**Title:** Warmer spring temperatures in temperate deciduous forests advance the timing of tree growth but have little effect on annual woody productivity

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*NOTE: In general, this needs to be condensed. The typical length of an article with 3-4 modest display items (figures and tables) is 2000-2500 words (summary paragraph plus body text). We’re currently at ~3116 words and 1 modest + 2 large display items. Articles typically have 30-50 references (currently ok there)*

# 1 (Summary paragraph)

As the climate changes, warmer spring temperatures are causing earlier leaf-out1–3 and commencement of net carbon dioxide (CO2) sequestration2 in temperate deciduous forests, resulting in a tendency towards increased growing season length1,4–6 and annual CO2 sequestration2,7–11. However, less is known about how spring temperatures affect tree stem growth, which sequesters carbon in wood that has a long residence time in the ecosystem12,13 or as wood products14. Here, we show that in two forests, warmer spring temperatures consistently shifted the woody growth of deciduous trees earlier but had no consistent effect on peak growing season length, maximum daily growth rates, or annual growth. The latter finding was confirmed on the centennial scale by 208 tree-ring chronologies from 108 forests across eastern North America, where annual growth was far more sensitive to temperatures during the peak growing season than in the spring. These findings imply that any extra CO2 sequestered in years with warmer springs7–9 is not allocated to long-lived woody biomass, where it could have a substantial and 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 (Body)

In recent decades, forests have sequestered ~20% of anthropogenic CO2 emissions, thereby slowing the pace of atmospheric CO2 accumulation and climate change15. A large portion of this CO2 sink occurs in temperate deciduous forests, with uptake of >100 Tg C yr-1 (>10% of the total forest C sink) attributable to environmental (as opposed to demographic) changes.16 The future behavior of this CO2 sink will play an important yet uncertain role in influencing atmospheric CO2 and climate change17,18.

In temperate deciduous forests, spring warming generally results in an increased growing season length, measured as the period over which trees have photosynthetically active leaves1,4–6 and the ecosystem is a net CO2 sink2. The expectation is that as growing season length increases, net annual carbon sequestered will increase as well (*i,e*, net ecosystem exchange, *NEE*)2,10,11,19, and [this expectation is represented in models](https://github.com/EcoClimLab/growth_phenology/issues/56).3,20 However, recent findings that positive effects of warm springs are compensated by negative effects of accumulation of seasonal water deficits3 and that sink factors can limit annual growth20,21 suggest that warmer spring temperatures and earlier leaf-out may not have a positive effect on C sequestration in trees.

While the responses of leaf phenology and seasonal CO2 sequestration to warming spring temperatures have been relatively well-studied1–6, we know very little about how the longest-lived component of fixed carbon in trees, the woody growth, 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 site22*. To our knowledge, the climate sensitivity of woody growth phenology and its link to annual growth has never been studied *in-situ* (but see Ref.21 for a controlled sapling experiment).

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 temperature or potential evapotranspiration between late spring and early summer23,24, with some hints that warmer springs may have a modest positive effect on growth24. Thus, tree-ring evidence does not necessarily align with the finding that warming spring temperatures increase annual CO2 sequestration, thereby providing a negative feedback to climate change2. 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.

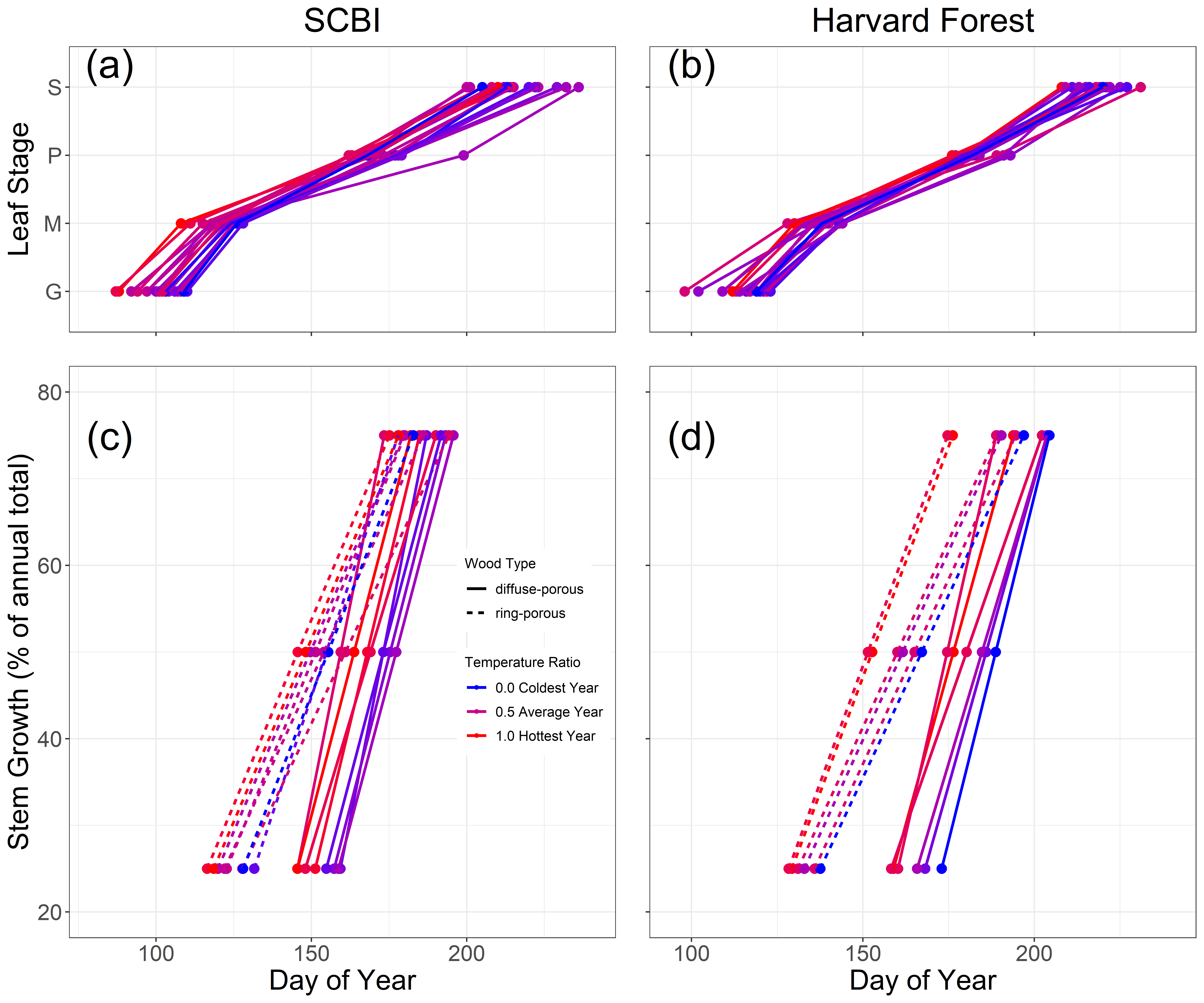
## Dendrometer band analysis

Using dendrometer band measurements taken throughout the growing season at the Smithsonian Conservation Biology Institute (SCBI; Virginia, USA; n = **146** trees from 2011-2020) and Harvard Forest (Massachusetts, USA; n = **755** trees from 1998-2003), we fit a growth model25 to determine the days of year where 25, 50, and 75% annual growth were 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 phenology22, and set in the context of leaf phenology (measured at ecosystem level via remote sensing).



**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.

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 Ref22, 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 2 | Leaf (a,b) and stem growth (c,d) phenology at the Smithsonian Conservation Biology Institute (a,c) and Harvard Forest (b,d).** Panels (a-b) show ecosystem-level leaf phenology, obtained from the MODIS Global Vegetation Phenology product (2001-2018), 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 SCBI (2011-2020) and Harvard Forest (1998-2003). 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.

Both leaf phenology and stem growth were sensitive to spring temperatures (Fig. 2, Extended Data Figures 4-6). 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 3-6), 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; Fig. 1). The strongest relationships, including but not limited to the critical temperature window (Extended Data Table 2), occurred for time windows closing 5 weeks prior to (Extended Data Figure 3).

For ring- and diffuse- porous species at both sites, warmer in the critical temperature window resulted in earlier achievement of growth milestones (Figs. 1, Extended Data Figure 4). Consistent with findings from previous studies27, the DOY of leaf greenup advanced with increasing during the critical temperature window (p=0.001). Specifically, greenup DOY advanced 4.5 days/C at SCBI and 2.4 days/ C at Harvard Forest ~~when comparing the years with the warmest and coldest mean during the critical temperature window~~, and mid-greenup also advanced, but to a lesser extent (Fig. 2). Similarly, at both sites, , , , and all decreased with mean during the critical temperature window (Figs. 1, 2; Extended Data Figures 4-6). Specifically, at SCBI, RP growth advanced 1.9, 1.5, and 1.1 days/ C for , , and , respectively, while DP growth advanced 3.5, 3.5, and 3.6 days/ C for , , and , respectively. At Harvard Forest, RP growth advanced 2.8, 5.0, and 7.2 days/ C for , , and , respectively, while DP growth advanced 7.9, 7.3, and 6.6 days/ C for , , and , respectively.

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 temperatures during the critical temperature window compared to those with cooler temperatures (Fig. 2), there was no consistent lengthening of . Specifically, because both and advanced 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 weak and inconsistent (Figs. 1, Extended Data Figures 4-6). Specifically, , which occurred very close to (on ; Extended Data Table 2), displayed either no relationship to mean during the critical temperature window (SCBI), or extremely small changes in opposite directions for ring- and diffuse- porous species (Harvard Forest). displayed no relationship with mean during the critical temperature window (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.

## Tree ring analysis

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 106 locations (Fig. 3, Extended Data Figure 1). For 12 species at SCBI and 4 species at Harvard Forest, ring width indices (RWI) rarely exhibited significant correlations to either or in the months corresponding to the critical temperature windows identified here (Fig. 3, 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 response to (Fig. 3). 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 4 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 3 | Sensitivity of annual growth, as derived from tree-rings, to monthly maximum temperatures, for 208 chronologies from 108 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.

The patterns observed at our focal sites were mirrored across an additional 192 chronologies from 106 sites (Fig. 3; Extended Data Figure 1)23. In total, our analysis included 208 species at sites distributed from Alabama (Lat = 34.35) to Michigan (Lat = 45.56) and spanning a 15 C range in April . Across all chronologies (focal sites included), RWI was significantly positively correlated with April for only 1% of records: 1 of 142 ring-porous and 2 of 66 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 53% (May: 47/142, Jun: 108/142, Jul: 90/142, Aug: 57/142) and 46% (May: 11/66, Jun: 53/66, Jul: 37/66, Aug: 22/66) 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.

## 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- 3). 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)2 and NEE.2 *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 the growth benefit of warmer springs is compensated by negative effects later in the growing season, with two primary possible mechanisms. First, stem growth, like leaf phenology20, may be sink-limited, such that an advance in the start of growth () would lead to an earlier depletion of resources needed for growth resulting in an earlier end to the season of rapid growth (). Warm springs may also be associated with greater seasonal water stress, effectively canceling out any positive effects of an extended growing period[3; ] or inducing the cessation of stem growth when a critical water deficit is reached28.

Spring warming at SCBI and Harvard Forest in the study years used here did not result in increased or summer water stress (SPEI; Supp(?) SPEI Figure). This suggests that even when warmer springs are not associated with greater seasonal water stress, the lack of increased stem growth still prevails at these sites. This could be because the woody growth at these sites are already limited by some mechanism.

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. 3, Extended Data Figure 7)24,29. 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 stress23. Linear models were run to examine the relationship between spring, summer and an interaction effect with ring-width for each of our 208 chronologies. The results indicated that, across all latitudes, the interacting effect of warmer springs and summers resulted in negligible increase of ring-width (supp (?) rw\_drought\_plot).  
*It is possible that an earlier start to the growing season may provide some buffer against drought later in the growing season30, potentially contributing to observed trends of declining drought sensitivity in the region24,31,32. (Is this relevent?)*(Neil suggested that the zhang paper would be good here but i’m not sure I see how…) *(ADD MORE ON DROUGHT HERE)*

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.10,11 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 period10,11. 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 from diameter measurements in the current year: either used for thickening of cell walls, a process that lags behind stem expansion33, or saved within trees as non-structural carbohydrates and used towards growth the following year34,35. In fact, [extension of our tree-ring analysis](https://github.com/EcoClimLab/growth_phenology/issues/57) showed a generally positive, although often non-significant, correlation between ring-width and previous year growing season in RP trees, indicating this may be a possibility. *very little correlation between April and growth the following year (5 of 142 RP and 3 of 66 DP species-site combinations), refuting the latter possibility*. We also cannot rule out the possibility that warm springs promote formation of more carbon-dense cell walls in the current of following year (**coauthors, do any of you know literature related to this?**); however, our results suggest that little of the extra C that may be fixed in these years goes into wood formation.

A second possibility is that any additional C fixed during years with warm springs that is not rapidly respired may be allocated, potentially in the following growing season, to plant functions other than stem growth, including respiration, reproduction, foliage, fine roots, or root exudates34. Stem growth is more sensitive to water deficit than is photosynthesis**muller\_water\_2011?**. [This seems to promote the investment of sequestered carbon into root growth in times of drought stress. Zoehner et al 202121 found that the proportion of root-to-stem growth increased under spring warming, suggesting that increased ecosystem sequestration resulting from spring warming may be promoting the growth of below-ground biomass. ~~However, this study was done under tightly controlled conditions within potted plants and does not represent the environmental conditions of forests.~~](https://github.com/EcoClimLab/growth_phenology/issues/72) Most of this carbon would have a relatively low residence time in the ecosystem34, although a small fraction would be incorporated into soil organic carbon pools *with residence times rivaling that of wood [REFS]*. Notably, turnover of extra C fixed during years with warm springs would often occur with sufficient temporal lag that it 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 that consider time frames of a year or less10,11. Studies examining long-term trends in growing season length and ecosystem C uptake2,7,8 – as opposed to their interannual variation – within or including the temperate deciduous biome showed increasing trends in both variables, suggesting that the C 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. *BUT SEE!!36 and****barichivich\_large-scale\_2013?*** *- these are focused on higher latitudes, but shows greater release of C in the fall!*

Thus, a distinction between interannual variation and directional change may be critical when considering how directional climate change is likely to affect tree growth and ecosystem C dynamics. In addition to the existence of temporal lags between C uptake and release, which introduce a lot of uncertainty34, trees are likely to acclimate *to some extent* to warming temperatures32,**gessler\_way\_2020?**, and on even longer time scales, we are likely to see changes in forest composition and 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 productivity37, and NEE.19 *Future research will be important to sorting this out.*

Despite remaining uncertainties, our findings contribute substantially to a broader picture of the influence of spring temperatures on forest ecosystem function. Warm spring temperatures result in earlier leaf-out (Fig. 2)1, an earlier start to net C sequestration2, and, as shown here, earlier initiation of stem growth (Figs. 1, Extended Data Figure 4). Yet, an earlier start to the growing season is not consistently associated with a longer peak growing season or increased growth (Figs. 1, 3), presumably because stem diameter growth is curtailed by C sink limitation20 or drought23,24,32.

As climate change accelerates and spring temperatures become increasingly warmer, growing seasons will start earlier, but this is unlikely to provide the sustained increase in carbon sequestration that is anticipated in most models (Fig. 1)20. 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. (*see* [*GitHub issue 56 on representation in models*](https://github.com/EcoClimLab/growth_phenology/issues/56))

# 3 content to incorporate or delete:

Warmer spring temperatures and earlier leaf-out are also linked to earlier leaf senescence38,39,**fu\_variation\_2014?**, apparently because of sink-limitation to CO2 sequestration20,28. Additionally, Warmer summer and autumn temperatures coupled with drought led to a delay of leaf senescence1,6,8,9,38,40,**xie\_predicting\_2018?** while heavy rainfall and heat stress led to earlier senescence**xie\_predicting\_2018?**. As a result, warming may advance or delay autumn senescence depending on timing of warming and water availability, with delays more common across eastern North America.3

These findings align with those of previous studies that suggest annual CO2 sequestration is more strongly linked to conditions in the peak growing season than to growing season length11,32 and with observations that warm springs result in earlier leaf senescence of deciduous trees because CO2 sequestration is sink limited.20,38 They contrast, however, with the expectation *in most models20* 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.

Under controlled conditions, spring warming increases biomass accumulation in trees, with a larger proportion of root growth compared to shoot growth21.

# 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.*), and 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 (Ref.24).

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 significant hurricane damage in 1938. Dominate species within the 35 ha ForestGEO plot are hemlock (*Tsuga canadensis*), oak (*Quercus spp.*) and red maple (*Acer rubrum*). 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.22

## Data collection and preparation

### Dendrometer bands

Metal dendrometer bands were 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. 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 vegetation 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 November 26, 2012. Timing of measurements at Harvard Forest were 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 raw 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 then return to a 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, cases where data were clearly wrong but with unknown causes were removed. If a majority of the data points fell into this class 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 removed 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, Harvard Forest = 34); (2) was standard deviations away from the mean for it’s xylem architecture group, year, and site (SCBI = 62, Harvard Forest = 106); (3) tree-years with small or negligible total growth ( < 0.02 mm; SCBI = 0, Harvard Forest = 66); (4) model fit predicted total yearly growth to take longer than 365 days, indicating poor model fit (SCBI = 181, Harvard Forest = 199); and (5) models with unexplained sharp spikes in growth rate (SCBI = 0, Harvard Forest = 3). At Harvard Forest the tag years removed through this method were 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)*.

### 3.0.1 Leaf phenology

Leaf phenology data for the years 2001-2018 were extracted for SCBI and Harvard Forest from the MCD12Q2 V6 Land Cover Dynamics product (informally called the MODIS Global Vegetation Phenology product).41

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

### 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;]42 and trees found newly dead in annual tree mortality in 2016 and 2017(24*If we’re citing a method from the helcoski paper, do we need to do this ‘briefly’ section? I would remove.)*. 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 106 deciduous and mixed forest sites in Eastern North America23,**maxwell\_sampling\_2020?** (**OTHER REFS??**). 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.43,44 *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.45 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.46 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.43 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.43* 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/>;].47 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.4.04,48 again via the ForestGEO Climate Data Portal v1.0.47

## 3.1 Analyses

### 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*.49 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 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 work/ 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.50

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.

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# References

1. Jeong, S.-J., Ho, C.-H., Gim, H.-J. & Brown, M. E. Phenology shifts at start vs. End of growing season in temperate vegetation over the Northern Hemisphere for the period 1982. *Global Change Biology* **17**, 2385–2399 (2011).

2. Keenan, T. F. *et al.* Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* **4**, 598–604 (2014).

3. Buermann, W. *et al.* Widespread seasonal compensation effects of spring warming on northern plant productivity. *Nature* **562**, 110–114 (2018).

4. Menzel, A. & Fabian, P. Growing season extended in Europe. *Nature* **397**, 659–659 (1999).

5. Menzel, A. *et al.* European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976 (2006).

6. Ibáñez, I. *et al.* Forecasting phenology under global warming. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3247–3260 (2010).

7. Keeling, C. D., Chin, J. F. S. & Whorf, T. P. Increased activity of northern vegetation inferred from atmospheric CO 2 measurements. *Nature* **382**, 146–149 (1996).

8. Dragoni, D. *et al.* Evidence of increased net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. *Global Change Biology* **17**, 886–897 (2011).

9. Crabbe, R. A. *et al.* Extreme warm temperatures alter forest phenology and productivity in Europe. *Science of The Total Environment* **563-564**, 486–495 (2016).

10. Zhou, S. *et al.* Explaining inter-annual variability of gross primary productivity from plant phenology and physiology. *Agricultural and Forest Meteorology* **226-227**, 246–256 (2016).

11. Fu, Z. *et al.* Maximum carbon uptake rate dominates the interannual variability of global net ecosystem exchange. *Global Change Biology* **25**, 3381–3394 (2019).

12. Xue, B.-L. *et al.* Global patterns of woody residence time and its influence on model simulation of aboveground biomass. *Global Biogeochemical Cycles* **31**, 821–835 (2017).

13. Russell, M. B. *et al.* Residence Times and Decay Rates of Downed Woody Debris Biomass/Carbon in Eastern US Forests. *Ecosystems* **17**, 765–777 (2014).

14. Profft, I., Mund, M., Weber, G.-E., Weller, E. & Schulze, E.-D. Forest management and carbon sequestration in wood products. *European Journal of Forest Research* **128**, 399–413 (2009).

15. Pan, Y. *et al.* A Large and Persistent Carbon Sink in the World’s Forests. *Science* **333**, 988–993 (2011).

16. Pugh, T. A. M. *et al.* Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences* **116**, 4382–4387 (2019).

17. Arora, V. K. *et al.* Carbonconcentration and carbonclimate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences* **17**, 4173–4222 (2020).

18. Friedlingstein, P. *et al.* Global Carbon Budget 2020. *Earth System Science Data* **12**, 3269–3340 (2020).

19. Churkina, G., Schimel, D., Braswell, B. H. & Xiao, X. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology* **11**, 1777–1787 (2005).

20. Zani, D., Crowther, T. W., Mo, L., Renner, S. S. & Zohner, C. M. Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees. 7 (2020).

21. Zohner, C. M., Renner, S. S., Sebald, V. & Crowther, T. W. How changes in spring and autumn phenology translate into growth-experimental evidence of asymmetric effects. *Journal of Ecology* **109**, 2717–2728 (2021).

22. D’Orangeville, L. *et al.* Peak radial growth of diffuse-porous species occurs during periods of lower water availability than for ring-porous and coniferous trees. *Tree Physiology* (2021) doi:[10.1093/treephys/tpab101](https://doi.org/10.1093/treephys/tpab101).

23. D’Orangeville, L. *et al.* Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Global Change Biology* **24**, 2339–2351 (2018).

24. Helcoski, R. *et al.* Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. *New Phytologist* **223**, 1204–1216 (2019).

25. McMahon, S. M. & Parker, G. G. A general model of intra-annual tree growth using dendrometer bands. *Ecology and Evolution* **5**, 243–254 (2015).

26. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).

27. Friedl, M. A. *et al.* A tale of two springs: Using recent climate anomalies to characterize the sensitivity of temperate forest phenology to climate change. *Environmental Research Letters* **9**, 054006 (2014).

28. Lempereur, M. *et al.* Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: Implications for assessing forest productivity under climate change. *New Phytologist* **207**, 579–590 (2015).

29. Alexander, M. R. *et al.* The potential to strengthen temperature reconstructions in ecoregions with limited tree line using a multispecies approach. *Quaternary Research* **92**, 583–597 (2019).

30. Wolf, S. *et al.* Warm spring reduced carbon cycle impact of the 2012 US summer drought. *Proceedings of the National Academy of Sciences* **113**, 5880–5885 (2016).

31. Maxwell, J. T., Harley, G. L. & Robeson, S. M. On the declining relationship between tree growth and climate in the Midwest United States: The fading drought signal. *Climatic Change* **138**, 127–142 (2016).

32. Zhang, J. *et al.* Drought limits wood production of Juniperus przewalskii even as growing seasons lengthens in a cold and arid environment. *CATENA* **196**, 104936 (2021).

33. Cuny, H. E. *et al.* Woody biomass production lags stem-girth increase by over one month in coniferous forests. *Nature Plants* **1**, 15160 (2015).

34. Trumbore, S., Gaudinski, J. B., Hanson, P. J. & Southon, J. R. Quantifying ecosystem-atmosphere carbon exchange with a 14C label. *Eos, Transactions American Geophysical Union* **83**, 265–268 (2002).

35. Richardson, A. D. *et al.* Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytologist* **197**, 850–861 (2013).

36. Piao, S. *et al.* Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* **451**, 49–52 (2008).

37. Banbury Morgan, R. *et al.* Global patterns of forest autotrophic carbon fluxes. *Global Change Biology* gcb.15574 (2021) doi:[10.1111/gcb.15574](https://doi.org/10.1111/gcb.15574).

38. Zohner, C. M. & Renner, S. S. Ongoing seasonally uneven climate warming leads to earlier autumn growth cessation in deciduous trees. *Oecologia* **189**, 549–561 (2019).

39. Keenan, T. F. & Richardson, A. D. The timing of autumn senescence is affected by the timing of spring phenology: Implications for predictive models. *Global Change Biology* **21**, 2634–2641 (2015).

40. Vitasse, Y., Porté, A. J., Kremer, A., Michalet, R. & Delzon, S. Responses of canopy duration to temperature changes in four temperate tree species: Relative contributions of spring and autumn leaf phenology. *Oecologia* **161**, 187–198 (2009).

41. Friedl, M., Gray, J. & Sulla-Menashe, D. MCD12Q2 MODIS/Terra+Aqua Land Cover Dynamics Yearly L3 Global 500m SIN Grid V006. (2019) doi:[10.5067/MODIS/MCD12Q2.006](https://doi.org/10.5067/MODIS/MCD12Q2.006).

42. Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C. & Shen, X. Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot: *Ecological Archives* E094-195. *Ecology* **94**, 2111–2112 (2013).

43. Cook, E. R. A Time Series Analysis Approach to Tree Ring Standardization. vol. PhD (University of Arizona, 1985).

44. *Methods of Dendrochronology: Applications in the Environmental Sciences*. (Springer Netherlands, 1990). doi:[10.1007/978-94-015-7879-0](https://doi.org/10.1007/978-94-015-7879-0).

45. Cook, E. R. & Peters, K. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene* **7**, 361–370 (1997).

46. Jones, P. D., Osborn, T. J. & Briffa, K. R. Estimating sampling errors in large-scale temperature averages. *Journal of Climate* **10**, 2548–2568 (1997).

47. Anderson-Teixeira, K. *et al.* Forestgeo/Climate: Initial release. (2020) doi:[10.5281/ZENODO.4041609](https://doi.org/10.5281/ZENODO.4041609).

48. Harris, I., Osborn, T. J., Jones, P. & Lister, D. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data* **7**, (2020).

49. van de Pol, M. *et al.* Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution* **7**, 1246–1257 (2016).

50. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using **Lme4**. *Journal of Statistical Software* **67**, (2015).