Model from a 5 m x 5 m elevation layer collected at plot establishment. We used the *whitebox* package in R (Lindsay 2016; Wu & Brown 2022) to fill and breach this layer, calculate flow accumulation at each cell and then calculate TWI as . We defined tree size as the diameter at breast height (calculated from dendrometer band window measurement) at the previous census. We estimated crown exposure for each tree at each census using crown illumination index, an ordinal categorical variable from 1 to 5 (least to most exposed) measured at each dendroband census.

We calculated deciduousness as a species level trait using data published in Williams *et al.* (2008) for the top 30 species. We defined deciduousness as the mean proportion of canopy loss at maximum loss across individuals in the species, with a score ranging from 1 to 4 where 1 is most evergreen and 4 is most deciduous.  
Data was unavailable for *Alphonsea ventricosa*, an evergreen species, and so we manually assigned it a deciduousness score of 1, in the middle of the evergreen range. An alternate measure of deciduousness is the duration spent at maximum crown loss. This data was strongly correlated with the proportion of crown loss; we chose to use the proportion of crown loss because it was available for a larger list of species.

***Statistical methods***

We first modelled sensitivity as a simple random intercept model

We then used the predicted sensitivities from this model and tested their correlations with deciduousness using simple linear models.

To model the interactive effects of deciduousness and wetness on sensitivity, we modelled

We then calculated predictions across all combinations of values from observed maximum to minimum of TWI and deciduousness within this dataset.

To further disentange the microenvironmental drivers of drought sensitivity, we simultaneously modelled:

and

Simultaneously modelling the effect of variables on sensitivity and the effect of DBH on CII in this way allows us to disentangle causual linkages between these processes. We chose to model a species random effect on all slopes here to account for variation across species instead of specific traits which may have different effects with each of the variables. However, we also ran simpler models with species random effects only on the intercept, the results of which are reported in the Supplementary Material. Across all models, we used Gaussian priors for the distribution of the response variable sensitivity, considered CII as an monotonic predictor (ordered factor) and centred and scaled the other predictors. We modelled CII as an ordinal categorical variable with a cumulative logit link function. In the combined form, the model therefore used a multivariate distribution of Gaussian and logit.

All statistical analyses were performed using R version 4.4.0 (R Core Team 2024). Mixed models were fit through Bayesian regressions using MCMC methods using the package *brms* (Bürkner 2017). We ran 4 MCMC chains for 3000 iterations with 1000 of these set as warmup. We extracted draws, calculated distributions and checked convergence using functions from the *posterior* package (Bürkner *et al.* 2023; Vehtari *et al.* 2021).

# Results

## Drought characteristics

The two droughts analysed had distinct temporal climatic characteristics, with 2010 primarily a dry season drought and 2015 a wet-season drought (Table 1, Fig 1). In 2010, drought characteristics of lower precipitation, higher number of dry days, higher maximum temperature, higher VPD than the long-term mean and SPEI values below -1 occurred between February and April, in the dry season. On the other hand, in 2015, similar deviations occurred in May and June, in the wet season. In 2015, SPEI in May was -2, an anomalously low value that was not observed in any month in the entire dendroband census time period, suggesting a severe drought.

## Growth timeseries and Drought sensitivity

The increment timeseries using dendrometer band measurements revealed plot- and species-level patterns in interannual growth variation (Fig 2a). Median annualised growth rate across the years of measurement for the whole plot was 0.17 0.28 cm. Median annual increment differed by species with *Gluta obovata* having the lowest (0.06 0.2 cm) and *Dipterocarpus alatus* the highest (0.36 0.34 cm) among the 30 species analysed.

Drought years were associated with lower growth across the plot. The drought year 2015 had the lowest median annual increment 0.08 cm, 52.68% lower than the median across all years. In 2010, the median annual increment was 0.15 cm, 13.33% lower than the median across all years. While there were more species differences in median responses to the 2010 drought, all species had lower increment than a typical year in 2015. Besides decrease in magnitude of growth, the proportion of trees with negative growth was also higher in the drought years (Fig S4). Across the years, on average, 11.42% of the trees had negative growth, with a minimum of 6.7% in 2011. The drought year 2015 had the maximum proportion of trees with negative growth in the timeseries, 22.57%.

Trees on average had negative drought sensitivities for both droughts with considerable variation around it (Fig 2b). Median drought sensitivity across all trees in 2010 was -0.27 0.92 while in 2015 it was -0.55 0.98. In 2010, *Alphonsea ventricosa* and *Afzelia xylocarpa* had the lowest and highest median sensitivity of -0.94 and 0.65 respectively. In 2015, *Dimocarpus longan* and *Mitrephora thorelii* had the lowest and highest median sensitivity of -1.06 and 0.02 respectively.



***Figure 3: Variation in sensitivity among species*** in the Huai Kha Khaeng ForestGEO plot during droughts in 2010 and 2015. a) Relationship of the mean species sensitivities from model fits of an intercept-only model, with mean species deciduousness values. Line shown for significant correlation. b) Predicted sensitivity values across the observed range of deciduousness and topographic wetness index from a model with TWI, deciduosness and their interaction across all trees modelled for each drought year separately. For comments: <https://github.com/forestgeo/growth-precip-thailand/issues/12>

## Species effects on drought sensitivity

Deciduousness was associated with lower negative sensitivities in 2015, but not in 2010 (Fig 3a). Species median sensitivities in 2010 and 2015 were not correlated with each other (Pearson’s correlation coefficient r = 0.11, p = 0.57, Fig S5) but on average had lower mean and median sensitivities in 2015 than in 2010 (Fig S5), in alignment with median sensitivities across all trees. In 2015, predicted sensitivities from intercept-only models of sensitivity with a species random effect on the intercept showed a significant negative association with deciduousness value (r = -0.41, p = 0.03). On the other hand, in 2010, predicted sensitivities had no significant association with deciduousness (r = -0.05, p = 0.8). Moreover, models of all trees with TWI and deciduousness as predictors showed that the conditional effect of deciduousness on sensitivity (controlling for topographic wetness) was significant and negative in 2015 (-0.08; 90% CI -0.12, -0.04) but not in 2010 (-0.02, 90% CI -0.05, 0.02).

## Microenvironment effects drought sensitivity

The effect of wetness on sensitivity was different in 2010 and 2015, with 2015 effects interacting with deciduousness. Individual tree responses to drought were not correlated with each other (Fig S6). Across all trees, the model with TWI and deciduousness showed that TWI had no effect on drought sensitivity in 2010 (median effect =0, 90% CI -0.04, 0.03) but a positive effect in 2015 (median effect =0.05, 90% CI 0.01, 0.08). The interaction between TWI and deciduousness was not significant in 2010 (median effect =0, 90% CI -0.01, 0.02) but was significantly negative in 2015 (median effect =-0.02, 90% CI -0.03, 0). Combined, predicted sensitivities of deciduous trees was more negative than evergreen trees in 2015, with this effect stronger in wetter sites (Fig 3b).

The opposite effects of TWI on sensitivity in the wet and dry season drought, and the influence of deciduousness was also confirmed by models that controlled for crown exposure and size as well as species variation in intercept and slopes (Fig 4a). These models showed small negative sensitivities in wetter sites in the dry season drought (median effect =-0.04, 90% CI -0.09, 0.02), but strong positive effect of wetness in the wet season drought (median effect =0.05, 90% CI 0, 0.11). The positive effect of TWI in 2015 was, however, mainly due to the response of evergreen species; deciduousness had a significant negative correlation with the slopes of the TWI effect in 2015 (Fig 4b). Predictions across the range of observed variables also showed that deciduous species generally had larger negative sensitivities in 2015, which did not show increase with wetness (Fig 4c). On the other hand, neither the mean sensitivities across species nor their response to TWI was associated with deciduousness in 2010.



***Figure 4: Drivers of variation in sensitivity among individuals***. All panels represent model results from models (one for each year) predicting sensitivity with microenvironment conditions with species random effect on all slopes. a) Coefficient plots showing median effects and 90% CI for wetness, exposure and DBH of tree. b) wetness effect across all species and its relationship with deciduousness value. Line represents a significant correlation. c) Predicted relationship of drought sensitivity with topographic wetness index across all species derived from model predictions. Black line represents overall relationship; coloured lines for each species reflects deciduousness values. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/13>

Crown exposure was associated with stronger negative sensitivities in both droughts. In the same models with species random effects on intercept and slope, the simplex parameter for the ordered factor crown exposure in 2010 was significant and negative (median effect =-0.15, 90% CI -0.32, -0.07), while in 2015 the negative effect was not as strong (median effect =-0.06, 90% CI -0.17, 0.03). Predicted effects of crown exposure on sensitivity decreased monotonically, with a decrease to negative sensitivities in category 4 and 5 in 2010, but all crown exposure categories had negative sensitivities in 2015 (Fig 5b).

Accounting for effects of exposure, remaining effects of size on sensitivity differed between the two droughts. DBH was a significant predictor of exposure category, with larger DBH associated with higher exposure categories in 2010 (median effect =4.02, 90% CI 3.75, 4.29) and 2015 (median effect =4.2, 90% CI 3.92, 4.49) (Fig 5a). Controlling for this direct effect of exposure, the remaining effect of size *per se* was significantly positive in 2010, while it was weakly negative in 2015 (Fig 4a, Fig 5a).



***Figure 5: Effects of size, exposure and water availability*** from combined models. Hypothesised relationships between microenvironment variables and drought sensitivity with their modelled effects in the HKK ForestGEO plot in the droughts of a) 2010 and b) 2015. Solid lines represent relationships where 90% credible intervals do not overlap 0, blue and red lines represent positive and negative effects respectively and line thickness is scaled to the effect size. c) Modelled sensitivity across crown exposure classes in 2010 and 2015. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/14>

# Discussion

We show strong evidence that tropical tree drought sensitivity can be jointly and interactively shaped by drought characteristics, species adaptations and local environmental conditions (Table 1). Analysing two droughts in a 14-year dendrometer band timeseries, we found that tropical tree species and individuals grew less than average in drought years, reflecting in lower plot-level growth (Fig 2). Comparing across droughts, we found that despite the shorter duration of drought conditions, the wet-season drought elicited stronger responses across trees, but especially so for deciduous species that are expected to have stronger seasonality in growth phenology (Fig 3). Interestingly, in the wet-season drought, we also show that evergreen and deciduous species had divergent responses along a wetness gradient; evergreen trees fared better and deciduous species suffered worse declines in wetter sites (Fig 3b, Fig 4b). Further, besides consistent negative effects of crown exposure, we found that the drivers of variation among species and individuals in drought sensitivity were dissimilar between the drought events (Fig 4a). Water availability buffered exposure-associated growth declines through different mechanisms in the two different droughts - larger trees (with likely deeper roots) in the dry-season drought and trees in wetter sites in the wet-season drought suffered smaller declines in growth (Fig 5). Taken together, our analysis of tree growth in two different drought years, and spanning meaningful variation, shows that species and individuals can respond differently to different drought events. Despite stand-level growth declines in drought years, we show that these broad patterns belie enormous heterogeneity in individual and species responses to drought in tropical forests with possible consequences for the maintenance of species diveristy and ecosystem stability.

Our analysis spans representative spatial and ecological variation, but we are limited in quantitatively analysing differences among droughts and variation in drought characteristics, because of low sample size. Given the diversity of factors that can influence tree growth and drought sensitivity in tropical tree communities, our analysis of 30 species across size classes and habitats spans this ecological and spatial (environmental) variation realistically and beyond the scope of previous such analyses. Further, although estimates of woody growth from dendroband timeseries can have measurement biases because of stem water shrinkage and bark peeling (Chitra-Tarak *et al.* 2015), our results are robust to simplifying assumptions that account for these biases (Fig S–). However, given the relative shorter duration of the timeseries, the effort required to collect these data, and the unpredictability of drought events, our analysis only included two specific droughts. Thus, quantitative analyses parsing out the specific effects of drought characteristics like relative influence of timing and degree of anomaly are currently impossible, limiting interpretations. In temperate forests, long-term records from tree ring analyses could disentangle species and individual sensitivities to differing drought characteristics, as annual rings are formed by a majority of the species. Indeed McGregor *et al.* (2021) found that species sensitivities were different across drought events. However, as this accumulating dendrometer data record continues to grow, so does the potential to answer these questions across a wider range of forested ecosystems.

Tropical dry forests represent periodic hot/dry conditions, creating selective pressures for adaptative variation towards drought resistance, but this might not hold in other bioclimatic zones where adaptive pressures and thus ecological variability is different. Strong seasonality in tropical dry forests exerts selective pressures on hydraulic strategies and has resulted in diversification along the hydraulic safety-efficiency axis with diverse strategies to maximise tree vital rates (González-M. *et al.* 2021; Oliveira *et al.* 2021). The degree of adaptive variation along the water use axis might be comparable to other dry climatic systems (e.g. temperate drylands reported in Vasey *et al.* (2022)) but it may not apply to the wet or everwet tropics, where tree-environment relations and evolutionary strategies may be substantially different. Therefore, we caution that our results suggestive of community-level insurance effects under drought be interpreted carefully across forest types that may be structured primarily by nutrient limitation, fires, herbivory or pathogens. However, our inference on the effects of drought timing could be generalisable across wet and dry tropics in the light of emerging evidence that despite low seasonality in climatic conditions, everwet forest species also show seasonal growth patterns (Giraldo *et al.* 2023).

Despite consistent observations of growth declines at the plot level across drought events, we show that this scale obscures a variety of ecological responses at the species and tree level that are heterogeneous across drought events. Our finding that a wet season drought had bigger impact calls into question the generality of the findings of Zuidema *et al.* (2022), which found that in species with tree-ring chronologies, dry season drought was most impactful. (Care must be taken in interpretation, however, as the 2015-2016 wet season ENSO drought was stronger (Fig 1)). *Afzelia xylocarpa*, one of the few annual-ring-forming species in HKK is noteworthy with the most distinct response across the two events; it had the highest (positive) sensitivity in the dry season drought, but a large negative sensitivity in the wet season drought (Fig S5). More generally, past analyses of tree ring and census estimates of drought sensitivity in seasonally dry tropical forests may have been limited towards fast growing (measurable using tape) or few dry-associated species (that form annual tree rings) - and therefore capturing only the more dramatic effects. In contrast, our analyses reveal a range of responses, including the contrasting influence of deciduousness in the two different droughts, showing that ecological and evolutionary strategies may result in heterogeneous consequences. Distinct responses of species and individuals to drought characteristics suggests potential spatiotemporal insurance effects among tropical tree response to drought in alignment with recent global analyses (Liu *et al.* (2022)).

Drought sensitivity is often defined as a static species trait but our study reveals expanded dimensions of drought responses with possible consequences for management and restoration. Despite net decreased growth at the plot level (in agreement with landscape-scale in Aguirre-Gutiérrez *et al.* (2022) and Bennett *et al.* (2023)), we show evidence that the same strategies are not uniformly successfully across spatiotemporal climatic variation. Static traits are often used to explain and predict forest responses to drought, especially in the tropics where long-term records are few (Guillemot *et al.* 2022; Vico *et al.* 2017). More inclusive frameworks for drought responses like Trugman *et al.* (2021) (on mortality) encompass ecological complexity and covarying traits with environment like, but they assume consistent sensitivity of individual trees across events. Our results, however, demonstrate an additional temporal dimension of variation, at least partially attributable to drought characteristics. Our results indicate that drought responses in tropical trees may not be a fixed response across events, but jointly shaped by species adaptations and local environmental conditions. Given these inconsistencies, diverse stands that may represent greater variation in ecological and evolutionary strategies, may have mechanisms for stable functioning under future droughts.

# Acknowledgements

We acknowledge the continued contributions of the Huai Kha Khaeng forest monitoring team in collecting data and maintaining the dendrometer bands. Ekaphan Kraichak and Kanisorn Chowtiwuttakorn helped with procuring elevation and climate datasets. José Medina-Vega, Valentine Herrmann and Eugenie Más provided input on improving analyses. KA was supported by the Smithsonian Institution Postdoctoral Fellowship and the ForestGEO Analytical Workshop, Asia 2024 in completing this work.

# References

Aguirre-Gutiérrez, J., Berenguer, E., Oliveras Menor, I., Bauman, D., Corral-Rivas, J.J., Nava-Miranda, M.G., *et al.* (2022). [Functional susceptibility of tropical forests to climate change](https://doi.org/10.1038/s41559-022-01747-6). *Nature Ecology & Evolution*, 6, 878–889.

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., *et al.* (2019). [Drier tropical forests are susceptible to functional changes in response to a long-term drought](https://doi.org/10.1111/ele.13243). *Ecology Letters*, 22, 855–865.

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., *et al.* (2017). [Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes?](https://doi.org/10.1088/1748-9326/aa5968) *Environmental Research Letters*, 12, 023001.

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., *et al.* (2015). [CTFS-ForestGEO : A worldwide network monitoring forests in an era of global change](https://doi.org/10.1111/gcb.12712). *Global Change Biology*, 21, 528–549.

Anderson-Teixeira, K.J., Herrmann, V., Morgan, R.B., Bond-Lamberty, B., Cook-Patton, S.C., Ferson, A.E., *et al.* (2021). [Carbon cycling in mature and regrowth forests globally](https://doi.org/10.1088/1748-9326/abed01). *Environmental Research Letters*, 16, 053009.

Anderson-Teixeira, K.J., Wang, M.M.H., McGarvey, J.C. & LeBauer, D.S. (2016). [Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db)](https://doi.org/10.1111/gcb.13226). *Global Change Biology*, 22, 1690–1709.

Bauman, D., Fortunel, C., Cernusak, L.A., Bentley, L.P., McMahon, S.M., Rifai, S.W., *et al.* (2022). [Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits](https://doi.org/10.1111/gcb.15982). *Global Change Biology*, 28, 1414–1432.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., *et al.* (2010). [Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate](https://doi.org/10.1126/science.1184984). *Science*, 329, 834–838.

Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015). [Larger trees suffer most during drought in forests worldwide](https://doi.org/10.1038/nplants.2015.139). *Nature Plants*, 1, 15139.

Bennett, A.C., Rodrigues de Sousa, T., Monteagudo-Mendoza, A., Esquivel-Muelbert, A., Morandi, P.S., Coelho de Souza, F., *et al.* (2023). [Sensitivity of South American tropical forests to an extreme climate anomaly](https://doi.org/10.1038/s41558-023-01776-4). *Nature Climate Change*, 13, 967–974.

Brando, P.M., Paolucci, L., Ummenhofer, C.C., Ordway, E.M., Hartmann, H., Cattau, M.E., *et al.* (2019). [Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis](https://doi.org/10.1146/annurev-earth-082517-010235). *Annual Review of Earth and Planetary Sciences*, 47, 555–581.

Bürkner, P.-C. (2017). [**Brms** : An *R* Package for Bayesian Multilevel Models Using *Stan*](https://doi.org/10.18637/jss.v080.i01). *Journal of Statistical Software*, 80.

Bürkner, P.-C., Gabry, J., Kay, M. & Vehtari, A. (2023). Posterior: Tools for working with posterior distributions.

Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H.S., Suresh, H.S. & Sukumar, R. (2015). [And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations](https://doi.org/10.1016/j.foreco.2014.10.007). *Forest Ecology and Management*, 336, 129–136.

Chitra-Tarak, R., Xu, C., Aguilar, S., Anderson-Teixeira, K.J., Chambers, J., Detto, M., *et al.* (2021). [Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest](https://doi.org/10.1111/nph.17464). *New Phytologist*, 231, 1798–1813.

Clark, D.A., Clark, D.B. & Oberbauer, S.F. (2021). [Annual Tropical-Rainforest Productivity Through Two Decades: Complex Responses to Climatic Factors, [CO2] and Storm Damage](https://doi.org/10.1029/2021JG006557). *Journal of Geophysical Research: Biogeosciences*, 126, e2021JG006557.

Clark, D.B., Clark, D.A. & Oberbauer, S.F. (2010). [Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO2](https://doi.org/10.1111/j.1365-2486.2009.02004.x). *Global Change Biology*, 16, 747–759.

Dahinden, F., Fischer, E.M. & Knutti, R. (2017). [Future local climate unlike currently observed anywhere](https://doi.org/10.1088/1748-9326/aa75d7). *Environmental Research Letters*, 12, 084004.

De Souza, B.C., Carvalho, E.C.D., Oliveira, R.S., De Araujo, F.S., De Lima, A.L.A. & Rodal, M.J.N. (2020). [Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest](https://doi.org/10.1007/s00442-020-04760-3). *Oecologia*, 194, 221–236.

García-Cervigón, A.I., Camarero, J.J., Cueva, E., Espinosa, C.I. & Escudero, A. (2020). [Climate seasonality and tree growth strategies in a tropical dry forest](https://doi.org/10.1111/jvs.12840). *Journal of Vegetation Science*, 31, 266–280.

Giraldo, J.A., del Valle, J.I., González-Caro, S., David, D.A., Taylor, T., Tobón, C., *et al.* (2023). [Tree growth periodicity in the ever-wet tropical forest of the Americas](https://doi.org/10.1111/1365-2745.14069). *Journal of Ecology*, 111, 889–902.

González-M., R., Posada, J.M., Carmona, C.P., Garzón, F., Salinas, V., Idárraga-Piedrahita, Á., *et al.* (2021). [Diverging functional strategies but high sensitivity to an extreme drought in tropical dry forests](https://doi.org/10.1111/ele.13659). *Ecology Letters*, 24, 451–463.

Guillemot, J., Martin-StPaul, N.K., Bulascoschi, L., Poorter, L., Morin, X., Pinho, B.X., *et al.* (2022). [Small and slow is safe: On the drought tolerance of tropical tree species](https://doi.org/10.1111/gcb.16082). *Global Change Biology*, 28, 2622–2638.

Intergovernmental Panel On Climate Change (Ipcc). (2023). [*Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*](https://doi.org/10.1017/9781009157896). 1st edn. Cambridge University Press.

Kunert, N., Zailaa, J., Herrmann, V., Muller-Landau, H.C., Wright, S.J., Pérez, R., *et al.* (2021). [Leaf turgor loss point shapes local and regional distributions of evergreen but not deciduous tropical trees](https://doi.org/10.1111/nph.17187). *New Phytologist*, 230, 485–496.

Lindsay, J.B. (2016). Whitebox GAT: A case study in geomorphometric analysis. *Computers & Geosciences*, 95, 75–84.

Liu, D., Wang, T., Peñuelas, J. & Piao, S. (2022). [Drought resistance enhanced by tree species diversity in global forests](https://doi.org/10.1038/s41561-022-01026-w). *Nature Geoscience*, 15, 800–804.

Luo, X. & Keenan, T.F. (2022). [Tropical extreme droughts drive long-term increase in atmospheric CO2 growth rate variability](https://doi.org/10.1038/s41467-022-28824-5). *Nature Communications*, 13, 1193.

McGregor, I.R., Helcoski, R., Kunert, N., Tepley, A.J., Gonzalez-Akre, E.B., Herrmann, V., *et al.* (2021). [Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest](https://doi.org/10.1111/nph.16996). *New Phytologist*, 231, 601–616.

Muller-Landau, H.C. (2008). Metal Band Dendrometer Protocol.

Naumann, G., Alfieri, L., Wyser, K., Mentaschi, L., Betts, R.A., Carrao, H., *et al.* (2018). [Global Changes in Drought Conditions Under Different Levels of Warming](https://doi.org/10.1002/2017GL076521). *Geophysical Research Letters*, 45, 3285–3296.

Oliveira, R.S., Eller, C.B., Barros, F. de V., Hirota, M., Brum, M. & Bittencourt, P. (2021). [Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems](https://doi.org/10.1111/nph.17266). *New Phytologist*, 230, 904–923.

R Core Team. (2024). *R: A language and environment for statistical computing*. Manual. R Foundation for Statistical Computing, Vienna, Austria.

Slette, I.J., Post, A.K., Awad, M., Even, T., Punzalan, A., Williams, S., *et al.* (2019). [How ecologists define drought, and why we should do better](https://doi.org/10.1111/gcb.14747). *Global Change Biology*, 25, 3193–3200.

Trugman, A.T., Anderegg, L.D.L., Anderegg, W.R.L., Das, A.J. & Stephenson, N.L. (2021). [Why is Tree Drought Mortality so Hard to Predict?](https://doi.org/10.1016/j.tree.2021.02.001) *Trends in Ecology & Evolution*, 36, 520–532.

Vasey, G.L., Weisberg, P.J. & Urza, A.K. (2022). [Intraspecific trait variation in a dryland tree species corresponds to regional climate gradients](https://doi.org/10.1111/jbi.14515). *Journal of Biogeography*, 49, 2309–2320.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.-C. (2021). Rank-normalization, folding, and localization: An improved Rhat for assessing convergence of MCMC (with discussion). *Bayesian Analysis*.

Vicente-Serrano, S.M., Beguería, S. & López-Moreno, J.I. (2010). [A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index](https://doi.org/10.1175/2009JCLI2909.1). *Journal of Climate*, 23, 1696–1718.

Vico, G., Dralle, D., Feng, X., Thompson, S. & Manzoni, S. (2017). [How competitive is drought deciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach](https://doi.org/10.1088/1748-9326/aa6f1b). *Environmental Research Letters*, 12, 065006.

Vinod, N., Slot, M., McGregor, I.R., Ordway, E.M., Smith, M.N., Taylor, T.C., *et al.* (2023). [Thermal sensitivity across forest vertical profiles: Patterns, mechanisms, and ecological implications](https://doi.org/10.1111/nph.18539). *New Phytologist*, 237, 22–47.

Vlam, M., Baker, P.J., Bunyavejchewin, S. & Zuidema, P.A. (2014). [Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees](https://doi.org/10.1007/s00442-013-2846-x). *Oecologia*, 174, 1449–1461.

Williams, L.J., Bunyavejchewin, S. & Baker, P.J. (2008). [Deciduousness in a seasonal tropical forest in western Thailand: Interannual and intraspecific variation in timing, duration and environmental cues](https://doi.org/10.1007/s00442-007-0938-1). *Oecologia*, 155, 571–582.

Wu, Q. & Brown, A. (2022). *’Whitebox’: ’WhiteboxTools’ R frontend*. Manual.

Zuidema, P.A., Babst, F., Groenendijk, P., Trouet, V., Abiyu, A., Acuña-Soto, R., *et al.* (2022). [Tropical tree growth driven by dry-season climate variability](https://doi.org/10.1038/s41561-022-00911-8). *Nature Geoscience*, 15, 269–276.

Zuleta, D., Duque, A., Cardenas, D., Muller-Landau, H.C. & Davies, S.J. (2017). [Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon](https://doi.org/10.1002/ecy.1950). *Ecology*, 98, 2538–2546.

Zweifel, R., Haeni, M., Buchmann, N. & Eugster, W. (2016). [Are trees able to grow in periods of stem shrinkage?](https://doi.org/10.1111/nph.13995) *New Phytologist*, 211, 839–849.