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Research

Changes in the climate suitability and growth rates of trees in eastern North America

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According to the 'fitness-suitability' hypothesis, ongoing changes in climate are expected to affect habitat suitability and hence species' fitness. In trees, differences in fitness may manifest as changes in growth rates, which will alter carbon uptake. Using tree-ring data, we calculated > 1.5 million annual stem growth rate estimates (standardized for tree size) for 15 677 trees representing 37 species from 558 populations throughout eastern North America. We used collections data and species distribution models to estimate each population's climatic suitability from 1900 to 2010. We then assessed the relationships between growth, suitability and time using linear mixed-effects models. We found that stem growth rates decreased significantly through time independent of changes in climate suitability and that relationships between growth rates and climate suitability were highly variable across species. Contrary to expectations, we found that growth rates were negatively correlated with species' climate suitability, a relationship that was consistent over time for gymnosperms and became more negative through time for angiosperms. These results may suggest that stem growth rates are not a good proxy for fitness and/or that unidentified factors may be slowing tree growth and outweighing any potential benefits of climate change and increasing atmospheric CO_2 concentrations. Regardless of the cause, this finding indicates that we should not count on the increased growth of eastern North American trees to help offset anthropogenic carbon emissions.

Keywords: CO_2 fertilization, dendrochronology, fitness-suitability hypothesis, species distribution models, suitability changes, tree growth rates, tree rings

Introduction

It has long been recognized that differences in environmental conditions determine habitat suitability and affect the performance of species, populations and individuals. This 'fitness-suitability' hypothesis (Liebig 1840, Shelford 1911) is a foundation of niche theory (Chase and Leibold 2003), underpins species distribution modeling

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(Guisan and Zimmermann 2000), and is integral to our understanding and predictions of how species will respond to climate change (Hamann and Aitken 2013).

Based on the 'fitness-suitability' hypothesis, changes in climate are expected to cause changes in habitat suitability for species and, therefore, affect species' fitness (Liebhold et al. 2004). This effect may manifest as altered species' growth rates (Purves 2009, Hubau et al. 2020), abundances (Iverson and Prasad 1998, Sporbert et al. 2020), distributions (Feeley et al. 2020, Margalef-Marrase et al. 2020), mortality (Druckenbrod et al. 2019) and/or reproduction (Hacket-Pain et al. 2018). In some cases, the impacts of these changes will be negative for a species (for example, if climate change causes reductions in habitat suitability this may lead to slower growth, decreased competitive ability and lower reproductive success), increasing the risk of extinction and potentially impeding ecosystem services. However, the opposite effect is also possible as climate change can increase suitability for some populations or species, with positive effects on fitness, performance and the provisioning of ecosystem services (Shestakova et al. 2015). For example, increased temperatures has led to greater tree growth and the 'greening' of some high latitude systems (Berner et al. 2020).

The effects of climate change on forests, and their constituent tree species, are of great interest given the importance of forests in the global carbon cycle and the many ecosystem services that they provide (IPCC 2021). One of the multiple ways that trees can respond to climate-driven changes in habitat suitability is through changes in their growth rates. Indeed, it is commonly hypothesized that rising temperatures and increasing atmospheric concentrations of CO_2 (i.e. $[CO_2]$) could lead to faster tree growth and increase the rate that forests uptake and store carbon, thereby creating a large net carbon sink that will help to offset anthropogenic greenhouse gas emissions (Shestakova et al. 2015). Accordingly, previous studies have posited that accelerated tree growth is responsible for much of the 'missing carbon sink' and plays a critical role in slowing climate change (Schindler 1999, Pan et al. 2011).

However, the idea that tree growth is accelerating due to warming temperatures and increasing atmospheric $[CO_2]$ remains controversial (Walker et al. 2021). Körner (2003) argued that the primary cause of faster tree growth is not carbon fertilization, but rather that purported increases in tree growth reflect the influence of measurement errors, successional dynamics, and/or idiosyncrasies (e.g. disturbances or local conditions). Indeed, several studies have shown that tree growth rates are stable or decreasing through time at the population or community level (Feeley et al. 2007, Clark et al. 2010, Gómez-Guerrero et al. 2013, Giguère-Croteau et al. 2019), and even when analyzing species at different locations along environmental gradients (Silva et al. 2010, Girardin et al. 2016, Girardin et al. 2022). A possible explanation for these conflicting results (i.e. some studies showing accelerating tree growth versus others showing decelerating growth) is the fact that studies are generally conducted at only a few sites and thus do not capture the full variability of growth responses that may be occurring across species' ranges. According to the 'fitness-suitability' hypothesis, we should expect that individuals/populations growing in areas where conditions are becoming more suitable through time should accelerate their growth while individuals/populations in areas where conditions are becoming less suitable through time should decelerate their growth. For example, tree populations in the hotter portions of a species' distribution may suffer from rising temperatures and exhibit decreasing growth, while populations of the same species in the colder portions of their distribution may benefit from rising temperatures and exhibit accelerating growth (Reich et al. 2015, Crous 2019) depending on the effects of biotic interactions (Paquette and Hargreaves 2021). In other words, if studies only examine a select subset of populations, then they are likely to find different results depending on where the study populations fall in the species' range and how suitability is changing for those specific populations. Likewise, since relative habitat suitability varies between species, individual sites will likely contain mixes of species in which growth is increasing and species in which growth is decreasing. Previous studies of tree growth rates have generally not accounted for the fact that tree populations are predicted to have different responses to warming based on the changes in habitat suitability where the sampling occurs, making it difficult to generalize or compare results between studies.

Furthermore, we expect that the effects of climate change on tree growth rates will differ based on phylogeny. Specifically, we expect that trees in the phylum Anthophyta (i.e. Angiosperms) may have different growth responses versus trees in the phylum Coniferophyta (i.e. Gymnosperms) because of differences in their life histories, methods of reproduction and wood anatomy. For example, angiosperms generally have longer and wider vessels that allow for more efficient water transport and better resistance to cavitation in comparison to gymnosperm's tracheids (Sperry et al. 2006, Chave et al. 2009), allowing them to outcompete conifers in many climates and habitats (Bond 1989).

Here, we leveraged a public database of over one million tree-ring measurements on 15 677 individual trees and 37 species to examine long-term and large-scale stem growth patterns measured at > 500 sites throughout eastern North America. Specifically, we aimed to answer four questions: Q1. Are spatial patterns of tree growth rates in eastern North America related to differences in climate suitability? Q2. Have tree growth rates changed through time (1900–2010)? Q3. Are these changes in growth rates through time due to changes in climate suitability? and Q4. Do these growth-suitability relationships differ between angiosperms and gymnosperms? Our a priori hypotheses were that tree growth rates would be positively associated with climate suitability through both space and time (in other words, tree populations located in areas with high climatic suitability should have faster stem diameter growth rates than tree populations located in areas with low climatic suitability (Liebig 1840, Shelford 1911, Chase and Leibold 2003) and changes in tree growth rates over the past century should be positively

correlated with species- and site-specific changes in relative suitability, with potential differences between angiosperms and gymnosperms. We focused our analyses on tree stem diameter growth rates because, to our knowledge, it is the only proxy for tree health and fitness that can be estimated through time at high resolution using present-day measurements. In addition, stem growth is directly related to the amount of carbon stored in trees and thus the ability of forests to act as carbon sinks.

Material and methods

Study area

We constrained our study to eastern North America (i.e. between 23 and 60° North latitude and between 50 and 100° West longitude). This area includes a large range of climate conditions due to the 37° latitudinal gradient that is encompassed, as well as differences in elevation (from sea level to approximately 1800 m a.s.l.), topography and distance to the coast.

Tree growth and study species

We used the International Tree Ring Data Bank (ITRDB) to calculate annual stem growth rates of trees in eastern North America between 1900 and 2010. The ITRDB is a collated and public database of tree-ring measurements that has proven utility for investigating long-term tree growth patterns (Klesse et al. 2018, Pearl et al. 2020, Stahle et al. 2020) and has a particularly strong representation in our selected study area (Zhao et al. 2018). We first downloaded all available tree-ring width (TRW) data available for the study area via the NOAA repositories (<www.ncdc.noaa.gov/paleo-search/>; accessed March 2018). We cleaned and filtered the ITRDB by screening for and removing outliers such as individuals not identified to the species level, individuals of species with distributional ranges only partially overlapping with our study area (e.g. *Pinus balfourniana*) or species known to be affected by invasive pests or diseases (e.g. *Castanea dentata*), and standardizing units of measurement and standardizing species names using the taxonomic name resolution service (TNRS) (Boyle et al. 2013). We further subset the database to include only trees with DBH (diameter at breast height) ≥ 10 cm and sites with ≥ 100 tree rings per species (for example, if a given site had two 50-year-old trees this site was included) to ensure enough replicates within species and locations. Moreover, we constrained our analysis to include only rings formed after 1750 CE to reduce possible errors associated with older measurements and due to reduced sampling densities of very old trees. Finally, we included only tree species with suitable data from multiple sites. After cleaning the database, we retained 1 816 177 ring width measurements from 15 677 individuals of 37 species in 558 sites (Supporting information).

We transformed the TRW data to basal area increment (BAI) ($mm^2\ year^{-1}$) because this metric better accounts for the genetic potential for growth, bole geometry, aging, site conditions and history (Fritts 1976) using the formula:

$$\mathrm{BAI} = \pi \times \left(\frac{\mathrm{DBH}_t}{2} - \frac{\mathrm{DBH}_{t-1}}{2} \right)^2 \quad (1)$$

where DBH is diameter at breast height and t is the year of the tree-ring formation. To estimate DBH, we assumed that the TRW was uniform in a circular cross-section of the tree (Peters et al. 2015) and that the oldest record in the sample corresponded to the tree pith (such that the tree radius at the start of any year is the sum of all older ring widths).

Given that tree growth inherently varies due to ontogeny, size, and/or other associated factors (such as competition for light and resources), we transformed BAI into a size-standardized metric of annual tree growth rate for subsequent analyses. For each combination of species and site (hereafter population), we fit a smoothing spline to the observed relationship between log(BAI) and the basal area (BA) at year of ring formation (Fig. 1B; Supporting information). This fitted curve indicates the expected annual growth for trees of each size in each population (Biondi and Qeadan 2008). The standardized growth of each tree in each year was then calculated as the difference between the observed and the expected growth predicted for its size:

$$\text{standardized growth rate} = \log\left(\text{observed BAI}\right) - \log\left(\text{predicted BAI}\right) \quad (2)$$

This standardized growth metric is unitless and indicates the deviation in observed growth versus expected or average growth of equal-sized conspecific trees growing in the same site. This regional curve standardization (RCS) is a common approach used to detect and characterize growth trends independent of tree size and has high sensitivity and reliability. That said, RCS may have low detection power for larger diameter trees (Peters et al. 2015) and is sensitive to some parameters used to fit the curve within the spline smoothing function, such as percentage of variance retained, and the length of window analyzed, that might affect the quantity of signal retained for the analysis (Cook and Peters 1981). In our analyses, we employed different smoothing parameters and selected the parameter value that resulted in relatively smooth growth versus size relationships (smoothing parameter = 1.2), thereby allowing for greater attribution of variation in growth to non-ontogenetic or size related factors such as differences in climate suitability over time.

Finally, to allow for comparisons with historical climate records (below) and to minimize temporal autocorrelations, we averaged the standardized growth rates in each population in overlapping 30-year periods from 1900 to 2010 at 5-year intervals (e.g. 1900–1930, 1905–1935, 1910–1940, …, 1995–2010) (Fig. 1C). The above analyses were performed using the package 'dplR' in R (Bunn 2008).

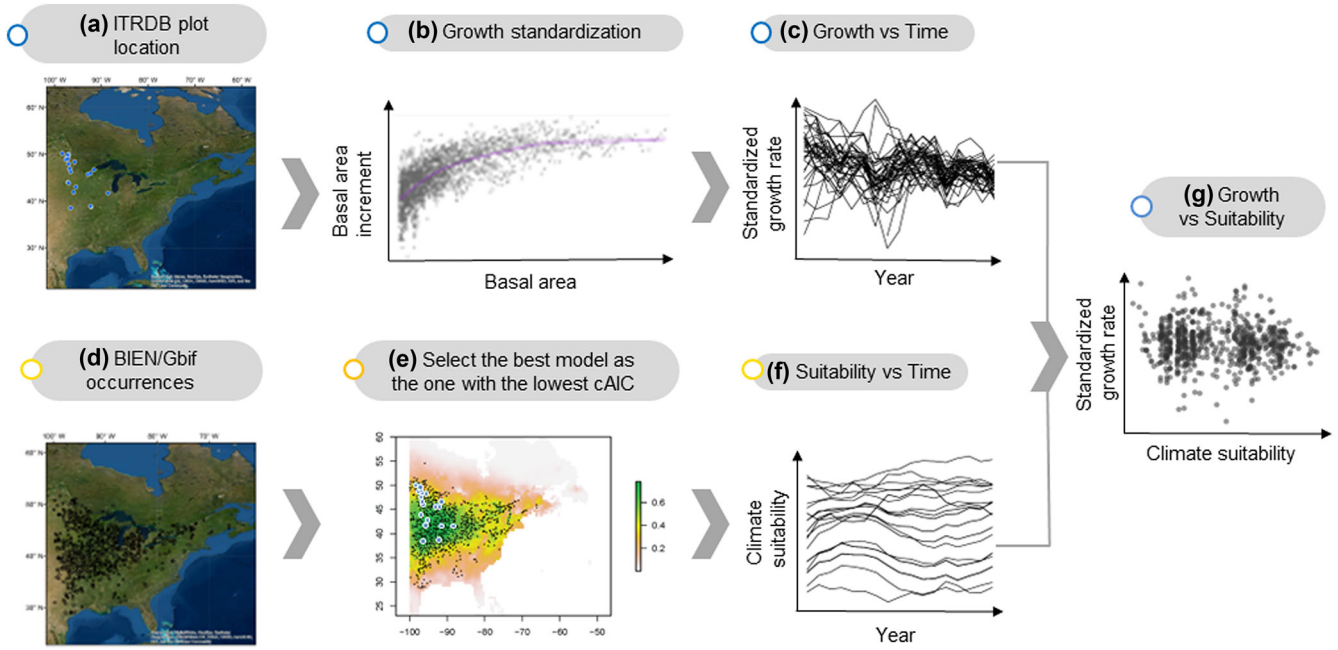


Figure 1. Conceptual diagram of the methods used to estimate the standardized annual growth rates (a–c) and relative climate suitability (d–f) for each individual tree and population (specific case shown for *Quercus macrocarpa*). (a) We obtained all available tree-ring width data for eastern North America from the ITRDB via the NOAA repositories. (b) To standardize tree growth rates, we transformed ring width to basal area increments and employed a regional curve standardization (RCS) approach. We calculated the annual log (BAI) for each individual and fit a smoothing spline function to the observed relationship to generate size specific expected growth rates within each population. (c) We then estimated the standardized growth rate of each tree in each year by calculating the difference of the observed and predicted (expected) rates. Finally, we calculated the mean standardized growth of each population in overlapping 30-year time periods 1900–2010 at 5-year increments. (d) To characterize changes in relative climate suitability for each population through time, we downloaded BIEN/GBIF occurrences. (e) We fit multiple models with different combinations of 1900–1930 climate predictors and selected the best model as the one with the lowest cAIC. (f) We then projected the selected SDM onto climate rasters for each of the 30-year time periods and extracted the 'probability of occurrence' at each site as a metric of relative climatic suitability for each population in each period. (G) Finally, we tested for relationships between the standardized growth rates and the relative climate suitability across time using mixed-effects models to account for species and site-level variability.

Climate suitability

To calculate time- and site-specific estimates of relative climate suitability for each of the 37 study species, we modeled the climatic niches of each species based on an independent dataset of collection and observation records from our study area. We downloaded all available occurrence records for our study species (> 5 million total occurrences) through the Botanical Information and Ecology Network (BIEN; accessed in July 2020) via the 'BIEN' package in R (Maitner et al. 2018) and from the Global Biodiversity and Information Facility (GBIF; accessed July 2020) filtering for georeferenced occurrences in North America without known geospatial issues e.g. large errors or suspicious coordinates. We removed records from outside the study region (i.e. 23–60° North and 50–100° West) and retained a maximum of one record per species per 30 arcminute raster cell to help control for spatial autocorrelation and spatial sampling biases. The resultant dataset consisted of 26 056 occurrences for the 37 study species, and all species had more than 200 occurrences (Fig. 1D; Supporting information). For each of these occurrence locations we extracted a set of 19 bioclimatic variables from the CRUCLIM 30-year average bioclimate time series with 30 arcminute resolution (Harris et al. 2014, Univ. of East Anglia 2015), which provides historic climatic data averaged for 30-year periods centered on the years 1915–1995 at 5-year intervals (e.g. 1900–1930, 1905–1935, 1910–1940, …, 1995–2010).

Using a combination of the occurrences and climate raster maps, we fit species distribution models (SDMs) for each species using the MaxEnt algorithm (Elith et al. 2011, Hao et al. 2020), the 'MIAmaxent' (Vollering et al. 2019), 'rjava' (Urbanek 2020) and 'rmaxnet' R packages (Baumgartner and Wilson 2021). For each species, we performed a forward stepwise model selection. Because the ordering of variables can matter in stepwise regression (Smith 2018), we ordered our climatic variables based on previous assessments about their relative importance in determining performance, fitness and distributions of trees at continental scales (Gentry 1988, Ter Steege et al. 2006, Kreft and Jetz 2007): annual mean temperature, annual precipitation, temperature seasonality, precipitation seasonality, mean diurnal range, max temperature of warmest month, min temperature of coldest month, precipitation of

wettest month, precipitation of driest month, isothermality, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter. We also included linearly transformed versions of the explanatory variables (i.e. derived variables) by rescaling each climatic variable to the range [0, 1] and by transforming each environmental variable around an optimum value that is found by looking at the frequency of presence (Vollering et al. 2019). Next, we selected the most parsimonious sets of explanatory variables (i.e. climatic variables) and derived variables (i.e. transformed climatic variables) retaining variables and first-order interactions with p-values ≤ 0.001. To build our SDMs, we used 10 000 random background points from within the geographic extent of the study area to act as pseudo-absences for each species. We randomly selected 5 subsets with 75% of each species' occurrences to train the model and used the remaining 25% for model testing. The predictors in our SDMs were the 1900–1930 climate variables, and we chose the 'best' model for each species as the one with the lowest cAIC (Warren and Seifert 2011). Subsequently, we re-estimated the model parameters using 100% of the occurrences. Lastly, we restricted the results to the range of the study area (Phillips et al. 2006) and rescaled them based on the projection data extent to calculate a 'raw' output that we converted to a logistic output ranging from zero to one (Fig. 1E). The most frequent climatic variables retained by the stepwise process to build the final SDMs were annual mean temperature, maximum temperature of the warmest month, mean temperature of the warmest quarter, annual precipitation and precipitation of the warmest quarter (Supporting information).

Finally, for each of the 37 species-specific SDMs that we created based on the 1900–1930 climate, we projected the selected SDM onto the raster of climate variables for each subsequent 30-year time period and extracted the 'probability of occurrence' at each of the ITRDB sites as a metric of relative climatic suitability for each species at each location in each period (Fig. 1F).

Relationship between changes in climate suitability and changes in tree growth rates

We used linear mixed-effects models (LMMs) to assess the relationship between the standardized tree growth metrics and estimates of relative climate suitability. To answer our research questions, we fit different LMMs in which we modeled tree growth as a function of climate suitability (Q1); time (i.e. year) (Q2); climate suitability, time and their interaction (Q3); and phylum, climate suitability, time and their interactions (Q4) as fixed effects (Table 1). We included nested random intercepts and slopes for the fixed effects varying among species. To answer Q1, we fit three mixed-effects models with different random structures to retain different sources of variability. Model 1 (M1) tests variability across space, model 2 (M2) tests variability across time and model 3 (M3) tests variability across space and time. To answer Q3 and Q4, we included the interaction between climate suitability and time as a fixed effect in order to test for the relationship between growth and suitability while allowing for possible changes in this relationship through time due to the effects of non-climatic factors (e.g. increasing atmospheric [CO_2]) or potential size/age-related biases in growth estimates (M5) (Peters et al. 2015). To answer Q4, we additionally tested for the interacting role of phylum (i.e. Anthophyta [Angiosperms] versus Coniferophyta [Gymnosperms]) with time (year) and relative climate suitability in explaining the standardized tree growth rates (M6).

We quantified the proportion of variance explained by the models based on the marginal R^2 (for the fixed effects) and the conditional R^2 (for the fixed and random effects combined) using the 'MuMIn' R package (Nakagawa and Schielzeth 2013, Bartoń 2020). Models were fit using the R package 'lme4' (Bates et al. 2015). All the analyses were performed in R ver. 4.0.5 (<www.r-project.org>).

Results

Standardized tree growth rates were not significantly related to relative climate suitability during the study period across either space (model 1; Supporting information), time (model 2; Supporting information), space and time together (model

Table 1. Relationships assessed between standardized tree growth rates (G) and relative climate suitability (S) using linear mixed-effects models accounting for multiple sources of variability: species, site and time.

Question	Model	Response variable	Fixed effects	Random effects (intercepts and slopes)	Lmer R notation
Q1	M1	G	S	Species/time (nested)	G ~ S (1 + S| species/time)
	M2	G	S	Species/site (nested)	G ~ S + (1 + S| species/site)
	M3	G	S	Species	G ~ S + (1 + S| species)
Q2	M4	G	Time	Species	G ~ T + (1 + T| species)
Q3	M5	G	S + Time + S*Time	Species/site (nested)	G ~ S*T + (1 + S| species/site)
Q4	M6	G	S + Time + Phylum + S*Time + Time*Phylum + S*Phylum + S*Time*Phylum	Species/site (nested)	G ~ S*T*Phylum + (1 + S| species/site)

3; Supporting information), or when analyzed considering a possible interaction between climate suitability and time (model 5; Supporting information). Nonetheless, standardized growth rates declined significantly over time ($p < 0.0042$; model 4, R^2 marginal = 3.68%, R^2 conditional = 42.17%; Supporting information), a pattern that was maintained even when climate suitability was included as an interacting factor with time (Fig. 2a; model 5; R^2 marginal = 3.13%, R^2 conditional = 32.24%; p = 3.24e-08; Supporting information).

The relationship between tree growth and climate suitability through time depended on phylum (model 6, R^2 marginal = 4.10%, R^2 conditional = 32.2%; Fig. 2b, Supporting information). For gymnosperm species (phylum Coniferophyta), the relationship between tree growth and suitability was consistently negative over time. In contrast, for angiosperms (phylum Anthophyta), there was no relationship between tree growth and suitability at the beginning of the study period (i.e. ~1900–1940), but it became strongly negative in later time periods (i.e. ~1970–2010) (Fig. 3; Supporting information). Climate suitability alone did not change significantly over time ($p > 0.05$, Supporting information).

All the relationships that we evaluated were highly variable across species (Fig. 4, Supporting information). Ten out of the 37 species significantly diverged from the average growth–suitability relationship tested in the model including phylum (model 6). One angiosperm (*Fraxinus nigra*) and two gymnosperms (*Pinus banksiana* and *Taxodium distichum*) had significantly negative relationships between growth and climate suitability, whereas four angiosperms (*Quercus alba*, *Q. michauxii*, *Q. stellata* and *Fagus grandifolia*) and three gymnosperms (*Picea glauca*, *P. rubens* and *Pinus resinosa*) had significantly positive relationships between growth and climate suitability (Fig. 4).

Discussion

Contrary to our a priori expectations based on the 'fitness-suitability' hypothesis, we did not find a significant positive relationship between the estimates of climate suitability and tree diameter growth rates (and hence presumably fitness) in eastern North America between 1900 and 2010. We instead found a negative relationship between tree growth and suitability that has been consistent over time for gymnosperms and tended to strengthen through time for angiosperms. However, even within the two phyla, growth–suitability relationships were highly variable among species supporting previous findings on the variability of species' responses to environmental variables (Girardin et al. 2022).

Both angiosperms and gymnosperms have species with negative (i.e. *Fraxinus nigra*, *Taxodium distichum* and *Pinus banksiana*) and species with positive relationships between growth and climate suitability (i.e. *Fagus grandifolia*, *Quercus alba*, *Quercus michauxii*, *Quercus stellata*, *Pinus resinosa*, *Picea glauca* and *Picea rubens*). Differences among species are likely attributable to their different life histories (i.e. occupying different positions in the fast–slow growth spectrum), different reproductive strategies, different growth forms (i.e. megaphanerophyte, mesophanerophyte, nanophanerophyte) (Salguero-Gómez et al. 2016), and contrasting wood anatomies and trait syndromes (Carnicer et al. 2013). Some of these differences may be more evident between phyla. For example, Angiosperms have longer and wider vessels that allow them to transport water at higher rates than gymnosperm's tracheids, which are more primitive cell types. But prioritizing water transport over hydraulic safety makes gymnosperms more vulnerable to cavitation (Sperry et al. 2006, Chave et al. 2009). As a result of their innovations in hydraulic transport and vascular capacities, angiosperms outcompete conifers under many modern climate conditions (Bond 1989, Zhang et al. 2017). Nonetheless, our results show that during the last decades (1970–2010) tree species in both phyla have experienced decreases in growth probably as a consequence of climate change – i.e. temperature increases and variations in precipitation regimes (Soh et al. 2019).

A possible explanation for the observed decreases in stem growth rates for many species, despite increases in estimates of climatic suitability, is that changes in other climatic and/

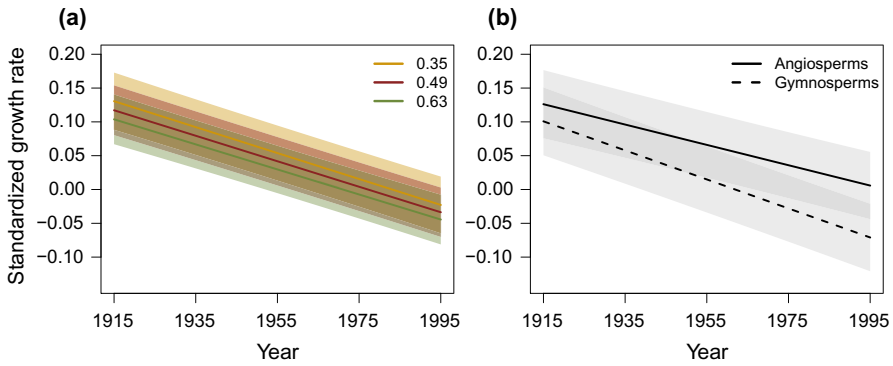


Figure 2. Standardized growth rates of trees in eastern North America were negatively related to time even after accounting for changes in relative climate suitability over the 110-year study period (a). The decrease in tree growth rates over time was more negative for gymnosperms (phylum Coniferophyta, dashed line) than for angiosperms (phylum Anthophyta, solid line) (b). Solid lines show the prediction from models 4 and 6 in (a) and (b), respectively. Different color lines in (a) illustrate three different climate suitability quantiles and their associated changes in growth over time. Shaded areas show the 95% CI.

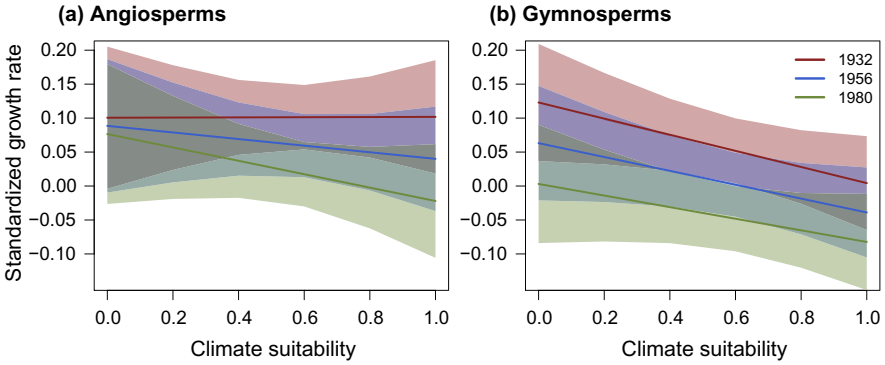


Figure 3. Standardized tree growth rates in eastern North America were more negatively related to climate suitability and time for gymnosperms (a) (phylum Coniferophyta) than for angiosperms (b) (phylum Anthophyta). Solid lines show the predictions from model 6. Different color lines illustrate the predicted growth for three time periods. Shaded areas show the 95% CI.

or environmental factors that we did not include in our study (e.g. evapotranspiration, precipitation frequency, drought length, freeze frequency, etc.) had negative effects that outweighed any potential benefits from the climatic variables that we did include in our SDMs (Anderson-Teixeira et al. 2021). Likewise, there might be different mechanisms involved in controlling tree growth rates; for example, Belmecheri et al. (2021) showed that recent precipitation increases in eastern North America have modified the CO_2 effect on intrinsic water use efficiency of temperate forests and therefore weaken the ability of trees to uptake and store carbon. It is also possible that stem growth is not indicative of overall tree fitness and that other metrics of fitness (reproduction, tree height or canopy size, root growth, etc.) show conflicting patterns with stem growth. Unfortunately, the data are not available to retroactively estimate these other components of tree fitness.

Independent of changes in relative climate suitability, there were widespread decreases in tree growth rates through time, but with species-level differences. We hypothesize that the observed slowing of tree growth rates over time is due at least in part to increasing competition and stand density in the eastern North American forests, especially in the last two decades as suggested by Woodall and Weiskittel (2021). Furthermore, many tree species in eastern North America have suffered from pests and pathogens during the 20th century (Cavender-Bares et al. 2019). For example, *Castanea dentata* was a major component of the eastern US forests before being decimated by chestnut blight, a bark fungal disease (Wang et al. 2013). We excluded *C. dentata* but retained several other species that may have been impacted by pest and pathogens, such as *Pinus banksiana*, *Pinus resinosa*, *Pinus taeda*, *Pinus strobus*, *Picea mariana*, *Fraxinus nigra*, *Larix laricina*, *Fagus grandifolia*, *Populus grandidentata*, *Quercus alba*, *Q. coccinea* and *Tsuga canadensis* among others (Cavender-Bares et al. 2019). When we analyzed our species-specific growth trends over time (Supporting information), we only observed abrupt decreases of growth (> 1 SD) in 8 out of 37 species (i.e. *Fagus grandifolia*, *Picea mariana*, *Picea rubens*, *Pinus echinata*, *Pinus strobus*, *Quercus coccinea*, *Taxodium distichum*, *Tsuga canadensis*) that might reflect new pests or pathogens impacting growth rates. However, growth declines were not synchronous between species or sites given the geographic extent of our data set. We did not expect the effects of the pathogens to be synchronous, but rather to have spread across the region over time, making the effects clearly asynchronous but more frequent, which in the long run will affect growth rates, so we cannot confidently attribute the growth decreases to these specific drivers.

While our results were contrary to our initial expectations, they were consistent with the findings of some previous studies assessing changes in tree growth rates in northern temperate and boreal forests (Silva et al. 2010, Girardin et al. 2016, Zambrano et al. 2017, Giguère-Croteau et al. 2019, Shestakova et al. 2019, Anderson-Teixeira et al. 2021). For instance, Zambrano et al. (2017) compared suitabilities from SDMs with growth rates from the FIA inventories for a 14 year period. Considering crowding index, they found a significant interaction between local competition and regional climatic suitability to be driving growth rate changes. Similarly, Shestakova et al. (2019) assessed growth rate synchronicity from boreal Eurasian forests from 1911 to 2013 and found a decreasing trend in the spatial synchrony of tree growth over the 20th century around the Ural Mountains, supporting different growth responses within and between species and indicating more divergent growth patterns with warming.

We recognize limitations in our analyses. For instance, there are several biases that are inherent in tree-ring measurements, some of which may have been exacerbated by using data from the ITRDB, which is collated from various studies and often lacks detailed metadata (Zhao et al. 2018). Dendrochronological sampling is typically biased towards large old trees (to maximize the length of the growth record) and individuals growing on the extremes of their distributions (to maximize the strength of the climate signal on growth), and generally excludes trees that die before sampling (although samples are sometimes collected from dead trees or stumps). To help minimize the effects of 'big-tree selection', 'marginal site selection' and 'slower grower survivorship' biases, we employed the RCS approach to calculate changes in the relative basal area growth rates of our 37 study species

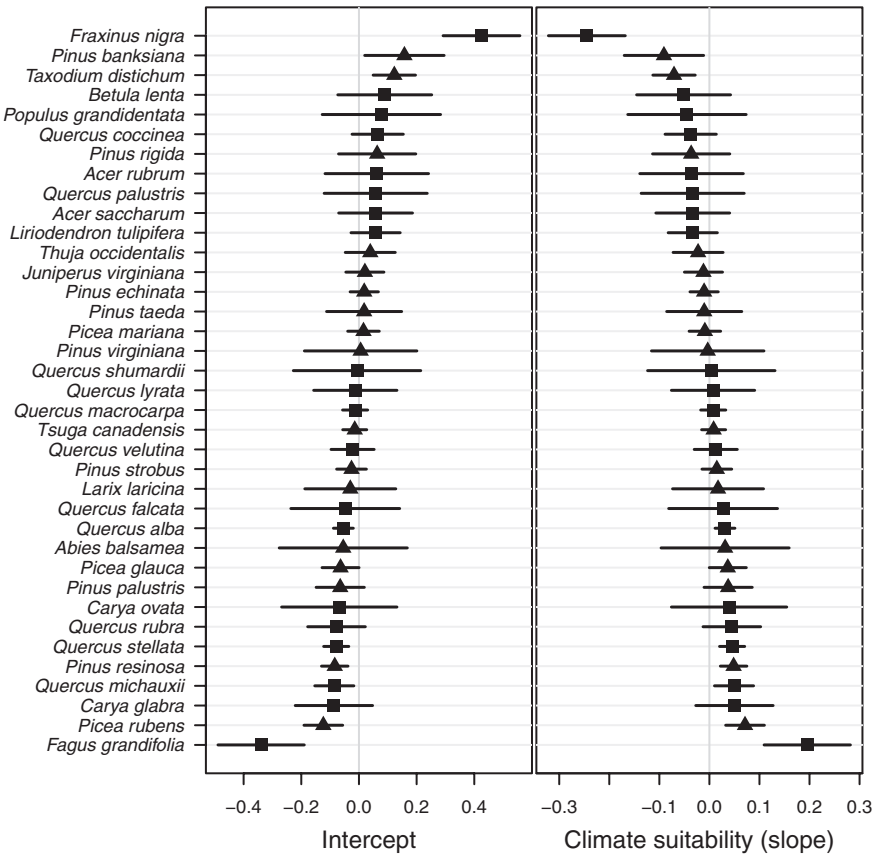


Figure 4. Relationships between standardized growth rates and climate suitability in eastern North America were highly variable across species. Species random intercepts and slopes for the model of standardized tree growth vs. relative climate suitability including time and phylum as interacting effects (Model 6).

across eastern North America and over a period of > 100 years. In fact, the age distribution of the trees included in our analyses were, on average, positively skewed (mean skewness = 0.53, median skewness = 0.54) across species, meaning that our results should not have been affected by the 'big-tree selection' bias (Supporting information). However, if biases continued to influence growth estimates even after RCS (Brienen et al. 2006, Bowman et al. 2013, Nehrbass-Ahles et al. 2014, Peters et al. 2015), they would be expected to cause increases in the apparent growth rates of trees over time, meaning that the rate of decreasing growth rate over time may actually be faster than what we observed.

Another potential limitation is that the SDMs that we used to estimate climate suitability may not be suitable for modeling species fitness or performance (McGill 2012) since our SDMs were based simply on the observed occurrences of species. In fact, the main sources of variability for suitability and growth were different: the highest proportion of variance for suitability is at the plot, genus and species levels, whereas growth variance was mostly concentrated at the year and family levels (Supporting information). Midolo et al. (2021) found that predicted suitabilities from SDM and species fitness relationships are rare (although they only evaluated spatial variation and they did not assess temporal variation), and van der Maaten et al. (2017) found that predictions of SDMs were related to temporal growth variation but not to spatial growth variation. Furthermore, we recognize some limitations specific to our SDM and suitability calculations. The spatial scale of the CRU TS3.10 climatic data that we used for building the SDMs is relatively coarse (e.g. 30 ArcMin, or 51.1 km at 23°N and 27.7 km at 60°N). However, it is one of the only climatic datasets that provide sufficient information to calculate bioclimatic variables over the entire 20th century (Harris et al. 2014, Univ. of East Anglia 2015). Likewise, the climate data we used did not include several climate variables which could have influenced suitability and growth – for example, the maximum or minimum temperatures of specific months, relative humidity or vapor pressure deficit. That said, the use of multiple occurrence datasets, the large number of occurrences used for each species, and the settings applied to build the SDM (e.g. limit the number of occurrences to one per pixel, five-fold cross-validation and forward model selection, etc.), all increase our confidence that the SDMs should accurately characterize changes in relative climate suitability through time.

Finally, habitat suitability and growth might be affected by other, non-climatic, environmental variables or events such as fires (Pellegrini et al. 2021), floods (Schongart et al. 2002, Jiménez Giraldo and del Valle 2011), hurricanes (Trouet et al. 2016), changes in soil nutrient concentration (e.g. due to

pollution or nitrogen deposition) (Eastman et al. 2021), forest succession (Bräuning et al. 2008, Brienen et al. 2009), and/or competition within and between species (Rozendaal et al. 2020), especially with invasive species (Grossiord et al. 2020). Additionally, the climate sensitivity of trees can be influenced by small-scale landscape features, such as topography or stand structure (Pederson et al. 2020, Zuleta et al. 2020), which were not included in our model. Stem growth rates can also be affected by changes in carbon allocation to other plant tissues or processes (e.g. root growth, leaf defense and/or reproduction) (Friedlingstein et al. 1999). Future studies looking at individual species can include more detailed ecological information about additional variables that may be affecting stem growth rates as well as more trees growing throughout the species' full distributional ranges to minimize any marginal site selection bias present in the ITRDB.

Despite these limitations (which are for the most part unavoidable when working with large complex datasets at continental and multi-decadal scales), our results provide strong evidence that tree stem growth rates in eastern North America are decreasing through time, but with large differences between phyla and species. Decreasing tree growth rates through time is contrary to the anticipated benefits of warming and increasing atmospheric [CO_2] (from approximately 300 parts per million in 1900 to 390 ppm in 2010 (IPCC 2021)). These results suggest that we cannot rely on an accelerated growth of trees in temperate forests to increase the rate of carbon sequestration in these ecosystems, even in populations where 'carbon fertilization' and climate change is expected to have positive effects (Büntgen et al. 2019). Decreases in tree growth may likewise have detrimental effects on other ecosystem services such as the provisioning of timber and climate regulation. Indeed, widespread decreases in tree growth may imply a weakening or 'saturation' of the terrestrial carbon sink, which can feedback to accelerate global warming. These results highlight the potential negative effects of climate change on North American forests, as well as the need for additional data on tree growth and fitness for more species and regions.

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Author contributions

Manuel Bernal-Escobar: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Daniel Zuleta**: Formal analysis (equal); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Kenneth J. Feeley**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

This article is entirely based on published data that are available for free and public download; no new data was used in this study. Tree-ring width data are available from the NOAA repositories (<www.ncdc.noEcolaa.gov/paleo-search/>). Occurence records are available from the Botanical Information and Ecology Network (BIEN) through the 'BIEN' package in R (Maitner et al. 2018), and from the Global Biodiversity and Information Facility (GBIF, dataset downloaded 27 May, <https://doi.org/10.15468/dl.wcej3s>). Climatic data are available from CRUCLIM, <http://dx.doi.org/10.4225/28/570DDDE168124> (Storlie 2016). Code is available from the GitHub Repository: <https://github.com/DanielZuleta/climate-suitability-tree-growth> (Zuleta 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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