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

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# Abstract (150 words)

The frequency and intensity of droughts are increasing across tropical forests, altering tree demography and its contribution to the land carbon sink. In seasonally dry 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 predict the drought sensitivity of tree growth in two climatically distinct droughts. Species and stems 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, with this difference worsened in wetter microclimates. Although exposed trees were more sensitive, access to water through larger size or topographic location buffered growth declines. Heterogenous responses of species and individuals to droughts indicate potential spatiotemporal insurance effects in diverse forests in the face of increased climate anomalies.

# Introduction

Tropical tree woody growth has long-lasting impacts on the terrestrial carbon pool, but it may be vulnerable to climate anomalies like drought.  
- Woody growth has one of the longest residence times in terrestrial carbon pool, contributing to long-lasting impacts on carbon removal from the atmosphere (Muller-Landau *et al.* 2021; Yang *et al.* 2021).  
- Climate anomalies like drought can lead to stand-level growth reductions, along with increased mortality (Bauman *et al.* 2022; Bennett *et al.* 2023).  
 - Seasonally dry tropical forests are especially vulnerable to ecological impacts of drought, being at the edge of plant thermal and water stress tolerance (Allen *et al.* 2017). - Within a stand, drought sensitivity varies among species and individuals, but the extent and drivers of this variation in drought responses is poorly understood.  
- With changing climate patterns across the global tropics, emergence of novel climatic regimes like “very extreme droughts” in recent decades (Dahinden *et al.* 2017; Luo & Keenan 2022), there is an urgent need to understand the drivers of this variation, to be able to predict and respond to forest drought responses.

Seasonally dry tropical forests can be vulnerable to droughts, despite trees being adapted to strong dry seasons.  
- Trees in seasonally dry forests are routinely exposed to hot, dry conditions in the dry season and may have evolutionary strategies like dry-season deciduousness and drought deciduousness for survival.  
- However, across the global tropics, drier forests show stronger sensitivities to drought-associated water stress (Aguirre-Gutiérrez *et al.* 2019; Bauman *et al.* 2022; Bennett *et al.* 2023). - One potential reason - thermal/water stress tolerance thresholds crossed (Allen *et al.* 2017).  
- Another reason: drought events are climatically different in timing and intensity, with trees exposed to drought conditions in different parts of their seasonal phenologies.  
- Morevoer, besides broad patterns at the stand level, species- and individual-level heterogeneity can lead to divergent responses with consequences for stand composition.  
- Some of the discrepancies between expectations from trees and observations at the stand-level may be resolved by considering factors that determine drought sensitivity across species and individuals

Trees in seasonally dry forests have strategies that span and interact across timescales to maximise growth and survival under hot/dry conditions.  
- evolutionary timescales - e.g. dry season deciduousness  
- Deciduous species, with shorter duration with leaves can have acquisitive strategies during leaf on (De Souza *et al.* 2020).  
- ecological timescales - e.g. distribution of trees in relation to wetness  
- Species distribution of evergreen species covarying with soil moisture (Kunert *et al.* 2021) and potentially affecting survival and growth.  
- ecophysiological - e.g. negative TLPs, plasticity in deciduousness (root/shoot) - Species with drought tolerant traits like deep roots, more negative turgor loss point and … can be more or less resistant to drought (Chitra-Tarak *et al.* 2021; Kunert *et al.* 2021).  
- Larger trees suffer more growth declines during drought (Bennett *et al.* 2015), exposed crowns -> more thermal stress (Vinod *et al.* 2023) although crown exposure -> more light -> more growth in normal years. - Some of these adaptations may confer drought sensitivity and buffer stem growth declines during drought years, or may tradeoff with advantages in normal years. - To understand drought sensitivity representative of stand diversity, trees across these strategies need to be analysed.

Drought sensitivity representative of stand diversity in seasonally dry tropical forests is difficult to assess using standard methods.  
- Annual tree rings - found in SDTFs but not many species,  
- Species with rings represent specific strategy to water use and growth - and often affiliated to drier microenvironments.  
- Tape measurements - more representative, but may not be annual because of effort  
- Even when tape measures are annual, not enough precision; error for each tape measure is 1mm, error for growth is at least 2mm. (Median annual growth across trees in HKK is ~1.4 mm, deviation from annual growth needs more precision).  
- In sum, these methods may only be capturing the most dramatic effects - the most severe droughts that affect ring-forming species or produce large-enough declines in fast-growing individuals.  
- Methods need to capture species strategies, distributions across microenvironments, and be precise enough.

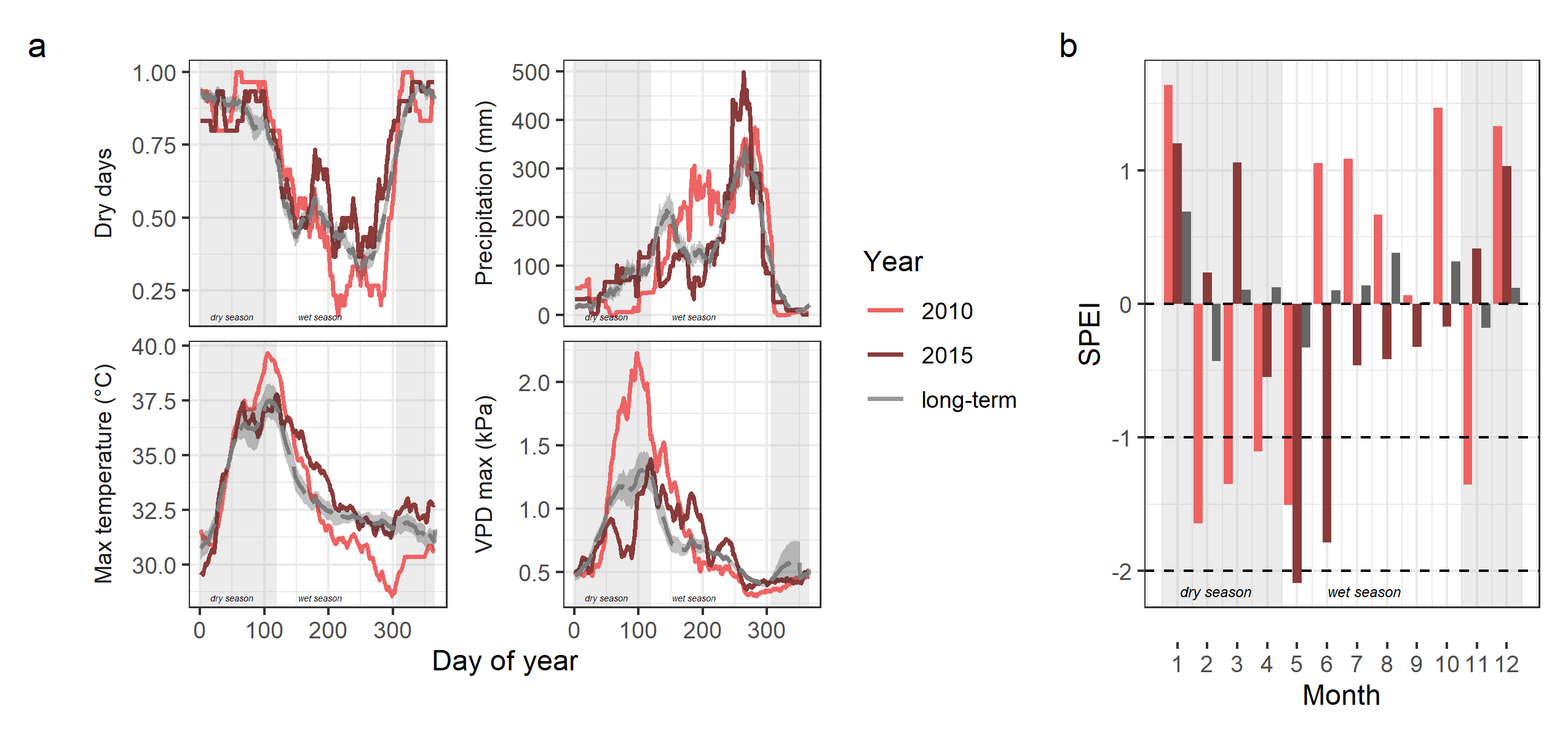
|  | 2010 | 2015 | evidence |
| --- | --- | --- | --- |
| **Drought characteristics** |  |  |  |
|  | dry season | wet season | Fig 1 |
|  |  |  |  |
| **Effect on species drought sensitivity** |  |  |  |
| Deciduousness | no | - | Fig 3 |
| 2010 sensitivity |  | no | Fig S- |
|  |  |  |  |
| **Effect on individual drought sensitivity** |  |  |  |
| TWI | - | + | Fig 3, 4 |
| Deciduousness:TWI | no | - | Fig 3 |
| exposure | - | - | Fig 4, 5 |
| other size effects | + | - | Fig 4 |
| 2010 sensitivity |  | no | Fig S- |

Here we examine individual tree growth during two known ENSO drought years within a 14-year record of dendrometer band measurements in a seasonally dry forest in Thailand to disentangle the drivers of tree growth sensitivity to drought. We hypothesise that tropical tree drought sensitivity is jointly shaped by species adaptations, individual microenvironments and drought characteristics. Specifically, we expect 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.

# 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 Huai Kha Khaeng ForestGEO plot. 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.

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 at breast height (DBH) 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]. Since this was dependent on the diameter measurement at installation, we used a direct measurement 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). We repeated the same steps using 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) Dsitribution 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***

Combining the growth timeseries from dendrometer band measurements with climatic information, we identified two drought years of interest - 2010 and 2015. To identify drought years, we identified years with low plot-level growth rate and combined this with information on ENSO events that affected the landscape. We chose to identify the years starting from the timeseries, instead of directly using climate variables and their deviation because drought definitions vary widely, and drought characterisation of a year can vary based on the definition selected. Moreover, broad definitions based on climate variables (often not measured at the location), may not capture ecological realities within the plot. Out of the two years with low plot-level growth, 2010 was a moderate ENSO event while 2015 was a very strong ENSO event. These years also corresponded with expert knowledge of major droughts that affected the region. 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 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 the long-term mean for each variable as the mean of the values of the rolling mean across all years of the dendroband measurements, and the standard error around this mean. We also used the SPEIbase dataset [REF] to calculate the Standardised Precipitation-Evapotranspiration Index, a drought severity index, calculated at the monthly scale. We report monthly SPEI for the two drought years along with long-term mean SPEI for each month.

***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. 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 annual increments from dendrobands from water-related growth or shrinkage, we also calculated growth occurrence using a zero-growth assumption (**zweifel?**). Under this assumption, positive DBH change is scored as 1 and any change <=0 is scored as 0. 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?**). 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 three species-level traits : deciduousness, maximum size and niche breadth. 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. We used data published in Williams *et al.* (2008) for the top 30 species. Out of these, 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. At the species level, we also calculated the maximum size across all individuals in the plot as measured in the 2008 whole-plot census. We calculated niche breadth as the standard deviation of TWI across all observed individuals of each species in the whole plot census in 2008.

***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 three species-level traits - deciduousness, maximum size and niche breadth using simple linear models.

To model the interactive effects of deciduousness 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 drivers of stem-level 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* [REF]. We ran 4 MCMC chains for 3000 iterations with 1000 of these set as warmup. We extracted draws, calculated distributions using functions from the *posterior* package [REF].

# 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 (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.

## Interannual growth variation 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. 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.



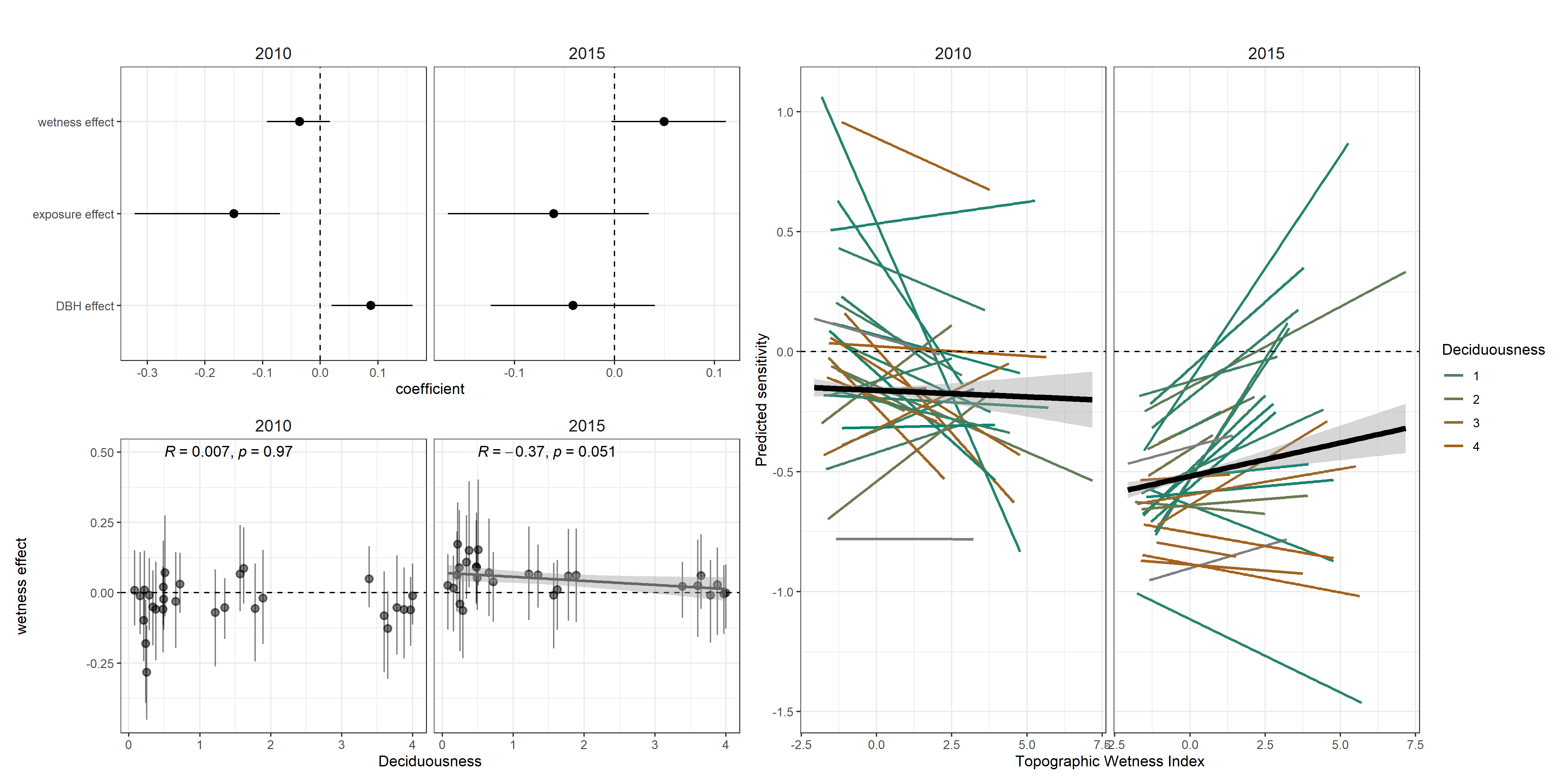
***Figure 3: Variation in sensitivity among species*** in the Huai Kha Khaeng ForestGEO plot during droughts in 2010 and 2015. For comments: <https://github.com/forestgeo/growth-precip-thailand/issues/12>

## Variation in sensitivity among species

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) but on average had lower mean and median sensitivities in 2015 than in 2010, 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).

The effect of TWI on sensitivity was different in 2010 and 2015, with 2015 effects interacting with deciduousness. 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.

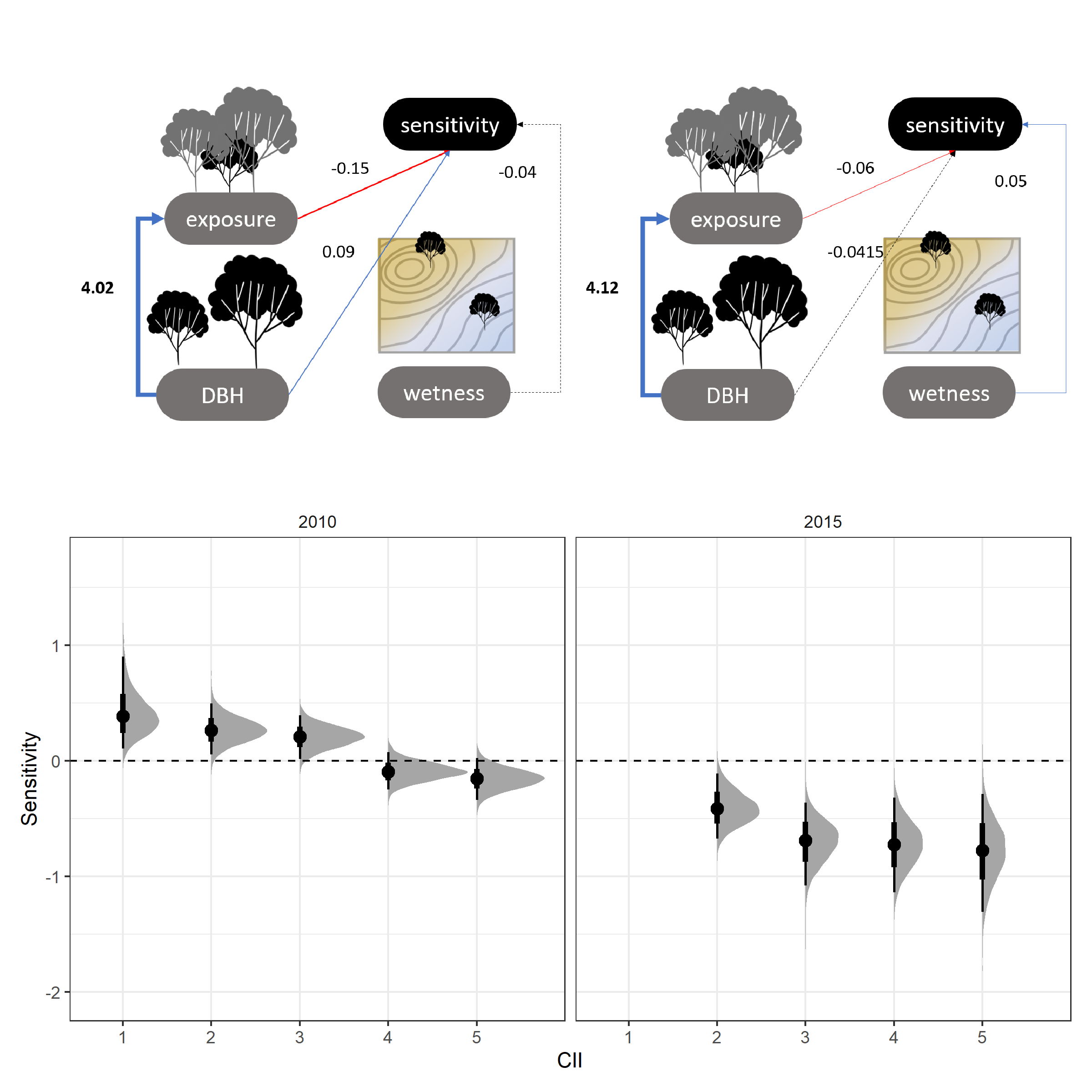


***Figure 4: Drivers of variation in sensitivity among individuals***. For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/13>

## Variation among individuals

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 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*** For comments - <https://github.com/forestgeo/growth-precip-thailand/issues/14>

# Discussion

Unordered points from Introduction - Many hydraulic-related traits vary with tree height (Vinod *et al.* 2023), including the frequency of dry season deciduous leaf loss – both within species and at the community level (**condit\_ref?**; **meakem?**). *caveat for species-level traits*

*for where else might they be allocating to?* - Some evidence that both understory and emergent species can have reduced survival during drought (Machado *et al.* 2023).  
- ENSO droguht changed regeneration dynamics in Thailand (Nutiprapun *et al.* 2023) - deciduous species have higher survival under multi-year droughts (**aguirre-guiterrez?** refs)

* (BCI light x size interaction in Rüger *et al.* (2011))
* Afzelia xylocarpa, one of the tree ring species had the most distinct (positive) sensitivity in the dry season drought *on how representative sampling is important*

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# Competing interests

# Author contributions

# Data availability

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