**Title:** Joint effects of climate, tree size, and year on annual tree growth derived using tree-ring records from ten globally distributed forests

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# Abstract

Tree rings provide a uniquely valuable long-term record for understanding how climate and other environmental drivers shape individual tree growth and forest productivity. However, conventional tree-ring analysis methods are not designed to simultaneously account for the effects of climate, tree size, and other environmental drivers on individual tree growth, which has limited the potential to use tree rings to understand forest productivity, its climate sensitivity, and its global change responses. Here, we develop and apply a new method to simultaneously model non-linear effects of primary climate drivers, reconstructed tree diameter (DBH), and year in generalized least squares models that account for the temporal autocorrelation inherent to each individual tree’s growth. We analyze tree-ring data from 3811 trees representing 40 species at 10 globally distributed sites, showing that water, temperature, DBH, and time have additively, and often interactively, influenced annual growth over the past 120 years. Growth responses were predominantly positive to precipitation and negative to temperature, with both included in 78% of top models, and with non-linear responses prevalent (*##%* of relationships). Interactions between DBH and climate were common (44% of cases tested). Growth rates – expressed as ring widths, basal area increments, or biomass increments – varied non-linearly with DBH. Accounting for DBH, growth rate declined over time for 90% of species-site combinations. These trends were largely attributable to stand dynamics as cohorts and stands age, which remain challenging to disentangle from global change drivers. By providing a parsimonious approach for characterizing multiple interacting drivers of tree growth, our method reveals a more complete picture of the factors influencing tree growth than has previously been possible. *As global change pressures intensify and the need to understand changing forest dynamics becomes increasingly urgent, we expect that this approach will prove valuable to understanding drivers of tree growth and forest change.*

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

# Introduction

Tree rings provide a long-term record of annual growth increments that is invaluable for understanding forests in an era of global change (Amoroso et al., 2017; Fritts & Swetnam, 1989; Zuidema et al., 2013). Spanning time scales of decades to centuries or even millennia, they provide by far the most robust method for characterizing the interannual climate sensitivity of tree growth (Bräker, 2002; Fritts, 1976) and how it has changed through time (Au et al., 2020; Babst et al., 2019; Maxwell et al., 2016; Sniderhan & Baltzer, 2016; Wilmking et al., 2020). Combined with forest censuses, they can be used to estimate forest woody productivity (Davis et al., 2009; Dye et al., 2016; Graumlich et al., 1989; Teets, Fraver, Hollinger, et al., 2018) and its climate sensitivity (Helcoski et al., 2019; Klesse et al., 2018; Teets, Fraver, Weiskittel, et al., 2018). Tree rings also provide the long-term perspective critical to understanding how slowly changing environmental drivers including rising atmospheric carbon dioxide (CO2) concentrations, changing climate, and other anthropogenic and natural changes are influencing tree growth and forest productivity (e.g., Levesque et al., 2017; Mathias & Thomas, 2018; Walker et al., 2020). This information is critical to predicting forest responses to anthropogenic changes, particularly climate change, and thereby reducing the enormous uncertainty surrounding future contributions of Earth’s forests to the global carbon cycle (Arora et al., 2020).

Yet, collection and analysis of dendrochronological records has traditionally been optimized to detect climate signals rather than to understand variation among trees, including size-related variation in climate sensitivity (e.g., Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021), and predict forest productivity, its climate sensitivity, and how it may be changing (Babst et al., 2018; Cherubini et al., 1998; Klesse et al., 2018; Nehrbass-Ahles et al., 2014; Wilmking et al., 2020). 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. To realistically estimate forest woody productivity, it is necessary to measure or model the growth rate of the individual trees within the stand based on the primary biotic and environmental drivers. Needed is an analysis framework that can capture the additive and interactive effects of climate, tree size (most commonly diameter breast height, DBH), and other environmental drivers (e.g., Evans et al., 2017; Klesse et al., 2020; Rollinson et al., 2021), which may often be best described by nonlinear functions (REFS, Rollinson et al., 2021). While multifactorial and sometimes non-linear individual-based analysis frameworks have been applied (e.g., REFS, Evans et al., 2017; Rollinson et al., 2021), their use has been relatively limited, and as a result we lack synthetic, global-scale understanding of some of the key questions that may be addressed using this such an approach (Table 1). Moreover, while tree-ring data has been used for benchmarking dynamic global vegetation models [DGVMs, e.g., REFS], an individual-based analysis approach focusing on multiple drivers including DBH would offer more opportunities for using tree-ring data as benchmarking tools for demographic DGVMs [[REFS?](https://github.com/EcoClimLab/ForestGEO-climate-sensitivity/issues/128)].

## 0.1 Climate sensitivity

The growth responses of trees to future climate variability and change will shape competitive dynamics, changes in forest composition, forest productivity, and climate feedbacks.

The classic dendrochronological approach to characterizing the climate sensitivity of tree growth describes linear relationships between a growth-limiting climate factor (moisture or temperature) and population-level growth responses captured in ring-width index chronologies [REFS]. While invaluable for applications such as reconstructing past climates [REFS] and useful developing a broad understanding of the climate sensitivity of forest productivity (e.g., Charney et al., 2016; Helcoski et al., 2019), capturing the substantial variation in climate sensitivity that can exist within a population [e.g., McGregor, Pederson(?)] requires an alternative analysis approach [e.g., REFS- rollinson, evans?]. In addition, a focus on linear climate responses to individual climate drivers misses nonlinearities and additive or interactive climate effects known to be widespread within forest settings (Rollinson et al., 2021; Wilmking et al., 2020; Woodhouse, 1999). Furthermore, for dendrochronological studies aimed at deciphering climate signals, DBH is not typically a variable of interest, and its influence is removed through detrending (Edward R. Cook & Peters, 1997), thereby eliminating the potential to directly model known interactive effects of DBH and climate on tree growth (Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021; Trouillier et al., 2019).

Over the vast majority of Earth’s forested regions, water is the primary climatic factor limiting tree growth [REFS]. Whereas the population-level growth responses captured in ring-width index chronologies [*sensu* REFS] are invaluable for applications such as reconstructing past climates [REFS], greater detail is needed to advance scientific understanding of the

*(cut most of this paragraph? but JB really liked it):* Dendrochronological methods to characterize the climate sensitivity of tree growth have been optimized to obtain the strongest possible climate signal for climate reconstructions, but face limitations when it comes to characterizing the long-term climate sensitivity of individual tree growth or stand productivity. Traditional methods begin by fitting a function (commonly an exponential curve or a spline) to the growth record captured by each core, extracting residuals around the long-term trends, and then standardizing and averaging the residuals across cores to form a species-level ring-width index chronology (Fritts, 1976; Speer, 2010). Climate signals are then identified by examining month-by-month or seasonal correlations of the ring-width index chronology to one or more climate variables over the current year and, typically, previous growing season (e.g., Fritts, 1976; Meko et al., 2011; Zang & Biondi, 2015). Following identification of the top climate driver(s), statistical models describing their relationships to tree growth can be used for applications such as climate reconstruction (e.g., Buntgen et al., 2011) or projection of tree growth responses to climate change (e.g., Charney et al., 2016). An important caveat for the latter, however, is that the slopes of correlations between climate variables and ring-width index chronologies are not identical to the mean slope of the relationship among individuals within the population, as the process of building species chronologies obfuscates individual-level responses (Carrer, 2011; Pederson et al., 2020). Although population-level climate responses have been approximated based on climate sensitives derived from species chronologies (e.g., Charney et al., 2016; Helcoski et al., 2019), the removal of individual-level variation prior to analysis of climate sensitivity limits potential for using species chronologies to characterize the climate sensitivity of stand productivity. In particular, analysis of species-level chronologies does not allow the direct characterization of known variation in climate sensitivity in relation to tree height, canopy position, or microhabitat characteristics such as topographic wetness index (e.g., Bennett et al., 2015; McGregor et al., 2020; Rollinson et al., 2021).

*(reword to ecology focus):* Dendrochronological studies most commonly focus on linear climate responses to individual climate drivers, thereby missing nonlinearities and additive or interactive climate effects known to be widespread within forest settings (Wilmking et al., 2020; Woodhouse, 1999). Nonlinearities in climate sensitivities of tree metabolism and growth have been observed across a wide range of spatio-temporal scales. Over time frames of seconds to days, photosynthesis and respiration display unimodal relationships to temporal variation in temperature, typically peaking at temperatures reflective of the environment to which the plant is adapted and acclimated (Kumarathunge et al., 2019). Across broad climatic gradients, annual forest productivity generally increases with temperature, precipitation, and potential evapotranspiration (PET) up to a point, after which it plateaus or decreases (Banbury Morgan et al., 2021; M. J. P. Sullivan et al., 2020). Filling a critical gap between short-term physiological responses and the global gradients representing millennia of community assembly and species adaptation, the annual growth records of tree rings capture tree growth responses to interannual climatic variation. Yet, because non-linearities are problematic for reconstructing climate variables (Esper & Frank, 2009), systems exhibiting these are typically not the first focus for sampling. Many worked around the non-linearity issues by sampling at sites with characteristics that result in trees being more climate-limited, though not all (E. R. Cook, 1982). Importantly, traditional analysis methods are designed around first-order linear growth-climate relationships (Fritts, 1976). *Dendrochronological studies allowing for nonlinear or threshold responses of tree growth to climate are less common (Cavin & Jump, 2017; Edward R. Cook & Johnson, 1989; Ljungqvist et al., 2020; Rollinson et al., 2021; Tolwinski-Ward et al., 2013; Tumajer et al., 2017; Woodhouse, 1999)* ***one could say these were a lot of citation for it to be uncommon. Perhaps make it more clear what aspects are less common?****, and we therefore know little about the nonlinearities in tree growth responses to interannual variation in climate that occur for trees within forest settings.* Furthermore, temperature and moisture are known to jointly shape tree growth (Beedlow et al., 2013; Foster et al., 2016) and forest productivity (e.g., Alexander et al., 2018; Banbury Morgan et al., 2021), yet growth sensitivity to their additive or interactive effects, potentially operating over different seasonal windows, is not commonly considered (but see Foster et al., 2016; Meko et al., 2011; Sánchez-Salguero et al., 2015), **largely because dendroclimate studies sample in such a way as to isolate one or other of moisture or temperature limitation.**

*(most of this is climate sensitivity changing with DBH):* Tree diameter at breast height (DBH) scales predictably with numerous traits affecting tree growth rate (e.g., height, crown size and position, root mass Enquist & Niklas (2002); Niklas (2004)] and therefore is itself linked to growth (e.g., Foster et al., 2016; Muller-Landau et al., 2006) and its climate sensitivity (e.g., Bennett et al., 2015; McGregor et al., 2020). However, for dendrochronological studies aimed at deciphering climate signals, DBH is not typically a variable of interest, and its influence, *along with the influence of stand dynamics in closed-canopy forests* , is removed through detrending (Edward R. Cook & Peters, 1997). Moreover, many studies constrain sampling to only trees in canopy positions or those that appear to be old (Fritts, 1976; Huckaby et al., 2003; Pederson, 2010). While convenient for developing long chronologies and identifying climate signals (Fritts, 1976), this approach is not optimal for subsequent inference of the climate sensitivity of forest productivity (Babst et al., 2018). Although climate correlations can be transformed to climate sensitivity (i.e., magnitude of response, *sensu* Charney et al., 2016) and scaled to characterize the climate sensitivity of stand productivity based on the scaling of ring width (RW) with DBH (Helcoski et al., 2019), they cannot be used to directly model known interactive effects of DBH and climate on tree growth (Trouillier et al., 2019). For example, drought sensitivity tends to increase with tree size (Bennett et al., 2015; Gillerot et al., 2020; McGregor et al., 2020), and responses to temperature can also vary with tree size or canopy position (Rollinson et al., 2021; Rossi et al., 2007). However, the removal of DBH signals via detrending makes it impossible to account for such size differences in climate sensitivity in a systematic, integrative way. To use tree rings to predict tree growth, ecosystem productivity, and forest dynamics, we need models that include DBH (e.g., Evans et al., 2017; Klesse et al., 2020) and its potential climate interactions (e.g., Rollinson et al., 2021).

## 0.2 DBH

## 0.3 Changing growth rates

*(keep mostly the same, but shift emphasis more towards ecology):* Characterizing how tree growth and forest productivity are responding to slowly changing environmental drivers is challenging and uncertain. Directional climate change (as opposed to interannual variation), rising atmospheric CO2 concentrations, and changes in atmospheric deposition of sulfur dioxide (SO2) and nitrogen oxides (NOx) are all potentially influencing tree growth (Belmecheri et al., 2021; Levesque et al., 2017; Mathias & Thomas, 2018; Maxwell et al., 2019; Takahashi et al., 2020; Walker et al., 2020). At the same time, stand dynamics influence growth: tree growth rates are sensitive to competition, the intensity of which tends to increase as forests mature, and to canopy position, which can change directionally as trees overtop or are overtopped by their neighbors. Moreover, carbon allocation to woody growth – as opposed to leaf or fine root production, reproduction, defenses, etc. – is known to decline as individual trees and forest stands age (Goulden et al., 2011; Pregitzer & Euskirchen, 2004; Thomas, 2011). However, tree size and time are almost inextricably linked (because each cored individual increases in DBH through time) and difficult to disentangle due to various sampling and analysis biases (Bowman et al., 2013; Brienen et al., 2017, 2012; Cherubini et al., 1998; Hember et al., 2019; Nehrbass-Ahles et al., 2014; Peters et al., 2015; P. F. Sullivan et al., 2016). Continued improvement of analytical methods, in combination with sampling approaches that minimize potential biases, will be important to disentangling DBH from time and detecting directional growth trends.

Here, we develop, and apply to ten forested sites spanning 52 degrees latitude, a new method that allows simultaneous consideration of the effects of primary climate drivers (i.e., the most influential climate variables and the seasonal window over which they operate), tree size, and calendar year on annual tree growth. This approach allows us to address the following questions and associated hypotheses (Table 1) for a globally distributed tree-ring dataset: (1) How does interannual climate variation shape annual tree growth (ring width, RW)? (2) How does growth rate vary with DBH? (3) How have growth rates changed through time?

**Table 1 | (DRAFT hypothesis table– needs to be filled in and condensed/ cleaned up)**. ….

| Focal questions, hypotheses, and specific predictions | frequency observed\* |
| --- | --- |
| ***How does interannual climate variation shape annual tree growth?*** |  |
| **Multi-month drought limits growth, but water responses are nonlinear.** |  |
| Water influences growth over relatively long seasonal windows (≥3 months). | 7 / 10 sites |
| Growth respones to water are predominantly positive, | 98% (42/43) SSC |
| ...but these positive responses decelerate or decline at high precipitation. | 76% (32/42) SSC |
| **Over shorter time scales, high temperature (T) limits growth, often nonlinearly.** |  |
| Growth is most sensitive to T over relatively short seasonal windows (≤3 months). | 9 / 10 sites |
| Growth responds more strongly to maximum T or PET than to minimum T. | 8 / 10 sites |
| Growth respones to T are predominantly either negative… | 13 / 38 SSC |
| …or non-linear concave down. | 18 / 38 SSC |
| However, there are cases where growth increases with T. | 7 / 38 SSC |
| **Climate sensitivity often varies with tree diameter (DBH).** | **49% of SSVC** |
| Water and DBH have an interactive effect on RW. | 16 / 36 SSC |
| Temperature and DBH have an interactive effect on RW. | 12 / 32 SSC |
| ***How does growth rate vary with DBH?*** |  |
| **Growth rate, by any metric, varies nonlinearly with DBH.** | **X% of SSVC** |
| RW declines with DBH for light-demanding species, | 46% (6/13) SSC |
| ...but increases with DBH for shade-tolerant species. | 73% (8/11) SSC |
| Basal area increment (BAI) peaks at intermediate DBH. | 95% (41/43) SSC |
| Biomass increment (∆AGB) peaks at intermediate DBH. | 98% (42/43) SSC |
| ***How have growth rates changed through time?*** |  |
| **Growth rates of most forest tree populations have declined through time.** | **90% of SSC** |
| In secondary or disturbed forests, growth rates of most species have declined. | XX / XX sp. at 7 sites |
| In relatively undisturbed old-growth forests, growth rates of some species has declined, | XX / XX sp. at 3 sites |
| ….whereas others have increased. | 3 / XX sp. at 3 sites |
| \*SSC= species-site combinations; SSCV=species-site-variable combination | |

# Materials and Methods

## Data sources and preparation

We analyzed tree-ring data, most most of which was collected for earlier studies (see references in Table 2), from 10 sites ranging from 9.15 to 61.30 N latitude and representing a wide range of forest and tree types: tropical broadleaf deciduous and evergreen, temperate broadleaf deciduous and conifer, and boreal conifer (Tables 2, S1, S2). Nine of these sites (exception: LT) were co-located with large forest dynamics plots of the Forest Global Earth Observatory (ForestGEO, K. J. Anderson-Teixeira, Davies, et al., 2015; Davies et al., 2021). Trees were cored within the ForestGEO plots (n=5 sites) and/or nearby within similar forest types (n=5 sites), following a variety of sampling protocols designed to meet the varied objectives of the original studies (Tables S1, S3). There was wide variation in the distribution of record start years, which approximate the age distribution of sampled trees (Figs. S1-S10). In using this diversity of data sources, we ensured that our approach could handle challenges presented by varying methodologies and forest types.

**Table 2 | Sites included in this analysis**. Here and throughout, sites are ordered by descending mean annual temperature. Additional site information is provided in Appendix S1 and Table S1, and tree species and sampling details are detailed in Tables S2-S3.

| site code | site name | location | July T (°C)\* | Jan T (°C)\* | MAP (mm)\* | vegetation type(s) | n species | n cores | original publication(s) |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| BCNM | Barro Colorado Nature Monument | Panama | 26.6 | 25.5 | 2,627 | BD, BE | 3 | 84 | Alfaro-Sánchez, Muller-Landau, Wright, and Camarero 2017 |
| HKK | Huai Kha Khaeng | Thailand | 25.7 | 22.4 | 1,428 | BD, BE | 4 | 470 | Vlam, Baker, Bunyavejchewin, and Zuidema 2014 |
| SCBI | Smithsonian Conservation Biology Institute | Virginia, USA | 24.3 | 0.9 | 1,018 | BD, NE | 14 | 704 | Bourg et al. 2013; Helcoski et al. 2019; Gonzalez-Akre et al. 2020 |
| LDW | Lilly Dickey Woods | Indiana, USA | 24.0 | -2.2 | 1,099 | BD | 6 | 170 | Maxwell, Harley, and Robeson 2016 |
| HF | Harvard Forest | Massachusetts, USA | 21.6 | -5.1 | 1,104 | BD, NE | 4 | 366 | Alexander et al. 2019; Finzi et al. 2020 |
| ZOF | Žofín Forest Dynamics Plot | Czech Republic | 18.1 | -2.0 | 731 | NE, BD | 4 | 2,059 | Šamonil et al. 2013; Kašpar, Tumajer, Vašíčková, and Šamonil, 2021 |
| NIO | Niobrara | Nebraska, USA | 23.4 | -6.5 | 520 | BD | 1 | 84 | Bumann et al. 2019 |
| LT | Little Tesuque | New Mexico, USA | 16.2 | -3.1 | 608 | NE | 2 | 34 |  |
| CB | Cedar Breaks | Utah, USA | 13.8 | -6.2 | 842 | NE, BD | 7 | 187 | Birch et al. 2020a-d |
| SC | Scotty Creek | Northwest Territories, Canada | 16.5 | -24.7 | 373 | NE | 1 | 443 | Sniderhan and Baltzer 2016 |
| \*Refers to 1950-2019 mean climate. | | | | | | | | | |

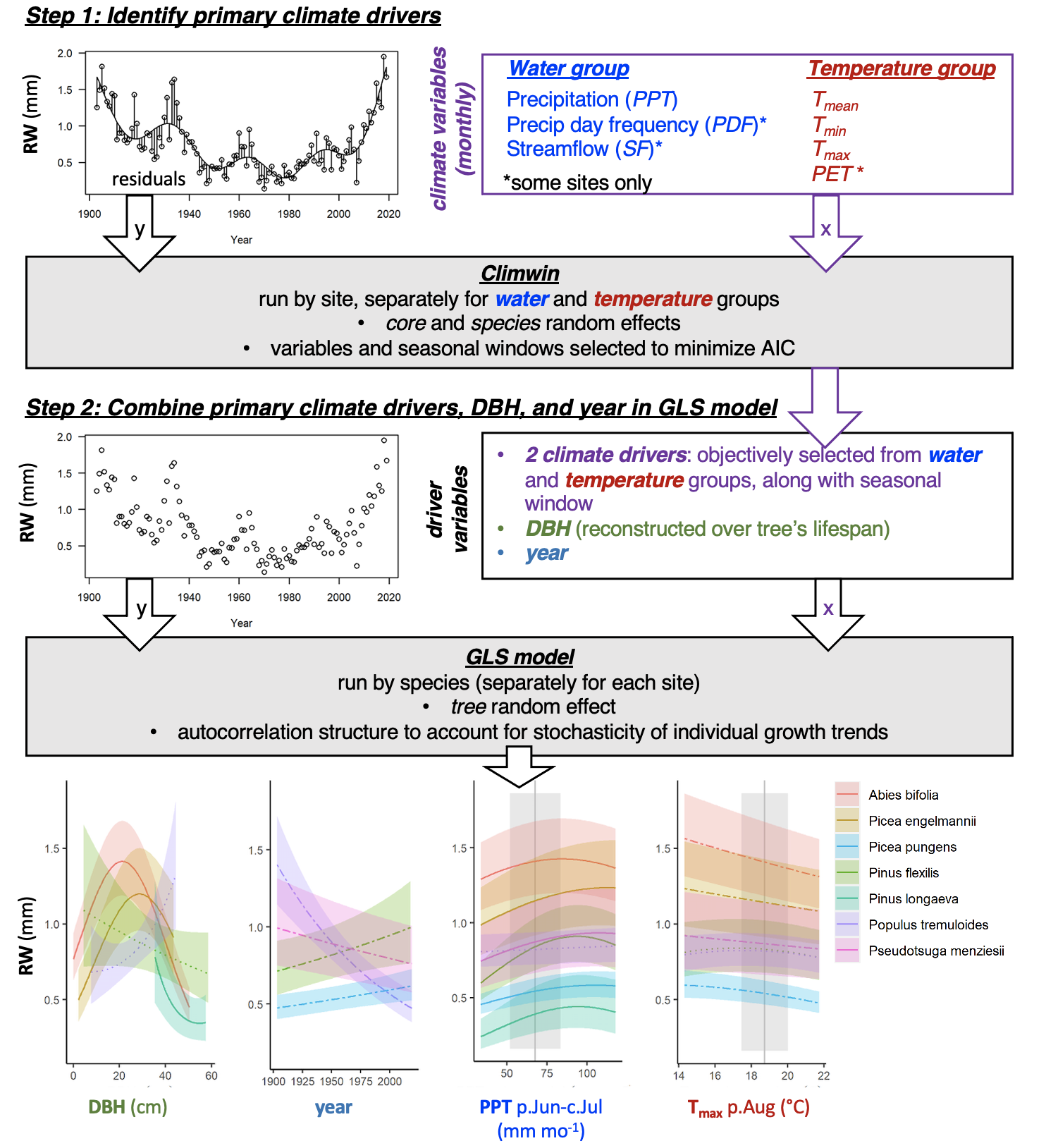
All tree cores **(n = XXXX)** were cross-dated and measured by the original researchers using standard dendrochronological practices (Stokes & Smiley, 1968). From among the full set of original RW measurements, we excluded cores for which we detected technical errors (e.g., labeling inconsistencies, obvious dating errors) that could not be resolved before finalizing the analysis. We also excluded records with small sample size or highly anomalous growth patterns, including (1) species with < 7 cores, (2) cores with < 30 years of record, (3) contiguous portions of cores containing large outliers (RW > mean plus 5 x SD of RW for the entire core), and (4) the final 20 years prior to death for trees cored dead. The final criterion was implemented to avoid periods of growth decline and potentially altered climate sensitivity prior to death (Cailleret et al., 2017; DeSoto et al., 2020). From analyses including DBH (see below), we further excluded (1) trees for which we lacked data required to reconstruct DBH, (2) trees for which there was a significant inconsistency between measured DBH and the sum of RW’s across the core (Appendix S2), and (3) poorly represented tails of the DBH distribution, starting where reconstructed DBH (see below) included < 3 conspecific trees. In total, this resulted in inclusion of 4655 cores from 3811 trees, 4513 of which (from 3705 trees) could be included in analyses with DBH (Table S3).

For each year in the tree-ring records, we reconstructed DBH, as detailed in Appendix S2. We applied allometric equations for bark thickness to account for changes in bark thickness as the tree grew (Appendix S2; Tables S2, S4). Once DBH had been reconstructed, we estimated basal area (, where is radius) and aboveground biomass (AGB). Biomass allometries for temperate and tropical species were calculated using the R packages *allodb* (Gonzalez-Akre et al. in revision) and *BIOMASS* (Réjou-Méchain et al., 2017), respectively. We then calculated basal area increment (, where is year) and aboveground biomass growth increments ().

Monthly climate data for 1901-2019 were obtained from CRU v.4.04 (Harris et al., 2014, 2020), and in a few cases corrected based on higher-resolution or local records (Appendix S3). Variables considered here included average daily minimum, maximum, and mean temperatures (, , , respectively); precipitation (PPT); and, when deemed reliable (Appendix S3), potential evapotranspiration (PET) and precipitation day frequency (PDF). For the one riparian site, NIO, we tested for an effect of stream flow (SF), for which we obtained data for the Sparks, Nebraska station (station code: 06461500; 42°54’14“N, 100°26’13”W) from the U.S. Geological Survey (USGS) National Water Information System (<https://waterdata.usgs.gov/nwis/uv/?site_no=06461500&agency_cd=USGS&referred_module=sw>). All ForestGEO climate records used here are archived in the ForestGEO Climate Data Portal, v1.0 (K. Anderson-Teixeira et al., 2020).

## Data Analysis

Data analysis consisted of two main steps: (1) identifying the primary climate drivers (i.e., variables and seasonal windows over which they are most influential on tree growth), and (2) combining these climate drivers, DBH, and year into a multivariate model (Fig. 1). The analysis was run separately for each site (step 1), site-species combination (step 2), and each response variable estimating different measures of tree growth (RW, BAI, or AGB). We note that the decision to identify primary climate drivers at the level of site, as opposed to species, was motivated by the expectation that differences in the most influential climate drivers across species in one site would be minimal compared to cross-site differences (Fig. 2); however, analyses focused on interspecific differences could optimize species-specific climate sensitivity estimates by fitting *climwin* individually by species.



**Figure 1 | Schematic illustration of the analysis process.** In step 1, the R package *climwin* (van de Pol et al., 2016) is used to identify the primary climate drivers in water and temperature variable groups for each site, defined as the variable-seasonal window combination that are most strongly correlated to the residual variation around splines fit to trends in growth (here, ring width, RW) for all cores sampled at the site. In step 2, a GLS model is used to produce a combined model with the previously identified drivers, reconstructed DBH, and year.

### Step 1: Identifying primary climate drivers

We used the *climwin* package in R (van de Pol et al., 2016) to identify the most important climate variable and the seasonal window over which its effect was strongest for each of two categories of variables: a temperature group (, , , and PET) and a precipitation group (PPT, PDF). To remove low-frequency variation that most likely represents responses to non-climatic drivers (*e.g.*, growth and aging of the tree, change in competitive dynamics, atmospheric pollution), we detrended the response variables by fitting penalized thin-plate regression splines in generalized additive models (GAM, functions *gam* and *s* in the R package *mgcv*, Wood, 2011) to individual growth records (RW, BAI, or AGB) from each core, and extracted the residual variation for each observation. The smoothing parameters were automatically selected by the *gam* function with generalized cross-validation (GCV). We then used *climwin* to identify the climate variables that most strongly correlated with the individual tree-level residuals of the growth variables, RW, BAI, or AGB, specifying quadratic fits to allow for potential nonlinearities in the climate response. Within *climwin*, we specified a mixed-effects model in which the fixed effects were the climate variables and the random intercepts were species (when n 3) and core identity (noting that these effects should be minimal given that residuals are centered around zero). For each climate variable, we ran permutations for all possible combinations of consecutive months within a 15-month period ending near the time of cessation of formation of each annual ring (Table S1). *Climwin* runs all potential models to select the best fit (lowest AIC), and does k-fold cross-validation in its computation of AIC to guard against over-fitting (van de Pol et al., 2016). For each group of candidate climate variables (water and temperature; Fig. 1), we selected the variable - seasonal window combination identified by *climwin* as having the lowest AIC as a candidate climate variable for the multivariate models.

We tested whether this process identified similar climate variable-month combinations to what would be identified using traditional methods for four species (detailed in Appendix S4). Furthermore, we explored alternate methods of climate variable selection for the two sites that have undergone the most rapid changes in climate and tree growth: LT, where increasingly warm drought has dramatically reduced growth (Touchan et al., 2011; Williams et al., 2013), and SC, where rapidly rising temperatures are causing permafrost thaw, which limits access to soil moisture during summer months and drives growth declines (Sniderhan & Baltzer, 2016). We ultimately determined that the method described above captured these sources of variation (Appendix S5).

### Step 2: Combining drivers in GLS model

Having identified the primary climate drivers in temperature and precipitation variable groups, we next combined climate variables (included in all models) and DBH (included in models with DBH and its climate interactions) into linear mixed-effects models (function *lme* in the R package *nlme*, Pinheiro et al., 2021), with core identity as a random intercept and yeaar as a continuous time covariate for the within-group correlation structure (function *corCAR1*). We will refer to this model as a generalized least squares (GLS) model (Fig. 1).

Prior to running the models, we checked for collinearity among the candidate variables using the *vifstep* function (Naimi et al., 2014) and removed any variable with a variance inflation factor > 3 (none required removal). Within the GLS models, our response variables were log[RW], log[BAI], or log[ AGB].

For each species independently, we ran every combination of the candidate climate variables and DBH, including both first- and second-order terms for each. For climate response, we allowed concave-down fits, but ignored any concave-up fits on the basis that these are not expected biologically.

As an example, a full model for log[RW] would look like this in *R*:

*lme(log[RW] ~ PET + I(PET^2) + + I(^2) + DBH + I(DBH^2)“, random = ~1|coreID, correlation = corCAR1(form=~yeaar|coreID), data = x, na.action =”na.fail“, method =”ML")*

where *x* is a complete data set (with no missing values) for one species at one site. The method is set to maximum likelihood (*ML*) during the fixed effect model selection phase, but to restricted maximizing likelihood (*REML*) for parameter estimation with the best model.

For models including interactive effects of climate and DBH, we tested for interactions between first-order linear terms for climate variables and DBH.

To test for year effects, we limited the analysis to species with reasonable coverage of the DBH x year matrix. Specifically, we required that the species be represented by cores from 3 trees and that the core record spanned 40% the total DBH range for 2/3 of the total time range analyzed. To avoid severe big-tree selection bias (Brienen et al., 2012), we also required that the minimum DBH sampled be 25 cm (exception: *Abies alba* at ZOF, where mature trees < 50 cm DBH are extremely rare). Species that failed to meet these criteria (n= 8; Table S3) were excluded from the analysis of temporal trends, but were included in analyses of climate and DBH and their interactions. We then ran models as described above, including a first-order linear effect of year. We note that the random effect of tree should, in theory, avoid analytical biases arising from persistent growth differences among individuals that are not accounted for by DBH or year (Brienen et al., 2017, 2012). To verify that GLS model trends for year were not an artifact of inherent covariation between DBH and year within each core, we compared GLS results to an analysis of DBH-growth relationships by decade (Figs. S58-S67).

Within each of three categories of models run (climate only, climate + DBH, climate DBH, climate + DBH + year), we selected as the top model that with the lowest AIC.

# Results

## Validation of the method

Our process identified similar primary climate drivers to those identified via established dendrochronological analysis methods for identifying climate signals (Figs. 2, S11-S14; Table S5; Appendix S4). While one-to-one correspondence of estimated slope coefficients describing the response of tree growth to interannual climatic variation was neither expected nor observed, estimates were correlated and rarely differed significantly (Appendix S4; S11-S14).



**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 S2) to potential evapotranspiration (PET). Panel (**a**) shows a matrix of Pearson correlations between ring-width index and monthly climate variables (produced using the bootRes package in R, Zang & Biondi, 2013). Black rectangle represents the period selected by *climwin* as the most influential window. Panels (**b-d**) give statistics for seasonal windows tested in *climwin*, where window open and close indicate months prior to current August, and cells across the lower diagonal indicate single-month tests (akin to panel **a**). Panels (**b**) and (**c**) give values of linear and quadratic terms for each seasonal window, and (**d**) gives the AIC for each. The seasonal window with the minimum AIC (1-3 months prior to August, or May-July; black circles), was identified as the most influential window. Panel (**e**) shows the correlation of individual-level residuals to PET, with the function fit in *climwin*. Finally, panel (**f**) shows the GLS model output, where PET was a candidate driver variable (along with PPT; DBH not included in this model). Plotted are responses of species for which PET was included in the top model, with best-fit polynomials plotted with solid lines when both first- and second-order terms are significant, dashed lines when only one term is significant, and dotted lines when neither is significant. Transparent ribbons indicate 95% confidence intervals. Species names corresponding to the codes are given in Table S2.

*Trends with year, when assessed, were consistent with those observed in a separate analysis of DBH-growth relationships by year (Figs. S58-S67).*

## Climate sensitivity

### Most influencial climate drivers

At each site, the three metrics of growth (RW, BAI, and AGB) exhibited similar patterns in the direction of response and relative strength of correlation to climate variables across the range of potential seasonal windows. However, the seasonal window exhibiting the strongest climatic effect on growth and even the most influential climate variable sometimes differed among the growth metrics (Figs. S15-S34). For eight of 20 site-variable group (i.e., water and temperature) combinations, both both the most influential climate variable and seasonal window were identical across growth metrics (e.g., Fig. S19). For nine site-variable group combinations, *climwin* identified the same climate variable and overlapping seasonal windows (e.g., Fig. S20), and in one case (at HKK) different variables ( and ) were selected with overlapping seasonal windows (Fig. S18). For just two site-variable group combinations (both variable groups at HF, where climate had only weak effects and mixed responses among species in the final models), *climwin* identified completely different seasonal windows and, for precipitation, different variables (PPT and PDF; Figs. S23- S24). Henceforth, unless otherwise noted, we focus on the climate sensitivities identified using RW as the growth metric and for the full set of cores (i.e., including those for which DBH could not be reconstructed).

Precipitation amount (PPT) was selected over precipitation frequency (PDF) as the top variable in five of the eight sites for which both variables were available (but had no significant main effect at one site, NIO), and was the only option at two sites (LT and CB). The most influential seasonal windows most commonly coincided at least partially with months of active growth in the current year (Fig. 3; Table S1): year-round in the tropics (BCNM and HKK) or late spring/ summer outside of the tropics (n= 5 of 8). In the tropics, the long time-windows over which precipitation was influential (12 mo at BCNM, 9 mo at HKK) also included the majority (BCNM) or all (HKK) of the dry season months (< 100 mm rainfall / month). Outside of the tropics, the most influential windows at three sites included the current growing season and extended back to the previous fall (LT, CB) or summer (SCBI), whereas they were limited to the current spring and early summer at LDW. At three sites (HF, ZOF, and SC), precipitation of the previous growing season was the most influential variable.

Within the temperature group (Fig. 1), the most commonly selected variables were and PET, which were identified by *climwin* as the top temperature-related driver at six and three of the 10 sites, respectively, noting that PET was not available for two sites. was identified as the top driver at BCNM, where it’s effects were only marginally significant for one species (Fig. 3), and was never selected as the top driver. The most influential seasonal windows for temperature tended to be shorter than those of precipitation (Table 1). They most commonly occurred during the current growing season (n= 5 of 10 sites), but there were cases where the most influential windows occurred during the preceding dry season (BCNM), late winter/early spring (HF, ZOF), or the previous growing season (NIO, CB). Temperature and precipitation variables were rarely influential over the same seasonal window (exception: LDW).

### Climate responses

Analyses of species-specific responses at each site used the GLS model to test for first- and negative second- order linear effects of both a precipitation and a temperature variable. Both a precipitation and a temperature variable were included in the top model for 78% (n=36 of 46) of site-species combinations (Fig. 3). There were seven site-species combinations for which only a precipitation term was significant (two at BCNM, three at SCBI, and two at LDW), two for which only a temperature term was significant (*Chukrasia tabularis* at HKK and *Betula papyrifera* at NIO), and none with no significant climatic effects on RW. Below, we summarize the precipitation and temperature variables included in these models and their direction of response.



**Figure 3 | Species-level responses of RW to climwin-selected variables in precipitation and temperature variable groups.** Primary climate drivers are coded on the x-axes as the climate variable abbreviation followed by the range of months (p=previous year, c=current year) over which it is most influential. For each species (color-coded as in Fig. 4), relationships are plotted if included in top model. For each relationship shown, other terms in the model are held constant at their median. Best-fit polynomials are plotted with solid lines when both first- and second-order terms are significant (t-test’s p-value <0.05), dashed lines when only one term is significant, and dotted lines when neither is significant. Transparent ribbons indicate 95% confidence intervals. Vertical grey lines indicate the long-term mean for the climate variable, shading indicates 1 SD.

Responses to precipitation amount (PPT) and frequency (PDF) were included in the best model for all but two species, and were predominantly positive (Fig. 3). Specifically, there were positive first-order linear terms for precipitation all but one species (*Tsuga canadensis* at HF; Fig. 3). Negative second-order terms were commonly included in the best model (32 of 42 with positive first-order terms), generally resulting in a deceleration or decline at the highest levels of precipitation, but occasionally producing a unimodal (e.g., several species at SCBI) or predominantly negative response (e.g., *Betula alleghaniensis* at HF; Fig. 3).

A temperature variable was included in the best model for all but eight site-species combinations, with predominantly negative responses, particularly at the higher end of the temperature range (81%; 34% with negative first-order term, 47% with positive first-order term but negative second-order term; Fig. 3). Within the tropics, there was minimal effect of temperature at BCNM and a negative effect of wet season for three of four species at HKK. For temperate sites with the most influential seasonal windows covering the current and/or past growing season, responses were universally negative (i.e., negative first-order linear or unimodal, peaking at temperatures lower than the long-term mean). In contrast, there were positive effects of Jan-March for all three species at ZOF and of March PET for *Tsuga canadensis* at HF, the latter contrasting with a negative response of the three deciduous species analyzed at HF (Fig. 3). At the highest-latitude site (SC), which has undergone rapid warming and permafrost melt, *Picea mariana* responded positively (but with wide 95% CI on the slope) to temperature over the full analysis period (1903-2013); however, responses were predominately positive prior to 1970 and predominantly negative afterwards (Fig. S55).

### Variation in climate sensitivity with DBH

Interactive effects of climate and DBH were found for 90 of the 203 (44%) species-variable combinations for which they were tested. For precipitation variables, interactions were significant for 16 of the 36 (44%) interactions with RW as the growth metric (Fig. S56) and for 17 of the 36 (47%) with BAI as the growth metric (Fig. S57). The majority of these interactions were positive (75% for RW; 65% for BAI), indicating that larger trees generally respond more positively to precipitation or its frequency (Fig. 4). Among the exceptions to this pattern (n=4 for RW, 6 for BAI), only a minority (n=1 for RW, 4 for BAI) occurred in species responding positively to precipitation in the current growing season.

Temperature variable interactions were significant for 38% of cases with RW as the growth metric (Fig. S56) and for 50% with BAI as the growth metric (Fig. S57). Directions of these interactions were mixed, with 5 of 12 significant interactions negative with RW as the growth metric and 10 of 16 significant interactions negative when BAI was the growth metric. For both RW and BAI, the majority of significant negative interactions (i.e., more negative/ less positive response of larger trees to higher temperatures) occurred in cases where the main effect temperature was negative (e.g., HKK, LT, CB; Fig. 4), whereas positive interactions were more common when the main effect of temperature was positive (e.g., HF, ZOF).



**Figure 4 | Examples of climate - DBH interactions for three species at three sites.** Shown are modeled response functions at the minimum and maximum and maximum tails of the DBH distribution. Other terms in the model are held constant at their median. Transparent ribbons indicate 95% confidence intervals. Vertical grey lines indicate the long-term mean for the climate variable, shading indicates 1 SD.

## Variation with DBH

When a precipitation variable, a temperature variable, and DBH were all included as candidate variables in the GLS models, typically all three were included in the top model, regardless of the growth metric used. Climate responses were generally similar to those described above for models without a DBH term, although some of the weaker climate responses were not consistently included in top models (e.g., responses at BCNM; Figs. 3, S35-S54). In general, DBH explained more variation in growth rates than did climate, but its relative importance varied across growth metrics and sites (Figs. S35-S54). The relative importance of DBH tended to be least for RW, intermediate for BAI, and highest for AGB (e.g., at SCBI; Fig. S39). However, there were exceptions, particularly when RW decreased steeply with DBH (e.g., LT; Fig. S49).

All three growth metrics, RW, BAI, and AGB, varied with DBH for most species at all sites (Fig. 5). For RW, DBH was included in the best model for 81% of species-site combinations (n= 35 of 43), and the majority of best models also included a significant second-order linear DBH term (n= 26, 21 of which were negative). There was substantial variation in these trends, with patterns mixed across both forests and species within a single stand (Fig. 5). On one end of the spectrum, some species exhibited maximum RW at low DBH, followed by fairly rapid declines in RW with increasing DBH. Species following this pattern either had low to at most intermediate shade tolerance (e.g., *Melia azedarach* at HKK, *Juglans nigra* at SCBI, *Acer rubrum* at HF, *Betula papyrifera* at NIO; *Populous tremuloides* at CB; Table S2) or grew in relatively open stands (e.g., both species at LT, *Picea mariana* at SC; Fig. 5). At the other end of the spectrum, some species had low RW at small DBH, increased to peak RW at intermediate DBH, and subsequently declined. These included, but were not limited to, shade-tolerant species at sites where they presumably established under closed-canopy conditions (e.g., *Trichilia tuberculata* and *Tetragastris panamensis* at BCNM; *Fagus* spp. at SCBI and ZOF, *Acer saccharum* at LDW, *Picea* spp. at ZOF and CB; Table S2).

Trends in both BAI and AGB were far more consistent across sites and species, most commonly increasing to a peak at intermediate DBH and then declining (Fig. 5). Best models for BAI included DBH and for 42 of 43 species (exception: *Acer rubrum* at HF), with a positive coefficient for DBH in 40 (exceptions: non-significant negative coefficients for *Pinus ponderosa* at LT and *Pinus longaeva* at CB, whose reconstructed DBHs did not extend down to 0 cm within the time frame analyzed) and near-universally negative coefficients for (exception: *Pinus longaeva* at CB). For AGB, models were even more consistent, with the best models for 98% of species containing a positive coefficient for DBH and a negative coefficient for (exception: *Pinus longaeva* at CB).



**Figure 5 | Growth sensitivity to DBH: (a) RW, (b) BAI, (c) AGB.** Relationships for species are plotted when included in the top model. Other terms in the model are held constant at their median. Best-fit polynomials are plotted with solid lines when both first- and second-order terms are significant (t-test’s p-value <0.05), dashed lines when only one term is significant, and dotted lines when neither is significant. Transparent ribbons indicate 95% confidence intervals.

## Effects of year

There was a significant effect of year in the GLS models for 31 - 32 (depending on growth metric) of the 37 species-site combinations tested (Figs. 6, S35-S54). In 90-91% of cases (depending on growth metric), the growth trend over time was negative. Declines were particularly dramatic for *Picea mariana* at SC, *Pinus ponderosa* at LT, all four species at HF, and several species at SCBI (Fig. 6). In such cases, models without year predicted declines in growth at large DBH that should more properly be attributed to the effect of year (Figs. S35-S54). Significant positive growth trends were observed for only three species (consistently across all three growth metrics), *Fagus sylvatica* at ZOF, *Picea pungens* and *Pinus flexilis* at CB, and all were modest compared to the steep negative trends observed for some species. Growth rate was consistently independent of year for only four species: *Chukrasia tabularis* at HKK, *Pinus strobiformis* at LT, and *Picea engelmannii* and *Pinus longaeva* at CB.

Effects of year and DBH interacted such that inclusion of year in models altered the shape of DBH responses, typically resulting in less pronounced growth declines with increasing DBH (Figs. S35-S54).



**Figure 6 | Effect of year, when included in the best model, on BAI.** For each species (all listed), relationships are plotted if the year effect could be analyzed and was included in top model. Other terms in the model are held constant at their median. Best-fit polynomials are plotted with solid lines when both first- and second-order terms are significant (t-test’s p-value <0.05), dashed lines when only one term is significant, and dotted lines when neither is significant. Transparent ribbons indicate 95% confidence intervals.

# Discussion

The long-term growth records contained in tree rings provide an exceptional tool for understanding past drivers of growth and anticipating future forest changes, yet traditional analysis methods were not designed to address questions that are critical to understanding whole-forest productivity (Table 1). Our novel method provides a powerful approach to elucidate how tree growth is simultaneously shaped by climate, tree size, slowly changing environmental conditions, and their interactions (Fig. 1). For each of these drivers individually, the method yields results that are consistent with those that would be obtained using established methods (Figs. 2, S11-S14, S58-S67; Table S5; see also Appendix S4). By allowing these factors to be considered simultaneously, our approach opens the door to robust analyses of the joint and interactive effects of climate, tree size, and other drivers. Applied across multiple forest types and species distributed globally across 10 sites, this method yields a more complete understanding of the drivers of variability and directional changes in tree growth over the past century (Tables 1-2).

## Climate sensitivity

Across diverse climates and forest types (Tables 2, S2), growth rates of 40 tree species generally responded positively to water availability (PPT or PDF) – at least up until the long-term mean – and negatively to temperature (usually or PET), with the exception of several positive responses at times and in places where temperature was limiting (Fig. 3). These findings are generally consistent with current understanding of global-scale patterns in climate sensitivity (Babst et al., 2019; Rozendaal & Zuidema, 2011): the majority of forests globally are moisture limited and respond negatively to temperature, with a shrinking area of temperature-limited forests in cold, humid regions (with SC falling near the transition zone). Within warmer regions, forests in humid climates can sometimes benefit from warm winter or spring temperatures (Babst et al., 2019; Tumajer et al., 2017), as we show for all three species at ZOF and one species at HF (Fig. 3). However, the predominantly negative temperature responses (Fig. 3) imply that warmer temperatures are likely to reduce growth across the wide range of forest types and climates represented here. This growth decrease at high temperatures is probably driven primarily by increased atmospheric dryness (PET or vapor pressure deficit) and ensuant exacerbation of observed water limitations (**REFS**) (Humphrey et al., 2021; López et al., 2021). This effect occurs in addition to the effects of precipitation (Fig. 3), highlighting the fact that precipitation and temperature jointly influence drought (**REFS?**), but, critically, tends to occur over shorter time-frames (usually 3 mo) than the effects of precipitation (usually 3 mo.; Table 1, Fig. 3). This suggests that relatively short periods of anomalously high temperatures and atmospheric dryness, themselves caused in large part by soil dryness (Humphrey et al., 2021), add to effects of prolonged periods of reduced precipitation to shape forest drought responses.

Our analysis differed fundamentally from most conventional approaches in testing for non-linear responses of growth to climate, finding that the majority of climate responses were nonlinear (Table 1, Fig. 3). This result, which is consistent with physiological expectations (**REFS**, Wilmking et al., 2020), indicates that the majority of tree-ring records examined here cover climate variation beyond the range over which the response is linear. The nonlinear form of most climate growth responses implies that as the climate changes, non-stationary climate responses, already common (Wilmking et al., 2020), could become more prevalent (Germain & Lutz, 2020).

We found that interactions between climate variables and DBH were common (44% of cases analyzed; Figs. 4, S56, S57). The most coherent pattern observed in this analysis was a tendency for larger trees to be more sensitive to precipitation and high temperatures (Fig. 4), consistent with widespread observations that larger trees are more sensitive to drought (e.g., Bennett et al., 2015; Gillerot et al., 2020; Hacket-Pain et al., 2016; McGregor et al., 2020; Pretzsch et al., 2018). An analytical structure such as ours that can account for this pattern and other DBH-climate interactions (e.g., Rollinson et al., 2021; Rossi et al., 2007) will be critical to using tree-ring records to understand and forecast the effects of climate on tree growth and forest productivity.

## Variation with DBH

Growth rate – whether measured as RW, BAI, or AGB – varied nonlinearly with DBH for the majority of site-species combinations (81 - 98% depending on growth metric; Fig. 5). Variation in these patterns – particularly for RW, for which variation was most pronounced – was driven by two primary, interrelated factors: species ecology and stand history. Species that would have established in fairly open conditions – i.e., shade-intolerant species (Table S2) and those at sites with more open canopies (e.g., LT, SC) – exhibited rapid initial growth, measured as RW, followed by a roughly exponential decline. Such patterns are consistent with dendrochronology’s “textbook” patterns of studies primarily based on trees that established in high-light environments, where declining RW is in part attributable to the geometric constraint that new growth is spread around an ever-growing circumference (Biondi & Qeadan, 2008; Fritts, 1976). However, within the forest settings studied here, the majority of species exhibited initially low, but increasing, RW. This latter pattern is consistent with the observation that when contemporary growth rates are compared across individuals within a closed-canopy stand (i.e., a “cross-sectional” analysis), RW increases continuously with DBH (e.g., K. J. Anderson-Teixeira, McGarvey, et al., 2015; Helcoski et al., 2019; Muller-Landau et al., 2006), or increases and subsequently decreases (Schelhaas et al., 2018).

We found evidence of saturation or decline in BAI and AGB for the majority (77%) of species-site combinations analyzed (Fig. 5), contrasting with findings of cross-sectional analyses showing that AGB increases continuously with DBH (Meakem et al., 2018; Stephenson et al., 2014), which has also been observed in tree rings (Foster et al., 2016). In large part, this discrepancy can be explained by differences between cross-sectional analyses and “longitudinal” patterns of individual trees through time (Forrester, 2021; Sheil et al., 2017). Declines in BAI and AGB at larger DBH are probably in part attributable to increasing allocation to reproduction (Thomas, 2011), and are also linked to slowly changing environmental conditions (e.g., successional changes in stand structure, climate change). Notably, inclusion of year in the GLS models tended to reduce the magnitude of BAI and AGB declines at larger DBH (Figs. S35-S54), suggesting that some of the declines (Fig. 5) are more properly attributed to the effect of year than DBH.

## Changing growth rates

Our analytical framework reconstructs growth changes in a sampled tree population over time while accounting for climate, DBH, and persistent growth differences among individuals (Fig. 1), thereby addressing some important challenges to obtaining unbiased estimates of growth trends. First, changes in climate can drive dramatic growth trends (e.g., declines at LT) and therefore must be factored out in order to capture the influence of other environmental drivers. Second, correcting for any relationship between tree growth rate and age or DBH (Fig. 5) is essential for unbiased reconstruction of growth trends, yet the reliability of existing analytical approaches remains mixed [**REFS**; Peters et al. (2015)]. A comparative analysis of several methods revealed low reliability of two of the most commonly used approaches, conservative detrending and basal area correction (Peters et al., 2015), both of which assume a constancy of growth in mature trees that is violated by the DBH growth trends observed here (Fig. 5). Our method is conceptually parallel to regional curve standardization, which performed better at growth trend detection in the analysis of Peters et al. (2015), but differs in that we standardize relative to DBH rather than age, correct for any trends in the most influential climate drivers, and include random effects of tree to account for persistent growth differences among individuals (see next paragraph). It is important to bear in mind, however, that growth trends in relation to DBH and year are linked, such that poor model representation of the ontogenetic effects of growth could bias estimated trends over time. While consistency in the direction of estimated temporal trends across growth metrics and relative to an alternative analysis method (Figs. S58-S67) rules out the potential for severe bias, the close linkage between DBH and calendar year implies that it is difficult, if not impossible, to fully disentangle the two statistically.

A third third important challenge is that persistent growth differences among individuals can bias estimated growth trends in positive or negative directions (Brienen et al., 2017, 2012; Groenendijk et al., 2015; Nehrbass-Ahles et al., 2014; van der Sleen et al., 2017). For instance, older trees, which provide the only records available for the earliest decades, are competitive winners that probably had above-average growth rates (Aubry-Kientz et al., 2015), which would upwardly bias average growth rate estimates for early decades (Groenendijk et al., 2015). While including a random effect of tree should help to avoid the the most severe potential biases associated with persistent growth differences across individuals, it is not possible to obtain fully representative samples of tree populations at all points throughout the history of a stand, as would be required to ensure unbiased representation through time (Bowman et al., 2013; Brienen et al., 2017, 2012). Thus, observed trends should be interpreted as representative of only the sampled population of trees, as opposed to all individuals of the species that existed throughout the time frame analyzed. Within this context, signals of changing growth rate over time are attributable to some combination of stand dynamics (e.g., recruitment and succession, changing stand structure) and environmental drivers (e.g., indirect effects of climate change, rising atmospheric CO2, deposition of SO2 and NOx).

Our analysis revealed that growth rates changed directionally for the majority (73-78%, depending on growth metric) of site-species combinations selected for analysis based on the sampling representation of DBH by year (Fig. 6). The majority of negative growth trends detected here (Fig. 6) are probably attributable to stand dynamics as cohorts and stands develop oer time, and are pretty typical of mixed-species stands that experience vertical stratification (Oliver & Larson, 1990). For species exhibiting a pulse of recruitment in the past followed by little subsequent recruitment (e.g., *Acer rubrum* and *Betula alleghaniensis* at HF; Figs. S1-S10), persistent differences in growth rates among individuals could produce a trend of declining growth, as faster-growing individuals reach various size thresholds earlier (Brienen et al., 2017; see also van der Sleen et al., 2017). Such a trend is not indicative of a directional response to changing environmental conditions that would be generalizable across stands (e.g., rising atmospheric CO2), but it does indicate declining growth of the species within the stand. This can occur, for example, when a species undergoes a dramatic decline in recruitment within a stand (e.g., *Quercus* spp. at SCBI; *Abies alba* at ZOF), such that fast-growing individuals disappear from progressively larger DBH classes as time proceeds. In secondary stands, particularly those where many of the sampled species recruited in pulses that were followed by low recruitment (e.g., SCBI, HF; Appendix S1, Figs. S1-S10), growth declines are consistent with the tendency for faster tree growth during early stand development (Lorimer et al., 1988; Lorimer & Frelich, 1989; Oliver & Larson, 1990), and with increasing competition and declining woody productivity as young stands mature (e.g., Goulden et al., 2011; Pregitzer & Euskirchen, 2004). Even within older forests, light-demanding species that establish in gaps (e.g., *Jacaranda copaia* at BCNM, *Populus tremuloides* at CB; Table S2) would tend to experience an increasingly competitive environment through time. For more shade-tolerant species in stands with no known major disturbance within the past 150 years (ZOF, CB), mixed growth trends probably reflect some combination of successional changes and shifting competitive advantages, perhaps in part driven by changing environmental conditions (Furniss et al., 2017; Vrška et al., 2009) or the lack of intermediate disturbances giving rise to increasing crowding (e.g., Lutz et al., 2009).

In a few instances, directional changes in growth are likely attributable to abiotic drivers. At Zofin, size-corrected growth rates were lowest in the 1970s and 1980s (Fig. S63), consistent with other studies from central Europe showing dramatic growth reductions due to acid deposition during this period (Elling et al., 2009; Šamonil & Vrška, 2008). Non-linear trends such as this would be more accurately described by a non-linear response function to year, or incorporation of data on pollution, but that is beyond the scope of the current analysis. In New Mexico (LT), where growth rates of *Pinus ponderosa* declined, it is possible that the primary climate drivers identified here do not capture all aspects of a strong regional warming and drying trend (Touchan et al., 2011; Williams et al., 2013). At Scotty Creek, in northern Canada, rapid warming is thawing permafrost and altering hydrologic conditions (Baltzer et al., 2014), resulting in high mortality, growth declines, and low recruitment of *Picea mariana* (Dearborn et al., 2020; Sniderhan & Baltzer, 2016); we attribute pronounced negative growth trends to a combination of successional declines and indirect climatic stress.

There is a notable lack of evidence that growth rates of any species benefited substantially from increasing CO2, corroborating previous analyses from HKK (Groenendijk et al., 2015; Nock et al., 2011; van der Sleen et al., 2015, 2017). With a few exceptions (*Fagus sylvatica* at ZOF, *Picea pungens* and *Pinus flexilis* at CB; Fig. 6), any growth benefit from elevated CO2 was outweighed by some combination of demographic or successional changes and chronic environmental shifts. This aligns with the preponderance of studies using tree rings to infer growth responses to rising CO2 (e.g., Girardin et al., 2016; Groenendijk et al., 2015; Hararuk et al., 2019; Walker et al., 2020), albeit contrasting with some (e.g., Hember et al., 2019; Voelker et al., 2006). A growth benefit of increasing atmospheric CO2 concentration is expected, based on physiological mechanisms, under water-limited conditions and has been observed in young forests in experimental settings (Walker et al., 2020). However, significant woody growth stimulation by elevated CO2 has not been observed in experimentally manipulated mature forests (Walker et al., 2020), and increasing CO2 does not appear to be a dominant growth driver for the trees in natural forest settings analyzed here.

## Conclusions

In this study, we present a novel robust approach that allows integrative analysis of factors that jointly influence tree growth (Table 1). Specifically, it allows us to demonstrate that (1) growth is generally simultaneously influenced by temperature and precipitation over different seasonal windows, (2) nonlinear climate responses and interactive effects of climate with DBH are common (Figs. 3 and 4, respectively), (3) growth – expressed in any metric – almost universally varies with DBH (Fig. 5), and (4) current or recently living trees commonly show growth declines in response to some combination of stand dynamics and environmental change (Fig. 6). While traditional dendrochronology methods, particularly those focused on climate reconstruction, generally sample and analyze data to minimize many of these effects, they are critical for understanding forest productivity in an era of global change. As global change pressures intensify and the need to understand changing forest dynamics becomes increasingly urgent (McDowell et al., 2020; Thom et al., 2017), we expect that this approach will prove valuable to understanding drivers of tree growth and forest change.

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# Authors’ contributions

KAT, VH, CR, RA, CP conceived the ideas and designed methodology; NP, CDA, RAS, TA, JLB, JDB, SB, PC, RH, JK, JL, EQM, JM, PS, AES, AJT, IV, MV, and PAZ collected the data; VH, BG, EGA, CD, and NP organized and analysed the data; KAT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

# Data availability

Code and full results are available via the project repository in GitHub (github.com/EcoClimLab/ForestGEO-climate-sensitivity) and archived in Zenodo (DOI: TBD) . Data for [# TBD] of the sites are archived in the The DendroEcological Network (DEN) database [SCBI, … ; Rayback et al. (2020)] and/or the International Tree-Ring Data Bank, ITRDB (CB; …).

# Supplementary files

Appendix S1. Site Details

Appendix S2. Methods for reconstruction of DBH

Appendix S3. Methods for climate data evaluation and correction

Appendix S4. Methods for comparing our approach with traditional methods

Appendix S5. Dealing with rapidly changing climate and tree growth

Table S1. Site Details.

Table S2. Species analyzed, their characteristics, and bark allometries applied.

Table S3. Sampling details for species by site.

Table S4. Allometric equations for bark thickness.

Table S5. Qualtiative comparison of results from this study with previous studies employing conventional methods.

Figures S1-S10. Density plots of core record start years by species for all sites.

Figures S11-S14. Comparison of our approach with traditional methods of identifying climate signals for four species.

Figures S15-S34. Climwin output for water and temperature variable groups at all sites.

Figures S35-S54. Best GLS models models excluding and including year for all sites.

Figure S55. Climate responses at SC before and after 1970.

Figure S56. All signficant climate - DBH interactions with RW as the response metric.

Figure S57. All signficant climate - DBH interactions with RW as the response metric.

Figures S58-S67. Relationships between DBH and BAI by decade for all sites.

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