**Title:** Warmer spring temperatures in temperate deciduous forests cause earlier tree growth but have little effect on annual woody productivity

**Authors (not yet complete, just alphabetical for now–final order TBD):**

Cameron Dow1

Albert Y. Kim1,2

Loïc D’Orangeville3,4

Erika B. Gonzalez-Akre1

Ryan Helcoski1

Valentine Herrmann1

Grant Harley

Justin Maxwell

Ian McGregor1,6

William McShea1

Sean McMahon7,9

David A. Orwig3

Neil Pederson3

Alan Tepley1,8

Kristina J. Anderson-Teixeira1,9\*

**Author Affiliations:**

1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; Front Royal, VA 22630, USA
2. Statistical & Data Sciences; Smith College; Northampton, MA 01063, USA
3. Harvard Forest, Petersham, MA 01366, USA
4. Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, NB, E3B 5A3, Canada.
5. Department of Geography & Geological Sciences, University of Idaho, ID, USA
6. Center for Geospatial Analytics; North Carolina State University; Raleigh, NC 27607, USA
7. Smithsonian Environmental Research Center, Edgewater, MD, USA
8. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada
9. Forest Global Earth Observatory; Smithsonian Tropical Research Institute; Panama, Republic of Panama

\*corresponding author: [teixeirak@si.edu](mailto:teixeirak@si.edu); +1 540 635 6546

# 1 (Summary paragraph)

(*word limit 200. italic=tentative*)

As the climate changes, warmer spring temperatures are causing earlier leaf-out1 and commencement of net carbon dioxide (CO2) sequestration2 in temperate deciduous forests, resulting in a tendency towards increased growing season length1,3–5 and annual CO2 sequestration[*6;7;8*;;9].10 However, less is known about how spring temperatures affect tree stem growth, which consumes only a modest portion of the carbon fixed annually11 but sequesters that carbon in wood that has a long residence time in the ecosystem12,13 or as wood products14. Here, we show that in two temperate deciduous forests, warmer maximum spring temperatures consistently shifted woody growth milestones earlier but had mixed, weak effects on peak growing season length, maximum daily growth rates, and annual growth. The latter finding is confirmed on the centennial scale by 207 tree-ring chronologies from 114 forests across eastern North America, which show that annual growth is by far more sensitive to temperatures during the peak growing season than in the spring. These findings align with eddy-covariance records showing that annual CO2 sequestration is more strongly linked to conditions in the peak growing season than to growing season length10, with observations that warm springs result in earlier leaf senescence15,16, and with evidence that forest CO2 sequestration is sink-limited16. They contrast, however, with the expectation *in most models16* that an earlier start to growing season would significantly increase the rate of biomass accumulation and thereby enhance the CO2 sink of temperate deciduous forests. Rather, our findings imply that *the extra CO2 sequestered in years with warmer springs6–8 is not allocated to the long-lived woody biomass C pool and is therefore unlikely to have a lasting impact on the forest C balance.* Thus, warming spring temperatures are unlikely to increase the woody productivity or strengthen the carbon sink of temperate deciduous forests.

# 2 (Introduction)

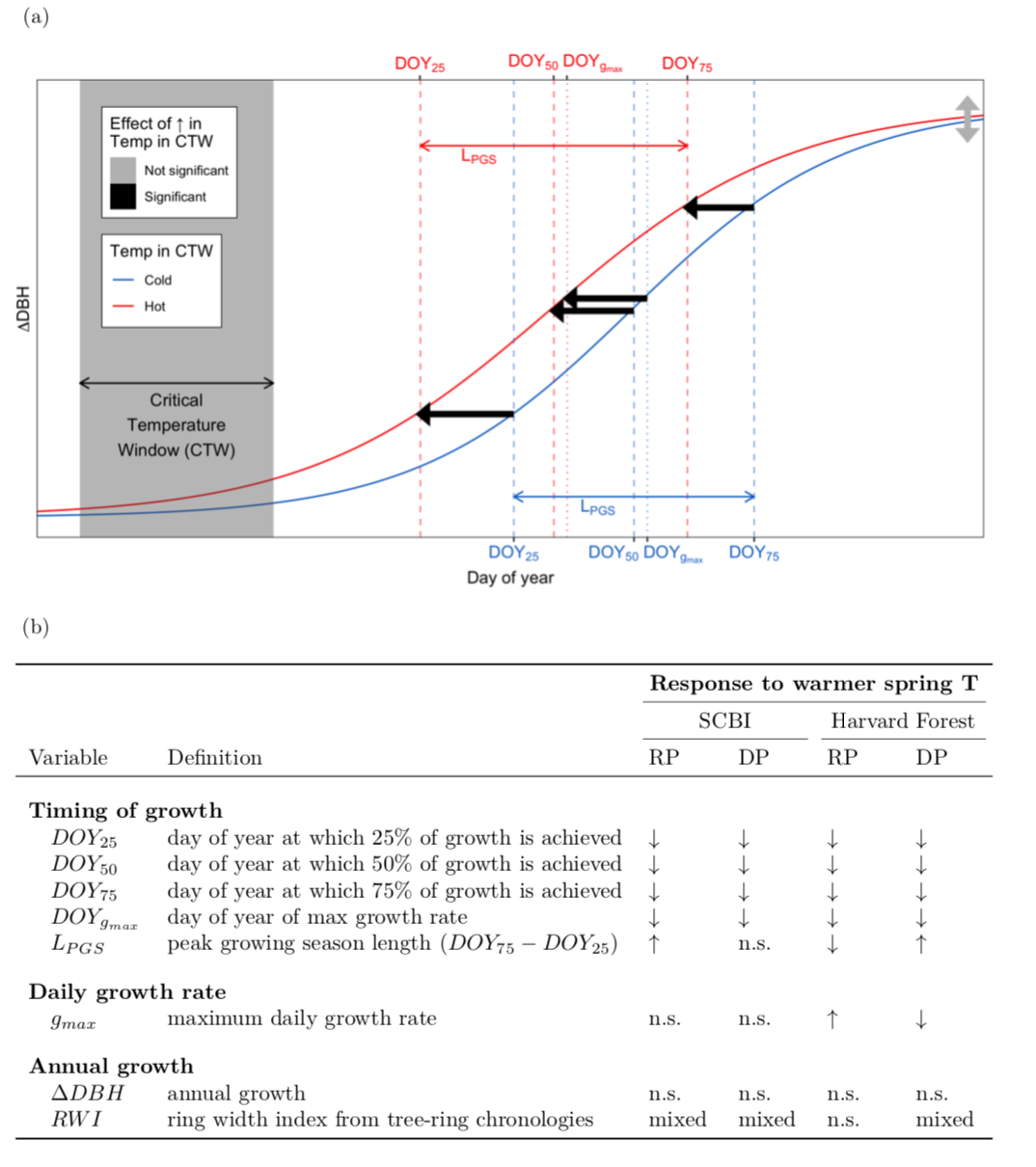
As Earth’s atmospheric CO2 concentrations and temperatures increase, the responses and feedbacks of forests will play an important yet uncertain role in influencing atmospheric CO2 and climate change17,18. Temperate deciduous forests, including those in eastern North America, *(have been net carbon sinks over the past several decades)*… *[Discuss this sink, mechanisms, uncertainties, ending with the point that one meaningful uncertainty is how the C sink will respond to warming springs]*

**In recent decades, warming temperatures have resulted in widespread phenological changes indicative of earlier arrival of spring20 and *often later autumn*1.** In temperate deciduous forests, spring leaf-out has been occurring earlier1, as has the beginning of the annual period of net CO2 sequestration[REFS]. Warmer spring temperatures and earlier leaf-out are also linked to earlier leaf senescence15,21, apparently because of sink-limitation to CO2 sequestration16. However, warmer summer and autumn temperatures can delay leaf senescence1,5,7,8,15,22. The net result is that spring warming generally results in an increased growing season length, measured as the period over which trees have leaves1,1,3–5 and the ecosystem is a net CO2 sink[REFS].

**The expectation is that as growing season length increases, net annual carbon sequestered will increase as well (*i,e*, net ecosystem exchange, )2,9,10,23.** *This expectation is represented in models.16* However, recent evidence that leaf senescence is induced when the seasonal carbon-sink capacities of trees are reached suggests that warmer spring temperatures and earlier leaf-out could advance autumn senescence and *will not necessarily lead to drastically increased C sequestration*16.

**We know very little about how the longest-lived component of fixed carbon, the woody growth of trees, is responding to warming spring temperatures.** In fact, we know little about the stem-growth phenology of temperate deciduous species, with multi-year records of growth phenology having been published for only one site.**doranngeville\_radial\_inreview?** *(We need to make sure we’re not missing anything.)* Tree-ring records, which can be used to examine correlations of annual growth to monthly temperatures but not to understand growth phenology, reveal that growth of temperate deciduous trees tends to be most sensitive to summer temperatures (REFS), with some hints that warmer springs may have a modest positive effect on growth (e.g., Refs.24 [MORE]). Thus, tree-ring records do not necessarily corroborate findings that warming spring temperatures lengthen the growing season and increase annual CO2 sequestration. Characterizing phenological responses of stem growth to warming spring temperatures is critical to bridging this conceptual disconnect and understanding how forest biomass growth is likely to change as the climate warms.

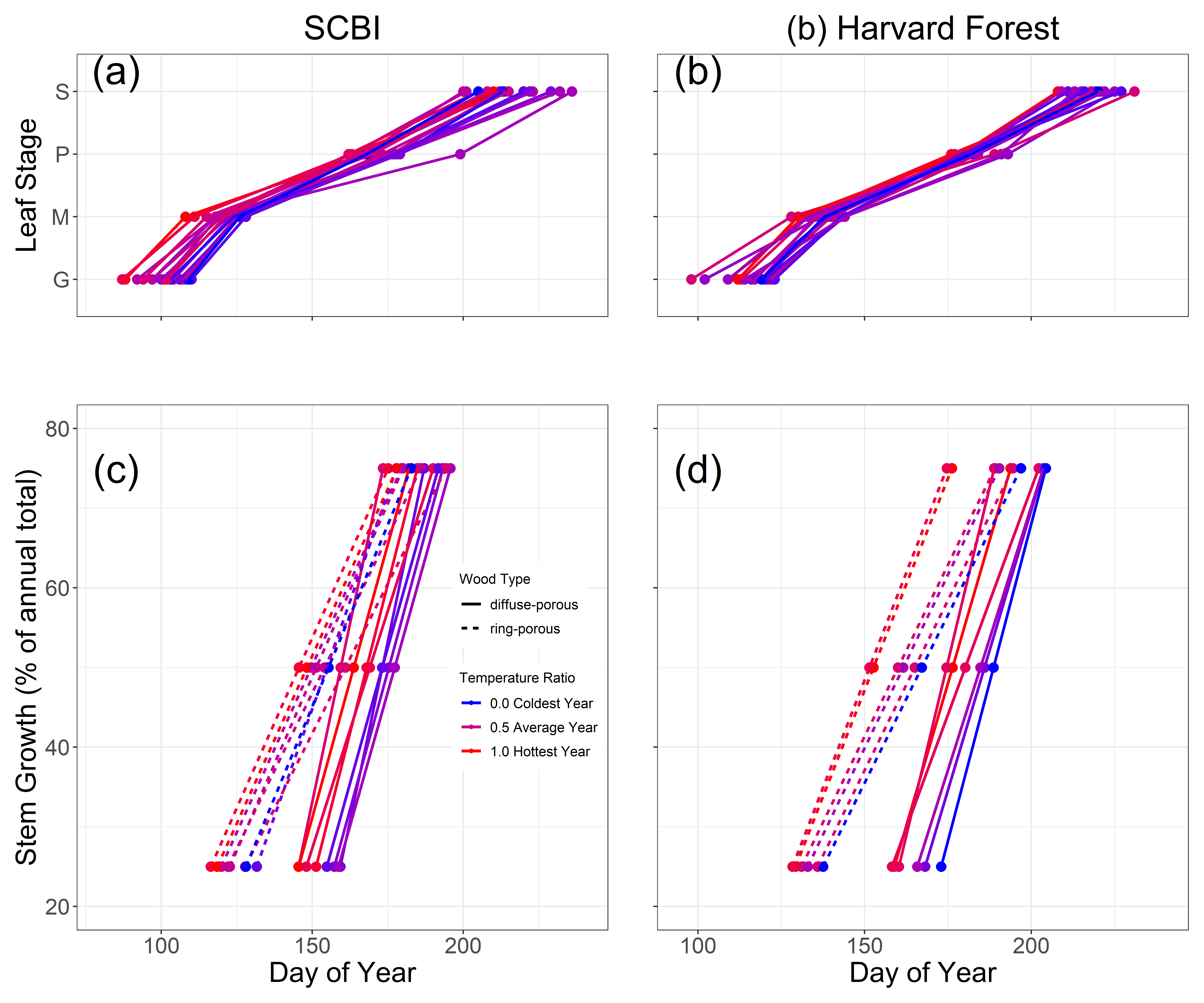
**Here, we characterize how early spring temperatures affect stem growth phenology, growth rates, and annual growth of temperate deciduous trees in two forests and annual growth across forests spanning eastern North America.** First, using dendrometer band measurements taken throughout the growing season at the Smithsonian Conservation Biology Institute (SCBI; Virginia; n = **146** trees over 10 years) and Harvard Forest (Massachusetts; n = **755** trees over six years), we fit a growth model25 to determine the days of year where 25, 50, and 75% annual growth was achieved (, , ), peak growing season length (-), maximum growth rates () and the DOY on which they occurred (), and total annual growth (; Fig. 1). This analysis was performed separately for ring- and diffuse-porous species, which differ in growth phenology**doranngeville\_radial\_inreview?**, and set in the context of leaf phenology at these sites.



**Figure 1 | Summary of tree growth changes under warmer spring temperatures.** (a) Schematic illustrating parameters of interest and summarizing how each responds to warmer maximum temperatures during a ‘critical temperature window’, defined as that with the strongest control over ; (b) Variable definitions and summary responses to warmer spring temperatures at two temperate forests and for two groups of broadleaf deciduous species (RP=ring porous; DP=diffuse porous), where up and down arrows indicate increases and decreases, respectively, ‘n.s.’ indicates no signficant correlation, and ‘mixed’ indicates a mix of signficant and non-signficant correlations, often in different directions.

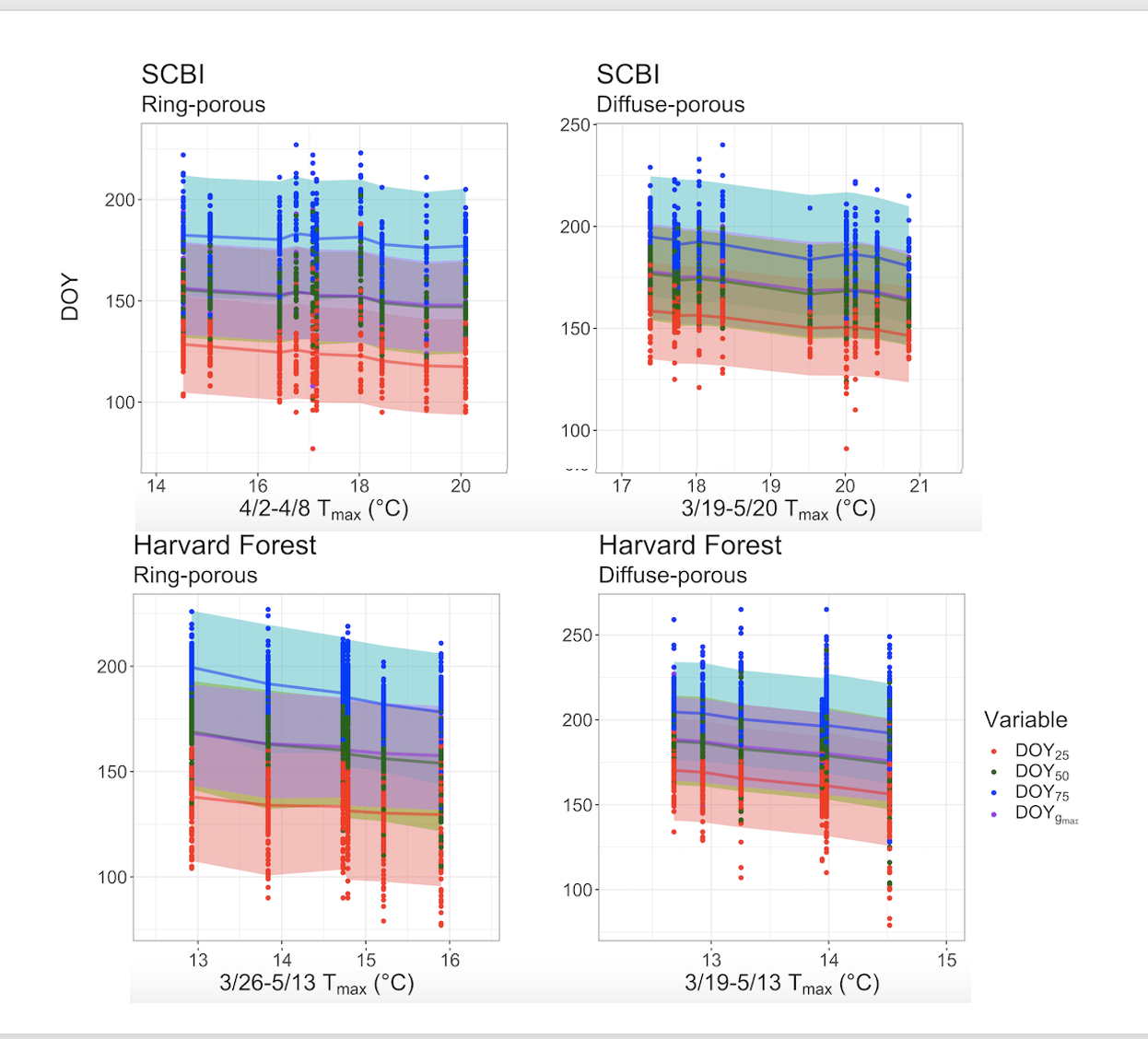
# 3 (Results)

Both leaf phenology and stem growth milestones occurred earlier at SCBI than at Harvard Forest, with stem growth milestones achieved on average 6-10 days earlier at SCBI (Fig. 2, Extended Data Table 2). Consistent with the results of Ref**doranngeville\_radial\_inreview?**, ring-porous species began growing earlier, reaching the benchmark earlier (by 31 days at SCBI and 32 at Harvard Forest), and their growth was spread out over a longer growing season (average 21 and 19 days longer at SCBI and Harvard Forest, respectively; Fig. 2, Extended Data Figure 2, Extended Data Table 2). Growing season length was similar across sites, with being, on average, only two days longer at SCBI for ring-porous species and less than one day longer for diffuse-porous species (Extended Data Table 2).



**Figure 3 | Leaf (a,b) and stem growth (c,d) phenology at the Smithsonian Conservation Biology Institute (a,c) and Harvard Forest (b,d) from 1998 to 2020 (when available).** Panels (a-b) show ecosystem-level leaf phenology, obtained from the MODIS Global Vegetation Phenology product, where G = Greenup, M=Mid-greenup, P=peak, and S=Senescence (i.e., beginning of green-down). Panels (c-d) show the dates at which stem growth milestones were acheived, on average, for sampled populations of ring-porous and diffuse-porous trees at each site. Mean temperature was calculated for each wood-type/site combination over the respective critical window, then turned into a ratio and assigned a color on a gradient where the coldest year in the sample is blue and the warmest is red. (**SHOULD WE COMBINE LEAF AND STEM PHENOLOGY ON A SINGLE PLOT WITH SEPARATE Y-AXES?** See [GitHub Issue #50](https://github.com/EcoClimLab/growth_phenology/issues/50). )

Both leaf phenology and stem growth were sensitive to spring temperatures (Figs. 2 -3). While the results described below were qualitatively consistent considering both maximum and minimum temperatures ( and , respectively) across a range of spring time windows (Extended Data Figures 3-7), we focused our analyses on the strongest relationships: responses to over the consecutive weekly time window between Jan. 1 and for which the correlation between and was strongest (henceforth, critical temperature window, CTW; Fig. 1). The strongest relationships, including but not limited to the CTW (Extended Data Table 2), occurred for time windows closing 5 weeks prior to (Extended Data Figure 3).



**Figure 2 | Relationship between growth parameters and climwin mean temperatures.** For each observed climwin mean temperature value, the posterior mean of the fitted day of year is represented by the solid blue line and 95% credible intervals are represented by bands. (**NOTE THAT THIS PARTIALLY REPLICATES EXTENDED DATA FIG 4**)

For both ring- and diffuse- porous species at both sites, warmer in the CTW resulted in earlier achievement of growth milestones (Figs. 1-3). Consistent with findings from previous studies[REFS], at our focal sites the DOYs of leaf greenup and mid-greenup (measured at ecosystem level via remote sensing) advanced significantly with increasing during the CTW (p=## and ##, respectively). Specifically, greenup DOY occurred 21 days earlier at SCBI and 7 days earlier at Harvard Forest when comparing the years with the warmest and coldest CTW , and mid-greenup also advanced, but to a lesser extent (Fig. 2). Similarly, , , , and at both sites all decreased significantly with CTW , advancing 1-8 days per degree Celsius during the CTW (Figs. 1- 3, 2; see also Extended Data Figures **4-6**).

Whereas the length of time between leaf greenup and senescence (*i.e.,* the day when greenness dropped below 90% of its peak) increased in years with warmer springs (Fig. 2), there was no consistent lengthening of the period of peak stem growth. Specifically, because – and not only – shifted earlier in years with warm springs, displayed mixed responses to spring temperatures (Fig. 1, Extended Data Figures **4-6**).

In contrast to the pronounced effects of on the timing of growth, its effects on and were less consistent and generally quite subtle (Figs. 1, 3). Neither maximum seasonal growth rate, , nor annual growth measured with dendrometer bands, , was consistently linked to early spring temperatures (Fig. 1, Extended Data Figures **4-6**). Specifically, , which occurred very close to (on ; Extended Data Table 2), displayed either no relationship to CTW (SCBI), or extremely small changes in opposite directions for ring- and diffuse- porous species (Harvard Forest), while displayed no relationship CTW (Extended Data Figure 4). Given the subtlety of these responses, a much longer record was needed to clarify what, if any, effect spring temperatures have on stem growth rates.

To understand how annual growth increments have responded to spring temperatures at the centennial scale, we analyzed tree-ring chronologies from our focal study sites (Extended Data Table 1) and across an additional 112 (Fig. 4, Extended Data Figure 1). For 12 species at SCBI and 3 species at Harvard Forest, ring width indices (RWI) rarely exhibited significant correlations to either or in the months corresponding to the CTWs identified here (Fig. 4, Extended Data Figure 7). Although correlations were rarely significant, there was a consistent pattern in responses to across all species at both sites: responses to were negative or neutral in all months from February to August, with the exception of one spring month at each site (April at SCBI, May at Harvard Forest) where growth displayed a positive or neutral responses to (Fig. 4). In these months, positive correlations to were statistically significant (at p=0.05) for one of nine ring-porous species at SCBI and one of two diffuse-porous species at each site. Starting in May at SCBI and June at Harvard Forest, negative correlations of RWI to were predominant, being statistically significant in at least one growing season month for all 12 species at SCBI and one of 3 species at Harvard Forest. Patterns in were fairly similar to those of , but weaker and more stochastic, with more (non-significant) correlations going in opposite directions (Extended Data Figure 7).



**Figure 4 | Sensitivity of annual growth, as derived from tree-rings, to monthly maximum temperatures, for 207 chronologies from 114 sites across eastern North America** (Extended Data Figure 1). Chronologies are grouped by xylem porosity and ordered by mean maximum April temperature. Chronology details are given in the Supplementary Information. (NOTE: Figure still needs some work. **COLOR SCALE IS A BIT OFF IN THIS COMPOSITE FIGURE (scales not identical across panels).** See [GitHub Issue #49](https://github.com/EcoClimLab/growth_phenology/issues/49).)

The patterns observed at our focual sites were mirrored across an additional 192 chronologies from 112 (Fig. 4; Extended Data Figure 1). In total, our analysis included # species at sites distributed from XXX to XXX and spanning a ## C range in April T. Across all chronologies (focal sites included), RWI was significantly positively correlated with April for only #% of records: # of # ring-porous and # or # diffuse-porous species-site combinations. In contrast, RWI was frequently significantly negatively correlated with during peak growing season months (May-August), with significant correlations for #% and #% of species-site-month combinations for ring-porous and diffuse-porous species, respectively. Again, generally exerted less influence over annual growth than (Extended Data Figure 7), with few significant correlations between spring and RWI.

# 4 (Discussion)

Together, our results demonstrate that warmer spring temperatures in the temperate deciduous forests of eastern North America advance the phenology of tree stem growth but have little effect on annual woody productivity (Figs. 1- 4). The observed advance in the timing of stem growth milestones under warmer springs is consistent with similar phenological advances observed for leaf development (Fig. 2)[**REFS**] and NEE [**REFS**]. *It would be interesting to compare the magnitude of these advances (days per degree C)* However, inconsistent with leaf phenology and NEE, we observed that the length of the period of most active stem growth does not increase under warmer springs. This suggests that stem growth, like leaf phenology16, may be sink-limited, such that an advance in the start of growth () accompanied by little change in growth rate () results in an earlier end to the season of rapid growth ().

The concept that stem growth is not enhanced under a longer growing season was supported by our tree-ring analysis, which showed that the effect of spring temperatures on annual growth is negligible for most species and locations, with at most modest influence for some species and locations (Fig. 4, Extended Data Figure 7)24,26. Rather, the primary effect of temperature on annual growth is a negative effect of during the peak growing season, which is most likely a signal of drought stress driven by increased vapor pressure deficit[**REFS**]. It is possible that an earlier start to the growing season may provide some buffer against drought later in the growing season, effectively reducing drought sensitivity, but this hypothesis remains to be evaluated.

Our finding that interannual variation in woody growth is more strongly linked to conditions during the peak growing season than to growing season length aligns with parallel findings for NEE.9,10 However, there is also a disconnect between the woody growth responses to spring temperatures observed here and parallel studies on NEE implying that annual C sequestration increases – at least modestly – with spring temperatures2 or with the length of the carbon uptake period9,10. We show that the extra C does not go into woody growth, raising the question of where this C goes. There are two main possibilities, which hold contrasting implications for the response of forest C balance to rising spring temperatures. First, C that is fixed in late summer or fall may be used for woody growth that is not apparent in the current year’s diameter increment: either used to provide extra thickening of cell walls, a process that lags behind stem expansion27, or saved within trees as non-structural carbohydrates and used towards growth the following year28,29. Tree-ring evidence from SCBI suggests that both processes may occur, and that this dynamic is likely complex24. Second, any additional C that is not rapidly respired may be allocated, likely in the following growing season, to plant functions other than stem growth, including respiration, reproduction, foliage, fine roots, or root exudates28. Most of this carbon would have a relatively low residence time in the ecosystem28, although a small fraction would be incorporated into soil organic carbon pools *with residence times rivaling that of wood [REFS]*. Notably, both of these involve lags of a year or more and would not be captured in interannual variation in NEE, implying that the long-term effect of lengthened growing season on NEE may not be captured in studies, including this one, that consider time frames of a year or less9,10. A study examining long-term trends in growing season length and NEE2 – as opposed to their interannual variation – showed increasing trends in both within the temperate deciduous biome, suggesting that the C that is not allocated to current year growth may have a fairly long residence time within the ecosystem; however, the amount and fate of this carbon remains unknown.

*(KAT edits end here)*

*There is a difference between interannual variation and directional change: the latter is likely to result in acclimatization, and eventually changes in forest composition/ adaptation.* If we look across spatial gradients where the latter have had time to play out, we see that longer growing seasons are correlated with greater tree growth[**REF?**], woody productivity30, and NEE.23

Our findings contribute to a broader picture of the influence of spring temperatures on forest ecosystem function. Warm spring temperatures result in earlier leaf-out (Fig. 2 , REFS), an earlier start to net C sequestration (REFS), and, as shown here, earlier initiation of stem growth (Figs. 1- 2). Yet, an earlier start to the growing season is not associated with a longer growing season (Figs. 1, 3)16 because growth finishes sooner under these conditions, presumably because of *C sink limitation*.16

As climate change accelerates and spring temperatures become increasingly warmer, growing seasons will start earlier, but this is unlikely to provide the increased carbon sequestration that is anticipated in most models (Figs. 1, 3, 4)16. Because of this, temperate deciduous forests are likely to sequester less CO2 than most models suggest, implying that these models are underestimating future overall atmospheric CO2.

# 5 (Content to incorporate)

31

From Neil:,3233

Geng et al. 2020 GCB- Climate warming increases spring phenological differences among temperate trees.

N. American strategies have conservative strategies when it comes to phenology, as historically they’ve been subject to more spring frosts. Thus, climate change is having less impact (Zohner et al., 2020); Leaf velocity discussion? - - RP trees BB = 25% and 75% leaf development = 50% growth.**doranngeville\_radial\_inreview?** Are DP trees leafing up earlier? If yes, how much earlier? Similar to 25,50,75% DOY retreat?

The timing of tree growth has profound impacts on ecosystem interactions, as well as dictates periods of highest drought sensitivity in temperate forests (Foster, 2014; D’Orangeville et al. in review).

# Methods

*We have not yet re-written the methods for Nature. Nature guidelines: Full methods, typically not exceeding 3000 words. May be subdivided by bold headings.*

## Study sites

Study sites included two temperate forests in the eastern United States, both part of the Forest Global Earth Observatory [ForestGEO; Anderson-Teixeira et al. 2015; Davies et al. 2021].

Our first study site was the forest dynamics plot located at the Smithsonian Conservation Biology Institute 5 km South of Front Royal, Virginia within the Blue Ridge Mountains (38.8935° N, 78.1454° W; elevation 273–338 m.a.s.l.). The forest here was established in the mid-19th century after conversion from agricultural fields. Dominate canopy species within the 25.6 ha forest plot include tulip poplar (*Liriodendron tulipifera*), oaks (*Quercus spp.*), hickories (*Carya spp.*). The climate is humid temperate, with a mean annual precipitation of 998 mm and temperatures averaging 1° C in January and 24° C in July ([helcoski\_growing\_2019]).

The second study site was Harvard Forest (42.5388° N, 72.1755° W, 340-368 m.a.s.l.), located near the central Massachusetts town of Petersham. Harvard forest is a secondary forest, having re-established following agricultural use *(time frame)* and signficant hurricane damage in *YEAR*. Dominate species within the 35 ha ForestGEO plot are hemlock (*Tsuga spp.*), oak (*Quercus spp.*) and maple (*Acer spp.*). The climate is temperate continental with a mean annual precipitation of 1120 mm and temperatures averaging -12° C in January and 19° C in July (D’Orangeville et al, ).

## Data collection and preparation

### Dendrometer bands

Metal dendrometer bands installed on a total of 463 trees within the SCBI and Harvard Forest ForestGEO plots (Extended Data Table 1). Bands were placed on dominant species, including two diffuse- and two ring-porous species at SCBI and eight diffuse- and three ring-porous species at Harvard Forest. Bands were measured with a digital caliper approximately every 1-2 weeks within the growing season from 2011-2020 at SCBI and 1998-2003 at Harvard Forest, respectively. The number of bands measured at each site fluctuated somewhat as trees were added or dropped (e.g., because of tree mortality) from the census. Across years, the number of bands sampled averaged *~135* (range: 99-145) at SCBI and *~717* (range: *700-755*) at Harvard Forest. In total, our analysis included 2459 tree-years (Extended Data Table 1).

Measurements were timed to begin before the beginning of spring growth and to continue through the cessation of growth in the fall. At SCBI, the median start date was 4/14, which was adjusted when early leaf-out of understory shrubs and herbs was observed, with the earliest start date being March 30, 2020. Measurements were continued through to fall leaf senescence, with the median end date being 10/17 and the latest end date was November 26, 2012. Timing of measurements at Harvard Forest was similar, with the median start date of 4/23 and median end date of 10/30. 1998 was an anomalous year where initial measurements were taken on 1/5, but not taken again until 4/15. The latest end date was November 11, 2002.

The dendrometer band data were manually cleaned by visual inspection before analysis. We screened for three classes of mistakes. First, when a weekly measurement was drastically different from previous week and following weeks, this was assumed to be a measurement error and the record was removed. Second, when measurements remained essentially unchanged for several readings, followed by a sudden jump followed by normal growth pattern, this was assumed to be a case where the band was stuck and then released. In these cases, the full annual record for the tree was removed. Third, there were cases where data were clearly wrong but with unknown causes. In cases where several measurements were an issue, they were simply removed. If there were no clear solutions to ‘fix’ the data, the entire year was removed from the analysis.

We fit the model of25 to define phenological dates and growth rates (Fig. 1). This five-parameter logistic model was fitted to dendrometer band data from each tree-year in R:

Here, and are lower and upper asymptotes of the model, corresponding to at the beginning and end of the year, respectively. are the modeled days of year (*i.e.*, julian days), is the day of year where the inflection point in growth rate occurs, *shapes the slope of the curve at the inflection point*, and is a tuning parameter controlling the slope of the curve toward the upper asymptote. *We note that the DOY on which maximum growth occurs, (Fig. 1) occurs on only when .* Using the optimized parameters for each tree-year, we then modeled throughout the year and extracted the intra-annual growth variables of interest (Fig. 1).

After fitting the25 model, we used a script to remove poorly fit models. Models were judged to be poorly fit if certain modeled growth characteristics fell outside of the acceptable range we determined. Modeled fits for tree-years were removed under five conditions: (1) single day growth rates were higher than 2 standard deviations away from the mean for each wood-type (SCBI = 2, HF = 34); (2) was standard deviations away from the mean for it’s xylem architecture group, year, and site (SCBI = 62, HF = 106); (3) tree-years with small or negligible total growth ( < 0.02 mm; SCBI = 0, HF = 66); (4) model fit predicted total yearly growth to take longer than 365 days, indicating poor model fit (SCBI = 181, HF = 199); and (5) models with unexplained sharp spikes in growth rate (SCBI = 0, HF = 3). At Harvard Forest the tag years removed through this method was proportional to the original sample size, indicating that no species or size class was disproportionately removed compared to others *(SI figure? data\_cleaning\_figure\_hf in manuscript folder)*. At SCBI a higher proportion of RP trees were removed–the majority in step 4 *(data\_cleaning\_figure\_scbi)*.

### 5.0.1 Leaf phenology

description here: <https://developers.google.com/earth-engine/datasets/catalog/MODIS_006_MCD12Q2#description>

MCD12Q2 V6 Land Cover Dynamics product (informally called the MODIS Global Vegetation Phenology product)34

### Tree rings

Dominant tree species were cored at both sites following sampling designs that covered a broad range of . We analyzed records for the dominant ring- and diffuse- porous species at each site (Extended Data Table 1), excluding species with other xylem architectures (*Juglans nigra* L. at SCBI, *Tsuga Canadensis* (L.) Carrière at Harvard Forest) At SCBI, cores were collected as described in.24 Briefly, cores were taken from living or recently dead trees 10 cm , including a randomly sampled subset of all dominant species within the ForestGEO plot [live trees in 2010-2011;]35 and trees found newly dead in annual tree mortality in 2016 and 2017.24 At Harvard Forest, …(*Neil can write this easily, or KAT probably has the info*) In total, we analyzed 926 cores from eleven species at SCBI and three species at Harvard Forest (Extended Data Table 1).

The tree-ring records from our focal sites were complemented with a much larger collection spanning **#** deciduous and mixed forest sites in Eastern North America. Again, species were limited to broadleaf deciduous species with clearly defined xylem porosity (i.e., excluding semi-ring porous).

All cores were mounted, sanded, cross-dated, and measured using standard methodology. We standardized ring-width series from each core via ARSTAN using a 2/3rds spline, where is the number of years in the series.36,37 *The following italic text is self-plagarized from Helcoski and needs to be reworded:)* *The influence of outliers in all series was reduced using the adaptive power transformation, which also stabilises the variance over time.38 Next, each series was stabilised using either the average correlation between raw ring-width series (rbar) method or a 1/3rds spline method to adjust changes in variance as series replication decreased towards the earlier portion of each chronology.39 The 1/3rds spline method was chosen when replication in the inner portion of each chronology (c. the inner 30–50 yr of each record depending on full chronology length) dropped below three trees. Once that step was complete, a robust biweight mean chronology for each species was calculated from the ring-width indices.36 We chose to use residual chronologies because the autoregressive standardisation process in creating them removes much of the tree-level autocorrelation in growth and these chronologies would most likely contain the most conservative information on drivers of interannual growth.36* We defined chronology start year (Extended Data Table 1) as the year where subsample signal strength (SSS) passed a threshold of SSS = 0.8, or where 80% of the population signal was captured in the chronology.

### Climate

For the dendrometer band analysis, we used climate data from local weather stations. Daily maximum and minimum temperatures ( and , respectively) for SCBI were obtained from a meteorological tower adjacent to the SCBI ForestGEO plot, via the ForestGEO Climate Data Portal v1.0 [<https://forestgeo.github.io/Climate/>;].40 Daily temperature records for Harvard Forest were obtained from the Harvard Forest weather station (Boose & Gould, 2004; Boose, 2018). The R package climpact () was used to plot temperatures for visual inspection. Climpact also identifies readings that were greater than 3 standard deviations away from yearly means. These points were labeled as outliers and removed from the dataset. Gaps in the SCBI meteorological tower data were subsequently filled using temperature readings obtained from a National Center for Environmental Information (NCEI) weather station located in Front Royal, Virginia (<https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00443229/detail>). (*how were gaps filled for Harvard? Or was the record good?*)

For the tree-ring analysis, we obtained monthly and data for 1901-2019 from CRU v.4.04,41 again via the ForestGEO Climate Data Portal v1.0.40

## Determining critical temperature windows

The period where the phenology milestone(s) were most affected by changes in early spring temperature was determined using the R package *climwin*.42 This package tests the correlation between one or more climate variables and a biological variable over all consecutive time windows within a specified time-frame, reporting correlation and $Delta AIC$ of each window. Here, we tested for correlation between temperature (, ) and over the time window from January 1 to the mean for the species group and site (Extended Data Table 2). *The critical time window is determined based on the subset of models that fall within the 95% confidence set.* Here, we focused on defining critical temperature windows for , as opposed to other growth phenology parameters (Figure 1), because we were interested in the influence of temperature on the initiation of woody growth. We note that other growth parameters would be controlled by different critical temperature windows; for example, at SCBI responds most strongly to May-July climate.24 Determining the climate variables that most strongly control all parameters is beyond the scope of this analysis.

## Hypothesis testing

(*This section needs more detail.*)

Correlation between these variables and spring temperatures were assessed using a linear mixed model in a hierarchical Bayesian framework.

Mixed effects models were used to test the response of growth phenology variables (, , , , , and ) to fixed effects of xylem porosity and mean temperature (, ) during the critical temperature window selected by *climwin*, along with random effects of species and tree. We ran separate models for each species group at each site, and for the response of all growth phenology variables to and . Models were run using the LME4 package in R.43

This mixed-effect model was run within a hierarchical Bayesian framework and fit using the rstanarm R interface to the Stan programming language.**rstanarm\_2020?** In all cases unless otherwise specified, all prior distributions are set to be the weakly informative defaults.

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# Author Contributions

# Additional Information

**Supplementary Information** is available for this paper.

Correspondence and requests for materials should be addressed to Kristina Anderson-Teixeira ([teixeirak@si.edu](mailto:teixeirak@si.edu)).

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