**Title:** Using tree-ring records to simultaneously characterize the influence of tree size, climate, and other environmental drivers on annual growth

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### Abstract

1. Tree rings provide a valuable long-term record for understanding how climate shapes forest productivity. However, traditional analysis methods have not been designed to simultaneously account for the effects of tree size and climate, which has limited the potential to use tree-rings to understand forest productivity in the current era of rapid climate change.
2. Here, we develop a new method that allows simultaneous non-linear modeling of the effects of objectively determined principle climate drivers and tree diameter. Specifically, we first identify the most important climate drivers using the climwin R package. We then include these in generalized least squares models that simultaneously fit the detrending splines needed to pull out climate signals and flexibly account for nonlinearity of responses to tree diameter and climate variables. We apply this method to tree-ring data from **#** species at **nine/ten** globally distributed sites spanning a wide range of forest types.
3. Our analysis identified similar climate drivers to those obtained via traditional methods, but revealed that non-linear responses to climate variables were common. Radial growth increments, basal area increments, and biomass increments all varied non-linearly with tree diameter. [*something about interactions between climate sensitivity and diameter*]
4. Our method provides a novel approach to objectively identifying the most important climate drivers of tree growth and combining them with tree diameter in nonlinear models. Our finding that nonlinear growth responses to climate variables are common contrasts with the assumption behind most contemporary dendrochonological analyses of the climate sensitivity of tree growth, but is consistent with physiological and ecological studies showing that biological rates often respond nonlinearly to climate drivers. The nonlinear relationship between tree diameter and growth rate implies that no metric of growth can be assumed independent of tree size, and therefore diameter must be accounted for in analyses seeking to quantify the impact of slowly-changing environmental drivers on tree growth. Our approach opens the door for using tree-ring records improved understanding of forest responses to climate change, while opening the door for simultaneous accounting of climate, tree size, and slowly changing environmental drivers.

**Keywords**: climate sensitivity; diameter; environmental change; Forest Global Earth Observatory (ForestGEO); generalized least squares; nonlinear; tree-ring

### Introduction

**Tree rings provide a long-term record of annual growth increments that is invaluable for understanding forests in an era of global change.** Spanning time scales of decades to centuries or even millennia, they provide by far the most robust method for characterization of the interannual climate sensitivity of tree growth (REFS) and how it is changing (e.g., Sniderhan & Baltzer, 2016; Maxwell, Harley, & Robeson, 2016). Combined with forest censuses, they can be used to estimate forest woody productivity (Graumlich, Brubaker, & Grier, 1989; Teets, Fraver, et al., 2018) and its climate sensitivity (Klesse et al., 2018; Teets et al., 2018; Helcoski et al., 2019). They may also be used to examine how tree growth is responding to pollution, including increasing atmospheric CO2 (reviewed in *Walker et al. in press*) and deposition of pollutants including sulfur dioxide (SO2) and nitrogen oxides (NOx) (Mathias & Thomas, 2018). This information is critical to predicting forest responses to climate change (*Walker et al. in press*; REFS), and thereby reducing the enormous uncertainty surrounding future contributions of Earth’s forests to the global carbon cycle (Friedlingstein et al., 2006). Yet, dendrochronological methods have been optimized to detect climate signals (DENDRO REFS) rather than to predict forest productivity and its climate sensitivity (Klesse et al., 2018). As a result, prevailing approaches hold a number of limitations for using tree-rings to address pressing questions concerning forest productivity in the current era of rapid environmental change.

**[limitations in how traditional methods look at climate variables]** - [subjectively selected variables (e.g., T, PPT, PDSI)] - [month-by-month, reflective of fact that historical climate data products are often presented at this time scale. While useful for characterizing how monthly climate influences annual tree growth, month is an arbitrary unit of time and this approach does not necessarily identify the most influential time windows –often several months–over which climate shapes tree growth. (*note that we use the monthly time step here–don’t set monthly resolution up as a problem we’ll solve*)] - [one variable at a time– no additive or interactive effects (although VS-Lite starts to get there), which are expected and have been observed for tree-rings (Foster et al. 2016)]

**Traditional methods characterize only linear climate responses. This conflicts with biological expectations.** Most biological rates—- from photosynthesis to animal metabolism—-display a unimodal relationship to temporal variation in temperature, wherein rates increase exponentially with temperature up to a point, typically reflective of the environment to which the organism is adapted / acclimatized, and decrease at higher temperatures (e.g., Slot and Winter 2017; Kumarathunge et al. 2019-cited in Helene’s Tansley review). Similar relationships have also been observed for moisture availability, particularly in environments that are not strongly water-limited. In trees, responses of photosynthesis and respiration to environmental drivers are typically observed over time frames of seconds to days, and therefore do not directly reveal how annual tree growth and forest productivity respond to inter-annual variation in climate. The annual growth records of tree-rings allow can be used to study interannual variation, but the standard practice in dendrochronology has been to fit linear relationships (exception is VS-Lite, which fits plateau(Tolwinski-Ward, Anchukaitis, & Evans, 2013)), and we therefore know little about what, if any, nonlinearities occur in tree growth responses to interannual variation in climate.

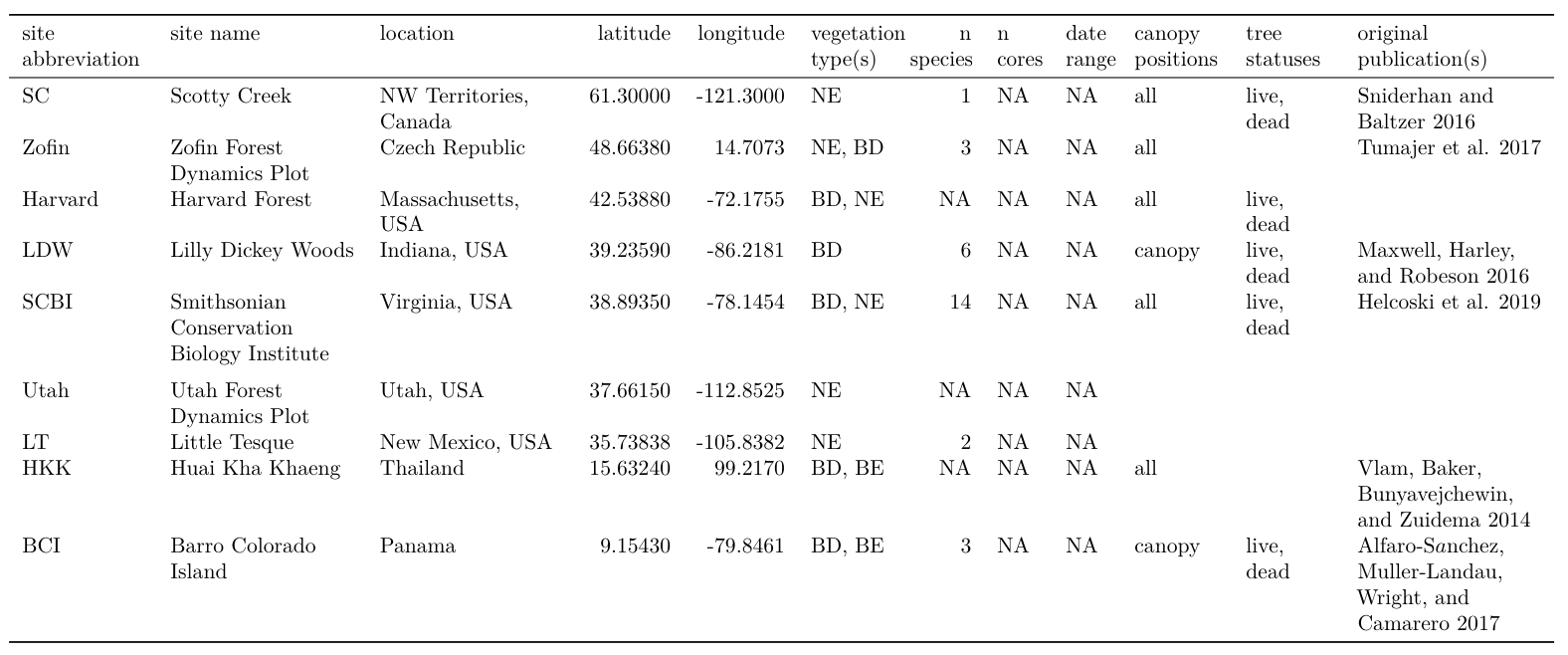
**Traditional methods do not characterize the effect of tree size or its potential interactions with climate variables.** Tree size (most commonly diameter breast height, ) is among the most important variables affecting tree growth rate [Muller-Landau et al. (2006); Foster, Finley, D’Amato, Bradford, & Banerjee (2016); REFS]. Radial growth increments (*i.e.*, tree-ring widths; ) may increase or decrease with tree size, often in a non-linear manner. Following a “juvenile growth phase”, which is typically removed in traditional dendrological analyses, may decline, particularly in open-grown conifers (??; DENDRO\_REFS). In contrast, in mesic closed-canopy forests, typically increases with tree diameter at breast height [; Muller-Landau et al. (2006); Anderson-Teixeira, McGarvey, et al. (2015); REFS, DENDRO\_REFS]. For dendrological studies aimed at deciphering climate signals, tree size is not typically a variable of interest, and its influence is removed through detrending (DENDRO\_REFS). While suitable for identifying climate signals (DENDRO\_REFS), this approach is not optimal for subsequent inference of the climate sensitivity of forest productivity. Although climate correlations can be transformed to climate sensitivity (*sensu* Charney et al., 2016) and scaled to characterize the climate sensitivity of based on the scaling of with (Helcoski et al., 2019), they cannot be used to characterize known interactive effects of and climate on tree growth. For example, larger trees tend to be more sensitive to drought [Bennett, McDowell, Allen, & Anderson-Teixeira (2015) ; McGregor et al. in revision; REFS]. Thus, to use tree-rings to predict for a forest where not every tree was cored, we need models that include tree size.

**Here, we develop a new method that allows simultaneous consideration of the effects of tree size, objectively determined principle climate drivers, and other environmental drivers on annual tree growth.** This allows us to ask: (1) What are the most important climate drivers of annual growth, and over which time windows? (2) What is the shape of the relationship between annual growth and climate drivers? (3) How do , , and aboveground biomass increments () vary with DBH? (4) Are interactions between DBH and climate drivers common?

### Materials and Methods

#### Data sources and preparation

We analyzed previously collected tree-ring data from # sites of the Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira, Davies, et al., 2015), plus one in New Mexico, representing a wide range of forest and tree types: tropical broadleaf deciduous and evergreen, temperate broadleaf deciuous and needleleaf evergreen, and boreal needleleaf evergreen (Table 1). Trees were cored within or close to (max distance: # km) the large forest dynamics plots following a variety of sampling protocols designed to meet the varied objectives of the original studies [Vlam, Baker, Bunyavejchewin, & Zuidema (2014); Maxwell et al. (2016); Sniderhan & Baltzer (2016); Tumajer et al. (2017); Alfaro-Sánchez, Muller-Landau, Wright, & Camarero (2017); Helcoski et al. (2019); MORE]. In using this variety of data sources, we encountered and solved a variety of challenges for analyzing existing tree-ring records with this approach.

**Table 1 | Sites included in this analysis** 

All tree cores were measured and cross-dated using standard dendrochronological practices. The full record for all cores was retained for analysis, with the following exceptions. First, we excluded species with <7 cores. Second, we excluded cores with <30 years of record. Third, for any sites with a record of > 10 mm within the first 15 years of the record, we excluded those 15 years. Fourth, for trees cored dead, we excluded the final 20 years prior to death to avoid periods of growth decline and potentially altered climate sensitivity prior to death (Cailleret et al., 2017) ; REF on climate sensitivity).

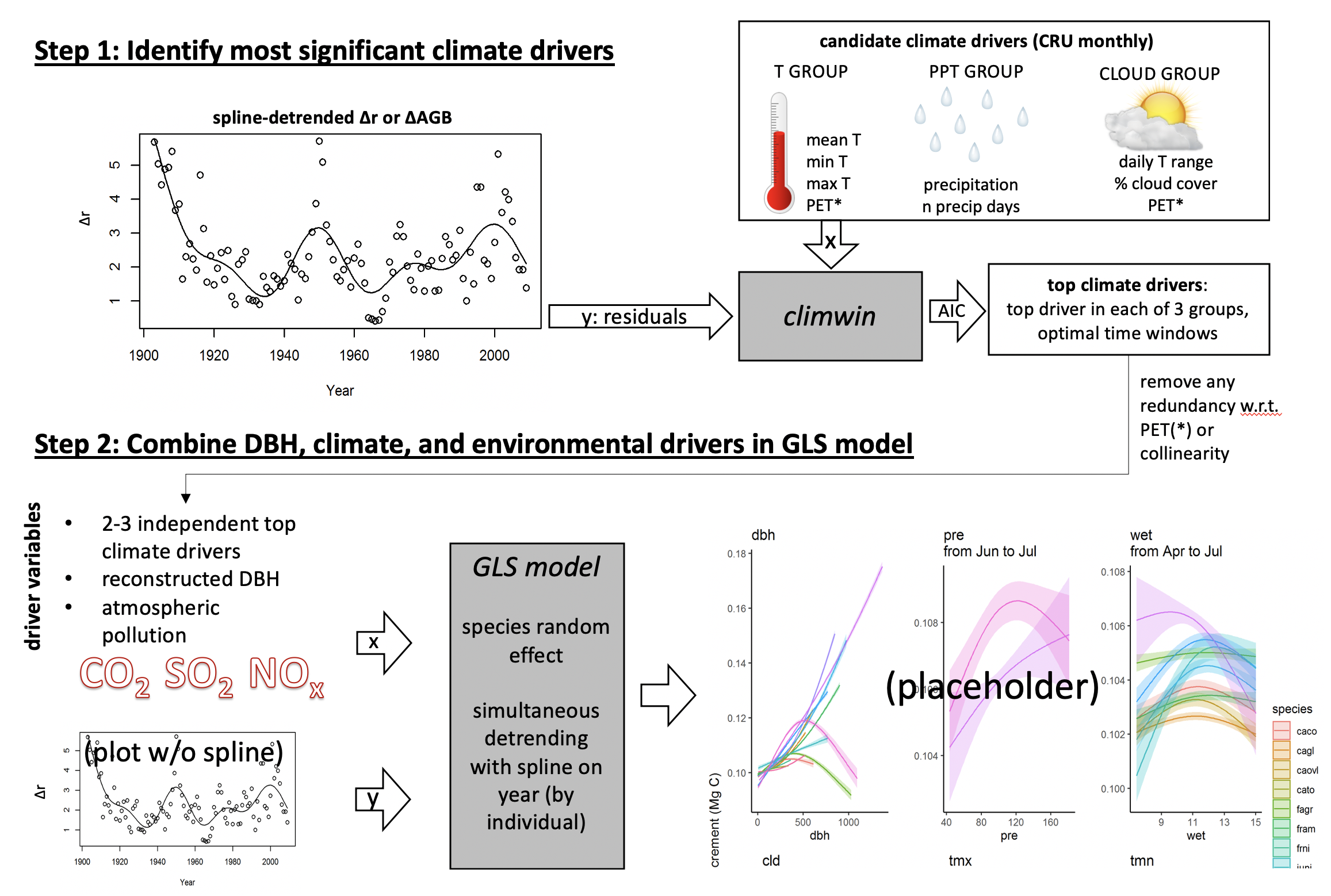
For each year in the tree-ring records, we reconstructed , as detailed in *Appendix S1*. In most cases, when a recent measurement was available, was reconstructed from the outside in. In cases where was not available, but when we knew that the core hit pith or could reasonably estimate how far off it was based on the curvature of the rings (DENDORO\_REF), was reconstructed from the inside out. In either case, we used allometric equations between and bark thickness to account for changes in bark thickness as the tree grew (Appendix S1; Table S2).

Once had been reconstructed, we calculated aboveground biomass growth increments () based on and . Specifically, for each year , we used biomass allometries to estimate based on and based on []. We then calculated as []. For temperate sites, biomass allometries were sourced from allo-db (DETAILS; Gonzalez-Akre et al. in prep). For tropical sites, biomass allometries were sourced from the BIOMASS package (REF).

Monthly climate data for 1901-20XX were obtained from CRU v.4.04 (Harris, Jones, Osborn, & Lister, 2014; Harris, Osborn, Jones, & Lister, 2020). Variables considered here included mean, minimum, and maximum temperatures; daily temperature range; precipitation; wet day frequency; cloud cover; and potential evapotranspiration (PET). In the CRU database, gaps are filled with monthly means… ([**ISSUE #45 in ForestGEO\_climate-senstivity**](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/45)**: handling gaps**). (*Describe criteria for excluding variables/ time frames.*) (*Describe BCI data.* )

#### Analysis methods

Our analysis consisted of two main steps: (1) identification of the most important climate drivers, and (2) combining and climate drivers into a multivariate model (Fig. 1). The analysis was run separately for each site.



**Figure 1 | DRAFT Schematic illustrating our analysis process.** This analysis is conducted separately for each site. (*CO2 needs to be removed from this figure.*)

*Identifying key climate drivers*

First, we identified the most important climate driver for each of three categories of variables: a temperature group (mean, min, and max temperature; PET), a precipitation group (precipitation, number of days with precipitation), and a group linked to cloud cover and temperature variability (“cloud” group; daily temperature range, percent cloud cover, and again PET). Because the variables in the cloud group are linked to both temperature and precipitation, this group was given lowest precedence in the variable selection process. These groups were defined based on the dependencies of these variables on one another in the CRU database (Harris et al., 2014, 2020), as well as climatological and biological considerations. Our first step was detrending to remove the influence of all non-climatic drivers (*e.g.*, growth and aging of the tree, change in competitive dynamics, atmospheric pollution), which is essential for identifying climatic drivers (DENDRO\_REFS). Specifically, we used a generalized least squares (GLS) model to fit a spline to individual tree growth records (, , or ), thereby producing residuals. We note that an an attempt at the analysis without detrending failed to produce results consistent with biological expectations and results obtained via traditional dendrochronological methods, and generally failed to identify significant climate drivers.

We then used the *climwin* package in R (REF) (Pol et al., 2016) to identify the most significant climate driver and time window for each of the three climate variable groups. *Climwin* searches through multiple climate variables and over a wide range of time frames to identify which are most strongly correlated to the biological variable of interest–in this case, residuals of , , or . We began by verifying that *climwin* identified similar climate variable-month combinations as what would be identified using traditional methods, as detailed in Appendix S2. (\*\*[ISSUE #35 in ForestGEO-climate-sensitivity](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/35))

Within *climwin*, we specified a mixed effects model using species and tree identity as random effects: residual ~ [climate] + (1 | sp) + (1 | treeID). Here, for each permutation, climate specifies one of the climate drivers in the climate variable group, analyzed over one of all possible combinations of time periods, at monthly resolution, starting in the previous May and ending in August of the current year. We note that analyzing all species together yields the most significant climate drivers across the full set of cores from each site (our goal here), whereas identification of the top climate drivers for individual species would be optimized by analyzing each species separately. *Climwin* can check for linear and quadratic relationships, and does k-fold cross-validation in its computation of AIC to guard against over-fitting (Pol et al., 2016). We specified quadratic relationships only because (i) quadratic relationships are more consistent with known biological mechanisms (see Introduction), (ii) preliminary tests revealed that quadratic fits usually had lower AIC, and when not there tended to be little difference in AIC and the curve would approximate a straight line, (iii) modeling only quadratic improves coding efficiency and speeds up the analysis process. For each group of candidate climate variables, we move forward with the best variable over the time window identified by climwin as a candidate climate variable for the multivariate models. If PET came out as the best variable in either the temperature or cloud group and there was any overlap in the time windows of variables from these groups, the cloud group variable was dropped from the analysis on the logic that it the top variables for these groups were too closely related.

A challenge to this system arose for the site undergoing most rapid climate change: Scotty Creek (*and NM*?). There, [temperatures have increased by X over X years]…, resulting in negative growth trends in basal area index (BAI) starting around 1950 and significant growth declines since 1970 in 56% of trees (Sniderhan & Baltzer, 2016). Problematically, correlating tree growth residuals from which climate-driven trends had been removed against the climate signal with a strong directional trend would not necessarily identify the most significant climate drivers. ([**ISSUE #25 in ForestGEO-climate-sensitivity**](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/25)**: How do we solve this?**)

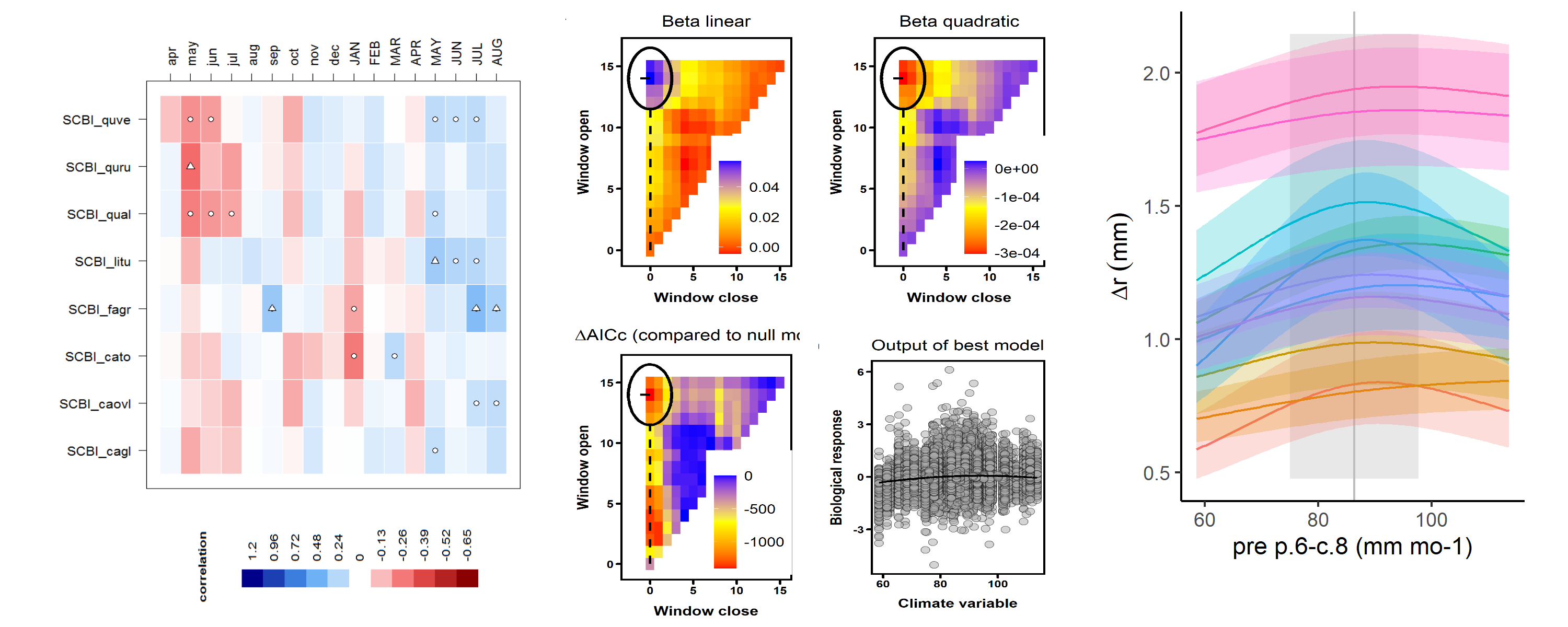
*Combining drivers in GLS model*

Second, we combined climate and reconstructed data in a GLS model (Fig. 1). We checked for collinearity among the full set of variables using the *vifstep* function (**REF**) and removed any variable with a variance inflation factor > 3. For each species (at each site) independently, we ran a GLS model including every combination of the candidate climate variables (as a 2-degree polynomial to allow quadratic curve), , and fit one year spline for each treeID, plus a random intercept for each tree. We also ran models with a spline of DBH (3 knots). Across all possible models, variable AICc weights were summed to determine which drivers are most important. We considered the model containing those variables as the top model.

### Results

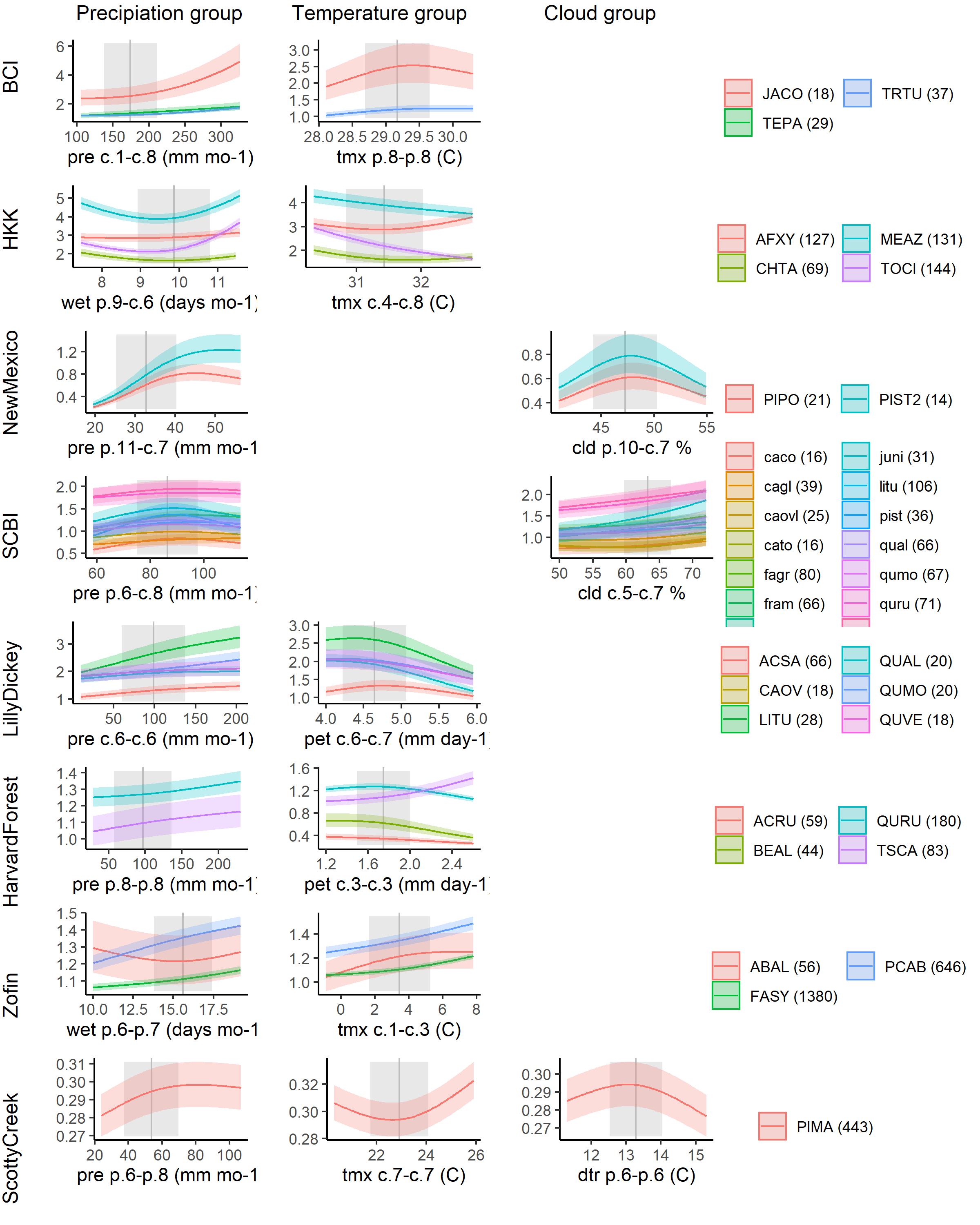
*Identifying climate drivers*

**Our process picked out similar climate drivers to what would be obtained via traditional methods (Figs. 2, S#; Appendix S2).**



**Figure 2 | Example comparison of climate sensitivity derived via traditional methods (**a**) and our approach (**b-f**).** Example is for the sensitivity of 14 species at SCBI (codes given in Table S1) to potential evapotranspiration (PET), identified by both traditional methods and our method to be among the top climate drivers. Panel (**a**) shows a matrix of Pearson correlations between ring- width index and monthly climate variables. Panels (**b-d**) give statistics for time windows tested in *climwin*, where window open and close indicate months prior to current August, and cells across the lower diaganol indicate single-month tests (akin to panel **a**). Panels (**b**) and (**c**) give values of linear and quadratic terms for each time window, and (**d**) gives the for each. The time window with the minimum (0-3 months prior to August, or May-Aug; black boxes), was identified as the optimal window. Panel (**e**) shows the correlation of individual-level residuals to PET, with the function fit in *climwin*. Finally, panel (**f**) shows GLS model output, where PET is one of several driver variables (*specify model*). Plotted are responses of species for which PET was identified as a signficant driver in the top model.

**The most influential climate drivers…[what tended to be selected?].** - Time windows - often current growing season - some exceptions - Selection within groups: - precip vs n precip days - temperature group: mean, min, max or PET? - t range group: which tended to be most important?



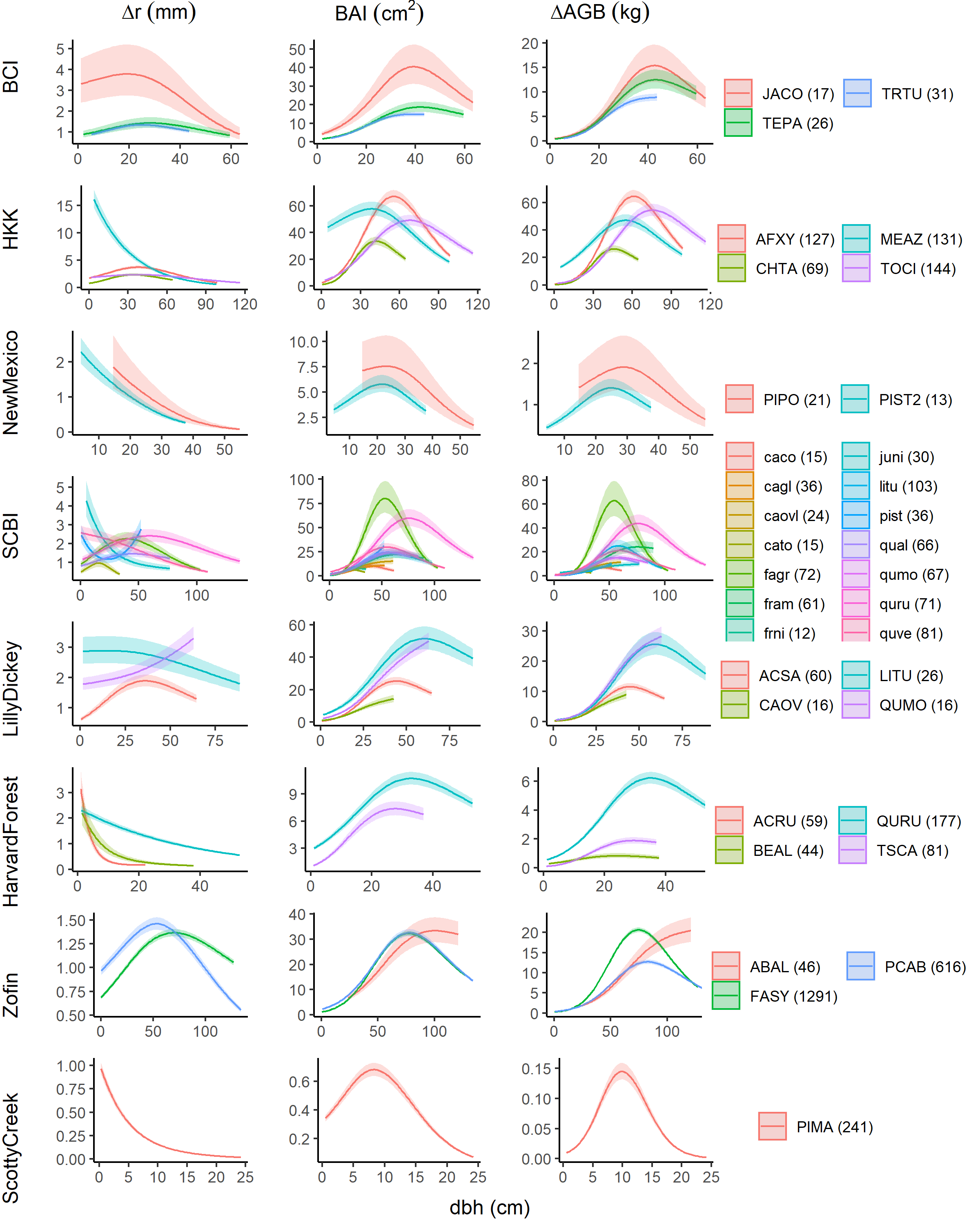
**Figure 3 | Climate senstivity for all sites.** Columns include the top variables in each grouping, with PET placed in the temperature group if included in the model. For each species, relationships are plotted if included in top model. Vertical grey lines indicate the long-term mean for the climate variable, shading indicates 1 SD. (IN-PREP FIGURE.)

*Climate sensitivity*

**Non-linear responses to climate variables were common (Fig. 3).** - Growth almost always increased with precipitation up to the long-term mean, but often declined under high precipitation. - The most common response to temperature was unimodal, often peaking within 1SD of long-term mean. (**depending on how strongly this comes out, may warrent separate paper**) - (results for cloudiness group)

*Influence of DBH*

\*\* , , and all varied with .\*\* For , the general tendency (with just a couple exceptions) was a decline with DBH, often following an initial increase (Fig. 4a). most commonly exhibited a unimodal relationship (Fig. 4b). also commonly exhibited a unimodal relationship, although tending to peak at larger DBH (Fig. 4c).

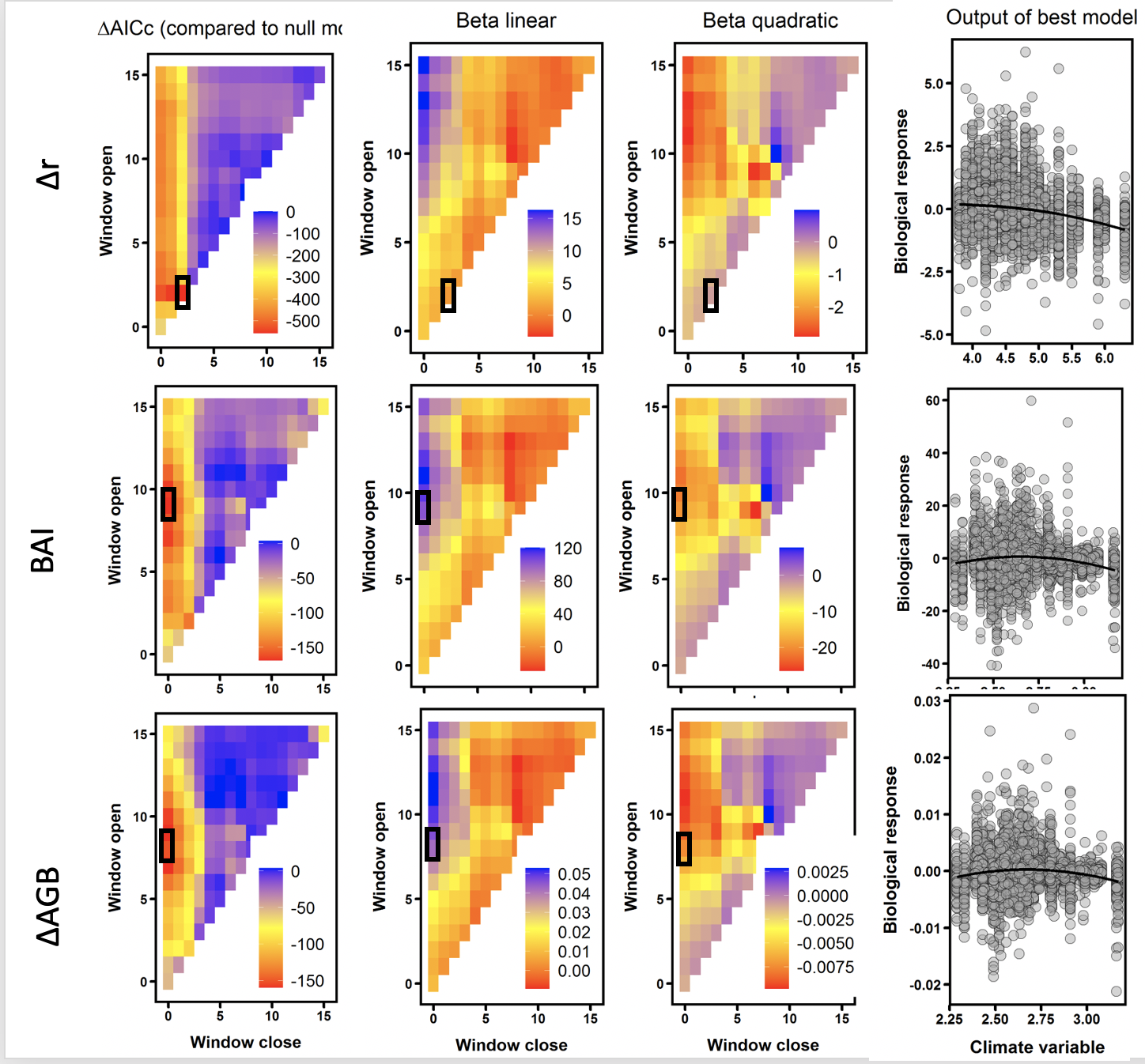


**Figure 4 | Growth sensitivity to DBH: (a) , (b) , (c) .** Only signficant relationships are shown. It’s tough to fit all the plots, so we may have to adjust this somehow.

*Climate-DBH interactions*

We get different climate sensitivity results with the different metrics of growth (Fig. 5?). Preliminary review of some early results indicates that the “landscape” of climate effects over various time windows is generally similar across the three metrics of growth, but that the optimal time window or even the top climate variable in a group can shift. (**See** [**ISSUE #40 in ForestGEO-climate-sensitivity**](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/40)).

The underlying cause of these differences would be differences in the variance structure, where growth residuals would tend to be greater (in absolute value) when growth rate is high. Thus, use of as a growth metric would tend to place proportionally more weight on smaller , whereas would tend to place more weight on larger individuals, with intermediate (Fig. 4). (**Christy, please check/revise**) The degree to which climate sensitivity landscapes differ across growth metrics should depend on the size structure of the data and the existence/strength of climate-DBH interactions.



**Figure 5 | Comparison of climwin output by growth metric:** Current example is PET at Lilly Dickey, selected mainly because data/model for other sites aren’t yet stable. (I’m not sure if this is interesting enough to present in the main text. If not, we should have at least one example in the SI)

**Table / figure on climate - DBH interactions?** (*See* [*ISSUE #42 in ForestGEO-climate-sensitivity*](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/42))

### Discussion

**We present a new method that allows simultaneous consideration of the effects of objectively determined principle climate drivers and tree size on annual growth.** Results are broadly consistent with those obtained by traditional methods, but offer several new insights.

On climate sensitivity: - Climwin step is problematic when climate is rapidly changing [ISSUE #25 in ForestGEO-climate-sensitivity](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/25).

**We recorded substantial variation in growth trends with , dependent largely upon species ecology and stand history (Fig. 4).** On one end of the spectrum, *Melia azedarach* at HKK had extremely rapid growth at small , with ranging up to ~15mm yr-1, followed by fairly rapid declines with increasing . This highly shade-intolerant species generally establishes in the open (Baker & Bunyavejchewin, 2006) and was sampled opportunistically outside the ForestGEO plot (Vlam et al., 2014), where it presumably established under open conditions. Similar patterns of approximately exponential decline in with were observed for conifer species at Little Tesque and Scotty Creek–both relatively open forests–and a number of species in mesic temperate forests (Fig. 4). At the other end of the spectrum, a number of species at sites where they presumably established under closed-canopy conditions (e.g., *Fagus* at SCBI and Zofin) had <1 mm yr-1 at small , increased to peak between # and # cm , and subsequently declined.  
A number of taxa showed different patterns at different sites; for example, *Acer* exhibited the first pattern at Harvard Forest and the second at Lilly Dickey. Similarly, patterns were mixed among species within a single stand (e.g., at SCBI and Harvard Forest). These variable patterns in with translated into differences in variation in and with , although trends in both of these were more consistent across sites and species, typically increasing to a peak at intermediate and then declining.

**Our analysis of growth trends with DBH yields several novel insights for dendrochronology and forest ecology.** First, the observation that typically declines with tree size in cored individuals, often following initial increase during juvenile growth phase, is consistent with many previous observations from tree-ring records (DENDRO\_REFS). This contrasts with patterns observed at the stand level [Muller-Landau et al. (2006); Anderson-Teixeira, McGarvey, et al. (2015); Piponiot et al. in prep]– presumably because [the sample of cored trees (survivors) doesn’t match forest composition] (*cite paper that I reviewed several years back;* [*Clark et al. 2007?*](https://esajournals-onlinelibrary-wiley-com.smithsonian.idm.oclc.org/doi/epdf/10.1890/06-1039.1)*;* [*Schleip et al. 2015*](https://onlinelibrary-wiley-com.smithsonian.idm.oclc.org/doi/abs/10.1002/env.2324)). This also contrasts with in [Helcoski et al. 2019](https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/nph.15906), where we show a positive relationship of radial growth to DBH from tree-rings. Our finding that is most commonly unimodal is surprising in that it contrasts with many previous findings and theoretical expectations (Stephenson et al, check Foster et al. 2006; check Piponiot et al. in prep). [EXPAND] declines at high are presumably because trees are investing fixed C elsewhere–for example, reproduction.

**These results have important implications for using tree-rings to infer growth responses to slowly-changing environmental drivers, including climate, atmospheric CO2, and deposition of SO2 and NOx.** …. Non-independence of from negates assumption that can be used as a DBH-independent metric of tree growth….

DBH is not always collected when cores are taken, and is not routinely preserved alongside tree-ring data. For example, the International Tree-Ring Data Bank (ITRDB) contains no structure for storing DBH records. DEN is new alternative.

Sets the foundation for considering other, slowly changing environmental drivers.

### Acknowledgements

Scholarly Studies

### Authors’ contributions

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