

PRIMARY RESEARCH ARTICLE

Global fading of the temperature–growth coupling at alpine and polar treelines

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Abstract

Climate warming is expected to positively alter upward and poleward treelines which are controlled by low temperature and a short growing season. Despite the importance of treelines as a bioassay of climate change, a global field assessment and posterior

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forecasting of tree growth at annual scales is lacking. Using annually resolved tree-ring data located across Eurasia and the Americas, we quantified and modeled the relationship between temperature and radial growth at treeline during the 20th century. We then tested whether this temperature–growth association will remain stable during the 21st century using a forward model under two climate scenarios (RCP 4.5 and 8.5). During the 20th century, growth enhancements were common in most sites, and temperature and growth showed positive trends. Interestingly, the relationship between temperature and growth trends was contingent on tree age suggesting biogeographic patterns in treeline growth are contingent on local factors besides climate warming. Simulations forecast temperature–growth decoupling during the 21st century. The growing season at treeline is projected to lengthen and growth rates would increase and become less dependent on temperature rise. These forecasts illustrate how growth may decouple from climate warming in cold regions and near the margins of tree existence. Such projected temperature–growth decoupling could impact ecosystem processes in mountain and polar biomes, with feedbacks on climate warming.

KEYWORDS

climate warming, forest limit, growth model, mountain ecosystems, tree rings

1 | INTRODUCTION

Mountain treelines are considered receptive monitors of the effects of climate warming on terrestrial ecosystems (Harsch et al., 2009; Holtmeier & Broll, 2005; Körner, 2012; Smith et al., 2009). Global average surface air temperature has increased by +0.8°C since 1900, but climate warming intensified since the 1980s at historically unprecedented rates, and this positive temperature trend is forecasted to continue and exacerbate during the 21st century (IPCC, 2014). Rapid climate warming along with the increase in atmospheric CO₂ concentration has translated into acceleration of tree growth at many altitudinal and latitudinal treelines worldwide (Devi et al., 2008; Liang et al., 2011; 2014; Trembl & Veblen, 2017). At such range-edge tree populations, radial growth is a more sensitive and close tracking cue of the interannual temperature variation than changes in treeline position, which shows lagged or nonlinear responses to climate warming due to demographic processes (Batllori & Gutiérrez, 2008; Camarero & Gutiérrez, 2004; Daniels & Veblen, 2004; Fajardo & McIntire, 2012).

Warming-triggered growth enhancement at treeline is expected to result in tighter coupling of tree meristems to air temperature as trees get taller (Körner, 2012). The enhanced growth and the relaxation of cold-temperature limitations will lead to enhanced reproduction, tree establishment, and, potentially, could induce long-term treeline shifts (Camarero et al., 2017; Harsch et al., 2009; Wiegand et al., 2006). Such treeline advance into treeless ecosystems could create new and different communities from those found near the forest limit. Forest expansion would affect carbon storage, nutrient cycling, and hydrological properties in mountains and boreal biomes, with significant feedbacks on climate warming

and human populations which depend on mountain water resources (Greenwood & Jump, 2014). If growth rates of treeline trees will be monotonically and tightly coupled to current and forecasted climate warming, treeline advance could be widespread and accelerated in the coming decades. This forest expansion could have large impacts on community assemblage and ecosystem functions. However, to properly project treeline shifts and dynamics, we need a sound global assessment and prediction of tree growth at treelines.

Although during the 20th century tree growth has positively responded to rising temperatures in most treeline sites (Salzer et al., 2009; Wilmking et al., 2004), recent investigations in these heat-limited environments have detected weak or even negative associations between growth and temperature due to nongrowing season conditions (Fajardo et al., 2019; Hofgaard et al., 2019; Piper et al., 2016). In addition, there is the divergence problem which describes a loss of responsiveness of tree growth to rising growing season temperatures in subarctic regions after the 1960s (Briffa et al., 1998). The low-frequency component of photosynthetic solar radiation has also been shown to explain part of the divergence problem in subarctic regions where tree growth is mainly driven by summer temperature (Kirilyanov et al., 2020). Such complex growth responses to temperature rise may depend on local climate conditions, treeline features (e.g., shape, size), and age structure or species-specific traits, making some treelines less valuable monitors of climate warming than expected (Davis et al., 2020). Moreover, if growth at the treeline is not primarily driven by regional or global changes in temperature, other local factors such as biotic interactions (competition, facilitation, or herbivorous activity) and local precipitation regimes should be also considered (Batllori et al., 2009; Liang et al., 2016; Sigdel et al., 2018; Wang et al., 2016). To reduce the uncertainties linked to the climate drivers of tree growth at

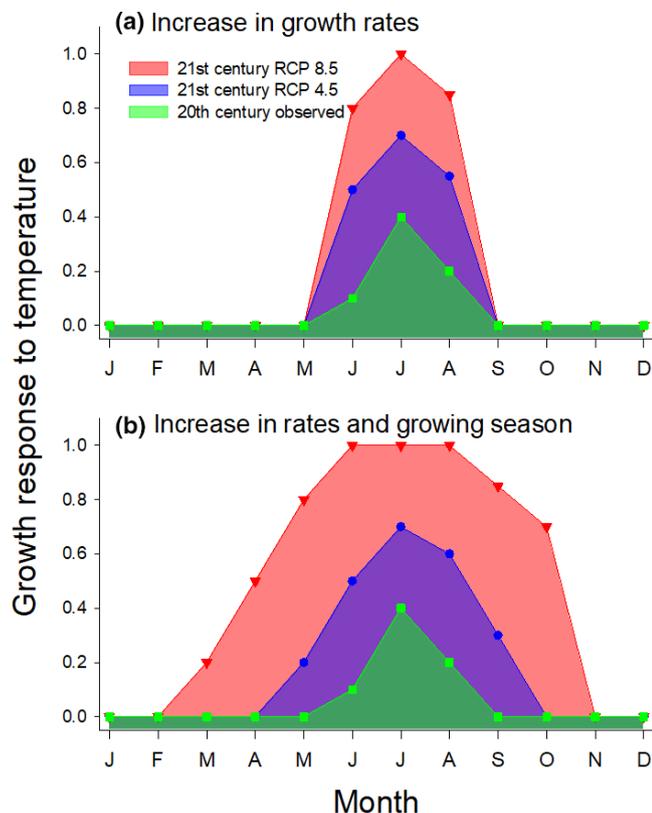


FIGURE 1 Expected model outputs used to forecast treeline growth responses to climate warming. Future responses could correspond to (a) an increase in growth rates and (b) increases in both growth rates and growing season length. The figure shows the monthly growth response for temperature (gT, y-axes; higher values indicate a lower limitation of growth by low temperatures) using the VS-Lite model for the period 1950–2004 (green lines and areas) and for the 21st-century projected climate under the RCP 4.5 (blue lines and areas) and RCP 8.5 (red lines and areas) scenarios. The temporal window (x-axes) spans from January to December in the northern hemisphere or from July to June in the southern hemisphere. The growing season goes from June to July or from December to January in the northern and southern hemispheres, respectively [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

treeline, we need intercontinental assessments encompassing multiple biomes, subjected to different climate conditions, and formed by different taxa. The current study aims to fill this research gap by analyzing 20th-century growth trends using tree-ring width (TRW) data from 37 Eurasian and American sites located in 13 regions representing most of the key treeline regions in the world. Reliable predictions of tree growth at treeline must be fed by climate projections, but, importantly, they also must be supported by long-term tree growth data at the margins of tree life-form existence. We need global scale ecosystem forecasts in response to climate warming, and this study aims at fulfilling this demand in the case of treelines.

One of the ecological challenges to accomplish continental assessment and forecasting of tree-growth trends at the treeline is explicitly incorporate local factors including climate, taxon, tree age, stand structure, or site topography. Here we use well-validated, climate-driven growth models that allow to: (i) determine the main climate drivers of growth variability; and (ii) forecast growth variability as a

function of different climate scenarios. Specifically, we modeled how the temperature–growth association will change for the representative concentration pathway (RCP) 4.5 and 8.5 emission scenarios which forecast moderate (0.9–2.6°C) to intense (1.4–4.8°C) warming for the late 21st century, respectively (see Sánchez-Salguero et al., 2017, 2018). We used the Vaganov–Shashkin-Lite process-based growth model (hereafter VS-Lite model), which is based on the relationships between radial growth and climate (Vaganov et al., 2006; 2011). The relationships between air temperature and radial growth are well established for alpine treelines (Liang & Camarero, 2018; Paulsen et al., 2000; Rossi et al., 2007). Having an increase in air temperature due to climate warming, growth is expected to improve. However, as already mentioned, growth enhancements can be lagged or minimal with respect to the temperature rise due to idiosyncratic regional (e.g., climate trends, radiation) or local (e.g., topography) factors. Our primary goal is to forecast the changes in coupling between rising temperature and growth at treeline over the 21st century (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study area

We defined the treeline as the ecotone going from the forest limit (with cover above 25%) to the tree limit where at least 2 m single-stemmed tall trees occur (Holtmeier & Broll, 2005). Following Harsch and Bader (2011), we classified four types of treeline forms: (i) diffuse, characterized by a gradual decrease in tree density and height with a prevalence of single-stemmed trees; (ii) abrupt, characterized by sharp transitions in tree density and height; (iii) island, characterized by the presence of clumped patches of trees or multi-stemmed, stunted (*krummholz*) individuals above the forest limit; and (iv) *krummholz*, characterized by the dominance of stunted, multi-stemmed trees usually forming contiguous bands above the tree limit. Intermediate types between these classes exist. The sampled area encompasses the main ranges where these four treeline types occur (Figures S1 and S2; Table S1). Thirty-seven treeline sites were sampled across five main biogeographic regions (Körner, 2012) including: the tropical zone (latitude 0–26°S; two sites), the warm-temperate zone (latitude 27–32°N; five sites), the Mediterranean zone (latitude 32°–43°N or S; 11 sites); the temperate zone (latitude 44°–57°N or S; 11 sites); and the boreal and subarctic zones (latitude 58°–71°N; eight sites).

2.2 | Field sampling

During several field campaigns, two to-the-pith long cores were extracted at a height of less than 30 cm from individual trees forming the treeline using increment borers (5.15 mm increment borer; Haglöf). Usually, either transects crossing the treeline ecotone (i.e., following the altitudinal gradient) or rectangular plots were sampled (Camarero & Gutiérrez, 2004). Transects or plots were located in

undisturbed, open ecotone, topographically homogeneous settings. They contained the uppermost forest limit and the treeline. All trees located in transects or within each plot were sampled and their diameter at breast height (measured at 1.3 m) and height were measured.

2.3 | Tree-ring width data

Tree cores were collected to estimate tree age and radial growth rates. Usually, two cores were extracted from each tree at the direction perpendicular to the maximum slope to avoid sampling reaction wood. Cores were air-dried, mounted on grooved wooden blocks, and sanded with sand paper of progressively finer grain size down to 600–800 grit. Samples were then visually cross-dated by detecting and noting characteristic rings. TRW was measured at a resolution of 0.01 mm using sliding stages, and the visual cross-dating was validated using the COFECHA software (Holmes, 1983). In those cases where samples had no pith because of the core mispointing or because the innermost rings were lost, pith-offset estimates were calculated. This was accomplished by fitting a geometric pith locator to the innermost rings and converting the distance to the theoretical pith into the number of missing rings (Duncan, 1989). We estimated tree age as the maximum number of tree-rings measured or estimated in each individual. We then adjusted this age by adding an estimate of the number of years from the base to the coring height following several field estimates and their high uncertainty (Devi et al., 2008; Liang et al., 2011). We estimated these years by counting annual whorls along the main stems or by counting rings in basal cross sections of small trees (saplings, seedlings) with heights from 0.1 to 1.5 m (Camarero & Gutiérrez, 2004).

The annually resolved TRW measurements were transformed into basal area increments (BAI) to account for the geometric constraints of an increasing surface area in ageing trees. We converted TRW into BAI assuming a circular outline of stem cross sections. Then, individual TRW and BAI series were obtained for the period 1901–2004, which was the overall best replicated time window, and site averages were also calculated. Normalized BAI for each tree at each site was calculated as the annual BAI for any given year divided by the sum of BAI values for the site.

We also converted TRW into dimensionless, ring-width indices (TRWi) to remove long-term trends in growth due to tree ageing by 67% cubic smoothing splines with a 50% cutoff frequency, which allows retaining information on common low-frequency tree-growth forcing (Helama et al., 2016). The resulting detrended series was pre-whitened with low-order autoregressive models to remove year-to-year growth persistence. Individual TRWi series were averaged for each site to obtain mean site series of TRWi using robust bi-weight means (Cook & Kairiukstis, 1990; Fritts, 1976). All stages of chronology building and growth–climate analyses were performed using the R statistical software (R Core Team, 2019). The dplR package was used to detrend TRW series and to calculate mean series or site chronologies of ring-width indices (Bunn et al., 2020).

2.4 | Climate data

The homogenized and quality-checked CRU T.S. 4.01 dataset (<http://www.cru.uea.ac.uk/data>) was used for the period 1901–2004 providing a reliable climate data source across all the study sites (Harris et al., 2014). This dataset contains monthly mean temperature and precipitation sum data gridded at a 0.5° spatial resolution that have been checked for homogeneity. We downscaled temperature and precipitation using the newly released (~1 km) data from the Climatologies at High Resolution for Earth's Land Surface Areas (<http://chelsa-climate.org>) product, which includes orographic predictors such as valley exposure for downscaling both precipitation and temperature (Karger et al., 2017). We calculated the climate parameters at every treeline site from that grid point of the 1-km pixel containing the closest location to the study site. The remaining elevational distance was accounted for by assuming a common altitudinal lapse rate of air temperature of -0.0055 K m^{-1} during the growing season (Körner, 2012).

2.5 | Climate–growth associations

To quantify climate–growth associations, we calculated mean TRW series at the site level. Within the developed TRWi chronologies, we considered the period 1950–2004, which corresponded to the most reliable time window of climate data. The relationships between monthly climate data (mean temperatures and precipitation) and TRWi series were assessed by calculating bootstrapped Pearson correlation coefficients, and also by fitting generalized least squares (GLS) regression models using the nlme R package (Pinheiro et al., 2018). Based on previous studies (Camarero & Gutiérrez, 2004; Liang et al., 2011; Salzer et al., 2009; Wilmking et al., 2004), the temporal window of growth–climate comparisons included from the previous September to the current October in the northern hemisphere and from previous March to current April in the southern hemisphere.

2.6 | Climate projections

Only those climate variables highly correlated with TRWi ($r > |0.30|$, $p < 0.05$) were considered in the climate-based models and TRWi projections under different climate scenarios. We focused on summer or winter temperatures in the northern and southern hemispheres, respectively. The climate data projected for the 21st century were downloaded and downscaled at a 0.5° spatial resolution from the fifth phase of the Coupled Model Intercomparison Project (ensemble CMIP5; Moreno & Hasenauer, 2016; Taylor et al., 2012). We used data for the scenario (RCP 8.5) that most closely tracked recent historical emissions (van Vuuren et al., 2011), and one lower emission scenario (RCP 4.5) in which the increase in annual emissions is more gradual during the early 21st century and declines after the mid-21st century. Specifically, the 4.5 and 8.5 RCP scenarios correspond to

radiative forcing values in 2100 of 4.5 and 8.5 W m⁻², respectively (van Vuuren et al., 2011).

2.7 | Statistical analyses of growth trends

The basic idea of these analyses was to compare and relate growth trends (BAI) as a function of growing-season temperature trends for the period 1950–2005. For each tree-ring series, the temporal trends in BAI and temperature were estimated using two simple linear regressions, each with calendar year as the explanatory variable (Huang et al., 2017). Specifically, we used BAI and growing season temperature (June–July in the northern hemisphere, December–January in the southern hemisphere) as response variables. Only trees with at least 25 rings measured in the period 1950–2004 were considered in the analyses.

To test for the relationship between growth and temperature trends, we applied linear mixed-effects models (Pinheiro & Bates, 2000). We used growth trend as the response variable, tree age and growing-season temperature trend as fixed factors, and site as a random factor. Site was a factor representing the different “treeline × species” interaction (37 levels). A first graphical examination of the model showed a heterogeneous distribution of residuals (Zuur et al., 2009), so we included a power variance structure to account for the spread of variation in the data as a function of estimated tree age (Figure S5). To select the most parsimonious model, we used a multi-model inference approach based on information theory (Burnham & Anderson, 2002). We ranked all potential models according to the second-order Akaike information criterion (AICc). The model showing the lowest AICc value and the largest Akaike weight (w_i , relative probability quantifying if the selected model is the best one) was selected as the best one. All statistical analyses were performed in the R environment (R Core Team, 2019). The lme function of the nlme package was used to fit the linear mixed-effects (Pinheiro et al., 2018). The MuMIn package was used to calculate the pseudo- R^2 of the model (Barton, 2012). The visreg R package was used to visualize regression models and calculate least-squares means (Breheny & Burchett, 2017).

2.8 | Process-based growth model

To understand the climatic drivers of tree growth and how they may change into the future, we estimated temperature parameters. We chose the VS-Lite model formulation (Tolwinski-Ward et al., 2011) that contains three parameters: a growth–temperature parameter (gT) and its two sub-parameters (T1 and T2). The gT parameter indicates the relationship between temperature and growth at a monthly temporal resolution. T1 and T2 indicate the threshold temperature below which growth cannot occur and the temperature above which growth is not limited by temperature, respectively. These two VS-Lite temperature parameters simulate nonlinear growth response to temperature by considering the threshold temperature (T1) of

cambial reactivation based on xylogenesis studies (usually from 3°C to 8°C; see Rossi et al., 2007), and the lower bound on temperature for optimal growth (T2) which would be between 9°C and 20°C (Tolwinski-Ward et al., 2011). To estimate model parameters, we followed a Bayesian approach (Tolwinski-Ward et al., 2013). Following Tolwinski-Ward et al. (2013), Tolwinski-Ward et al. (2016), the VS-Lite model relates the annual growth responses from September of the year prior to growth to October of the year of tree-ring formation in the northern hemisphere and from previous March to current April in the southern hemisphere (Rossi et al., 2007; Vaganov et al., 2011) to the sum of the minimum monthly temperature response (gT), modulated by day length or insolation (gE). This minimum allows for an important process-based nonlinearity depending on how temperature is limiting growth at treeline (Körner, 2012). We estimated gE from site latitude with no interannual variability. In the VS-Lite modeling approach, parameters were used to build simulated TRW chronologies for the 1950–2004 calibration period (TRWi_{VSL}). We then related the simulated tree-ring chronologies to the observed tree-ring chronologies (TRWi) from the observed tree-ring data (Tolwinski-Ward et al., 2013), allowing for estimation of all the above parameters. We assumed uniform priors for the growth function parameters, and independent, normally distributed errors for TRWi, and ran for 12,000 iterations with three chains (Tolwinski-Ward et al., 2011). We present the posterior median for each parameter (gT, T1, T2) for the calibration period to understand the temperature drivers on growth in the recent past. We also divided this calibration period into two subperiods to evaluate the temporal stability of the calibrated growth response functions (1950–1979, 1980–2004), withholding the second half for validation of the parameters estimated in the first half. Other parameters used in the VS-Lite model formulation (e.g., runoff, root depth) were retrieved from published studies (Sánchez-Salguero et al., 2017, 2018; Tolwinski-Ward et al., 2011;).

2.9 | Statistical growth models

We fitted growth models with climate covariates using GLS models (Pinheiro et al., 2018). All continuous predictor variables were standardized to give them the same weight in the fitted models (i.e., the mean was subtracted from each value and divided by the standard deviation), enabling the interactions to be tested and compared (Pinheiro & Bates, 2000). In addition, we evaluated the existence of multicollinearity among explanatory variables by calculating the variance inflation factor (VIF), which was always <2, indicating no redundancy problems (i.e., those variables are not collinear with the other variables in the model). The VIF was calculated as the ratio of the overall model variance to the variance of models including single independent variables. The stability and validity of GLS models were tested by a split-sample procedure by dividing the period into two subperiods of similar length (Fritts, 1976). We used the function step of the R package stats (R Core Team, 2019) and selected the final regression equations as those showing the lowest AICc values.

2.10 | Projected growth–climate associations

We used GLS models to project the TRWi of each site (hereafter TRWip) for the 2015–2049 and 2050–2100 periods under the two selected RCP scenarios. The VS-Lite model was fitted to estimate parameters (gT, T1, T2) from the TRWip. This allowed us to infer whether the relationships between climate and growth changed from the observed period (1950–2004) to the projected period (2015–2100) by comparing the gT in the two periods. We then generated a second synthetic TRW projection from VS-Lite (TRW_{iVSLP}), and compared the two projected TRW indices through Pearson correlations.

3 | RESULTS

3.1 | Temperature and growth trends at treeline

We found a general growth increase during the 20th century, with a more pronounced rising trend from the 1980s onward. There was, however, substantial variability among regions (Figure 2a). Overall, 80% of sites showed positive and significant ($p < 0.05$) growth trends. Growing season temperature trends were positive in most sites (Table S3).

Tree growth and growing-season temperature trends were positively related (Figure 2c). Higher growth and stronger temperature trends were observed in Pyrenees sites, whereas negative growth rates were found in some of the Rocky and Scandes Mountain sites

(Table S3). Additionally, some sites in the southern hemisphere showed substantial positive growth trends but no significant temperature trends (points in top left area of Figure 2c). Models also showed that basal area increment trends were related to tree age, but trees established before the 20th century also presented positive growth trends (Figures S3 and S4).

3.2 | Current temperature–growth associations

Growing-season (June–July or December–January) temperature was the most commonly observed and important driver of growth in 17 out of 37 sites during the 20th century (Figure 2c; Tables S4 and S5). On average, 50% of growth variation was explained by temperature. In the growth rate regression models (Table S5), 60% and 40% of the parameters retained by model selection corresponded to temperature and precipitation variables, respectively. At high-latitude sites, 80% of the regression parameters corresponded to July–August temperatures, while in mid- to low-latitude sites, 80% of the parameters corresponded to nonthermal factors. In one of the equatorial treeline sites (Cordillera Real-Peru) growth was negatively associated with temperature. The explanatory strength of temperature varied across locations, from 26% in that equatorial site to 70%–81% at high-latitude ones (Siberia, Scandes, and southern Andes). The percentage of growth variance explained by temperature (R^2_{adj} in Table S5) increased as treeline elevation decreased ($r = -0.33$, $p = 0.049$),

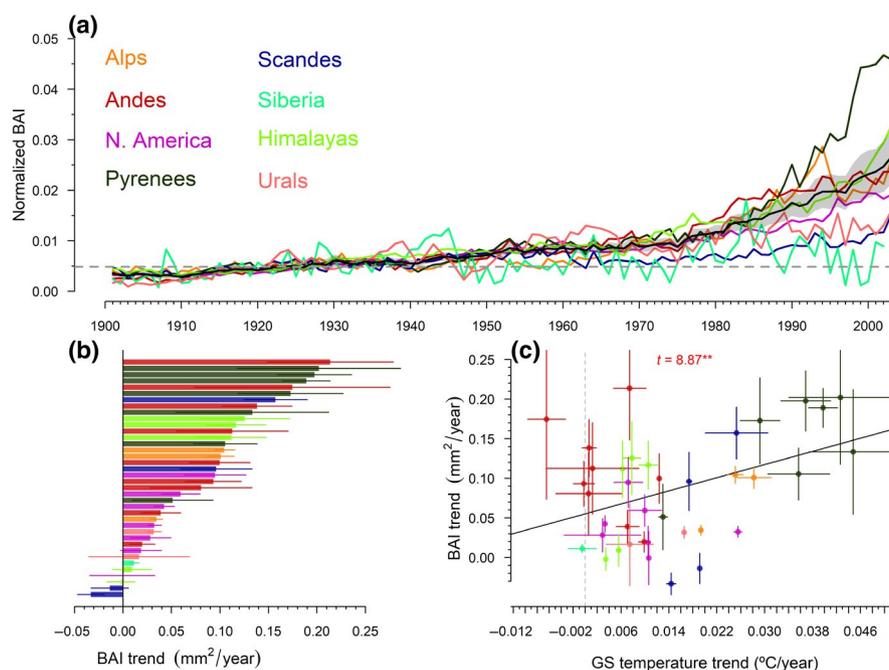


FIGURE 2 Observed and predicted growth (BAI) trends. (a) Growth trends (normalized BAI) during the 20th century for all study treeline sites. Colored lines indicate the growth for the 1901–2004 period in each region. The shaded area shows the 95% confidence intervals (CIs) of the averaged normalized growth across all treeline sites. (b) Observed BAI trends and (c) observed (points) and predicted (regression) BAI based on linear mixed-effects models as a function of growing-season (GS) temperature (June–July in the northern hemisphere, December–January in the southern hemisphere). Error bars indicate 95% CIs. In the plot (c) the t statistic of the regression is shown (** $p < 0.01$). The vertical dashed line indicates the zero value for the GS trend. In all plots treeline sites and regions are presented with the same colors [Colour figure can be viewed at wileyonlinelibrary.com]

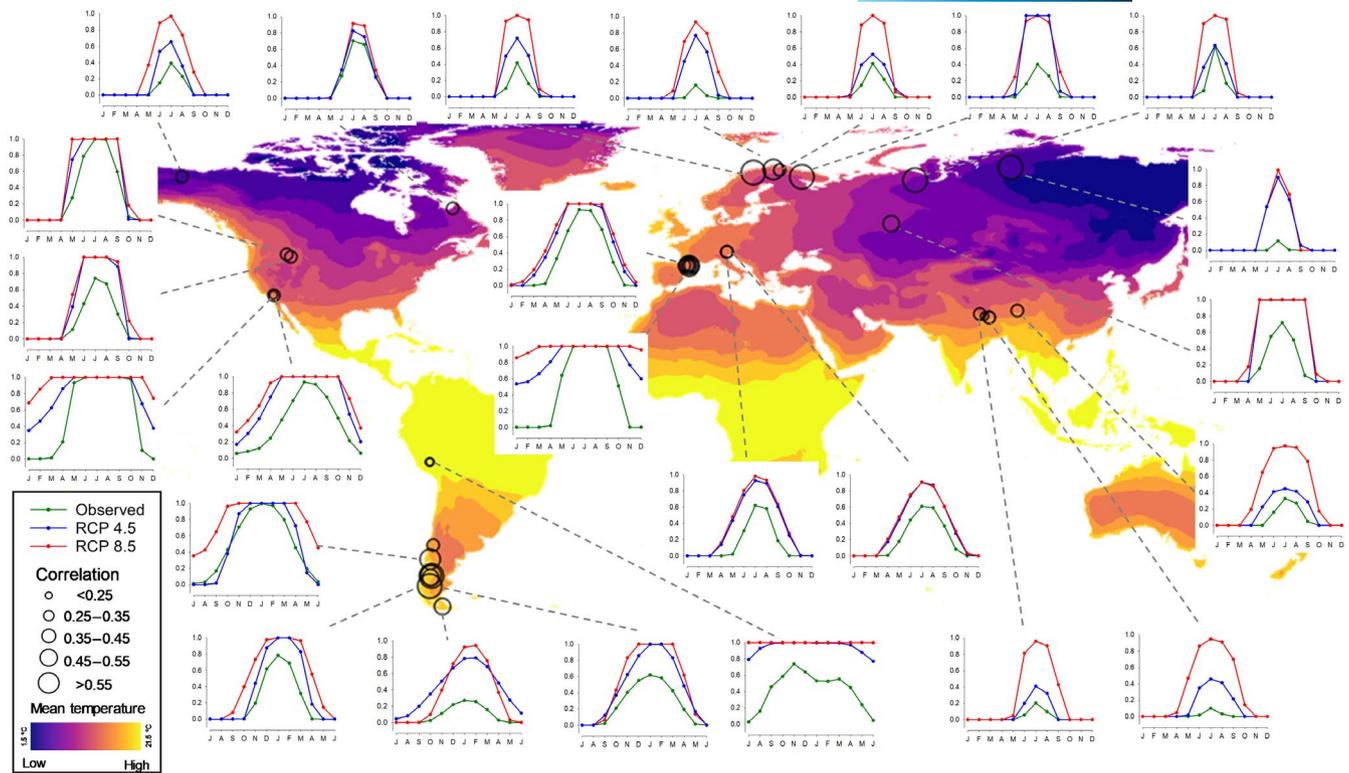


FIGURE 3 Simulated monthly growth response to temperature (gT) using the VS-Lite model. Monthly growth response curves for temperature (gT, y axes) using the VS-Lite model for the period 1950–2004 (green lines), and for 2050–2100 under the RCP 4.5 (blue lines) and RCP 8.5 (red lines) emission scenarios. The size of map symbols is proportional to Pearson's correlation coefficients calculated between observed and fitted mean ring-width site series. Correlation values higher than $|0.25|$ are significant at $p < 0.05$. Colored background shows mean growing-season temperatures [Colour figure can be viewed at wileyonlinelibrary.com]

and it was higher in abrupt *Nothofagus* treelines ($R^2_{\text{adj}} = 0.60 \pm 0.05$) than in diffuse ($R^2_{\text{adj}} = 0.48 \pm 0.03$) treelines ($t = 2.18$, $p = 0.037$).

3.3 | Forecasted growth responses to climate

Currently, non-limiting thermal conditions during at least 1 month within the growing season are observed in 8% of the sites, whereas this is projected to occur in 52% of them after 2050. This indicated that during the 21st century temperature might no longer constrain growth rates on over half of the treeline sites worldwide. This will effectively decouple tree growth from rising temperature trends (Figure 3).

The VS-Lite model reproduced the role played by low growing-season temperatures as the main constraint of tree growth in the 20th century (Figure 3; see also Tables S6–S8). In 80% of sites, the model predicted enhanced growth together with longer growing seasons in the warmest RCP 8.5 scenario, whereas 20% of sites featured just higher growth rates. However, under the RCP 4.5 scenario, only 50% of the sites are forecasted to show higher growth rates and longer growing seasons. In some sites, we found trivial differences in the growing-season temperature parameters between RCP 4.5 and 8.5 scenarios (e.g., Rocky Mountains, Alps, Pyrenees). This indicates that growth limitation by low temperatures could already fade out with the RCP 4.5 scenario. In a few sites (e.g., Peru, California, southern Urals), the predicted growing season would

extend from 2 to 6 months in the late 21st century when considering the RCP 8.5 scenario. The minimum temperature threshold for growth (T1) will decrease mainly in Fennoscandian, Siberian, tropical, and Mediterranean sites, and should be related to a relaxation in temperature limitation during the onset of the growing season. This would suggest for the next decades an earlier anticipation of the growing season toward current spring months. The decrease of T1 will be more marked in sites where increasing growth rates are predicted.

4 | DISCUSSION

In this study, we showed that trees growing in most treelines on four continents exhibited increasing growth rates over the past century—with a particularly acute acceleration since the 1980s—and these changes are strongly correlated with concurrent warming occurring at most sites. These findings and the 21st-century predictions of increasing growth rates are in line with previous xylogenesis studies, performed in the last 10 years when temperature increases have been the highest, which estimated that 75% of the final ring width depends on growth rate and 25% depends on the length of the growing season (Cuny et al., 2015). Despite the potential issue of the no-analog bias in defining the actual growth trends (i.e., old, slow-growing trees may be rare or absent in some treelines),

recent warming trends have important implications for tree growth and productivity in currently heat-limited subarctic and subalpine treeline environments (Camarero & Gutiérrez, 2004; Körner, 2012; Salzer et al., 2009). Nonetheless, our approach with the adoption of a forward model to detect future changes in physiological limitations to growth shows great potential for predicting nonlinear changes in treelines and other marginal ecosystems (Hofgaard et al., 2019; Sánchez-Salguero et al., 2018; Vaganov et al., 2006).

We identified that the 20th-century growth enhancements occurred at most of our sites underlining the previous conditions limited by temperature. However, projection of these same trees and sites to year 2100 suggest that this thermal limitation could disappear in half of the cases, leading to an increase in productivity and promoting treeline encroachment. A divergence between growing-season climate and growth has been interpreted as a loss of sensitivity to climate (divergence problem), particularly in boreal forests (Briffa et al., 1998). However, divergences from previous climate-growth associations may indicate the fading in climate constraints on growth as observed in arctic treelines (Hofgaard et al., 2019), and as forecasted by our simulations. The expected upward and poleward shift of current treelines must also be considered (Harsch & Bader, 2011), even though the response of treeline positions to warming can be lagged (Liang et al., 2011; Rees et al., 2020). If tree growth in the current treeline stands decouples from temperature at the end of the 21st century, this could be because those stands will become part of subalpine or boreal forests and not be part of treeline ecotones anymore (McIntire et al., 2016).

We found important biogeographic sources of variability in growth trends, climate trends, patterns of temperature limitation, and forecasted treeline dynamics (Camarero et al., 2017), which should be considered in further investigations. First, tree growth in the equatorial treeline (Peru) was poorly related to temperature as compared to high-latitude sites (Siberia, Scandes, and southern Andes). This finding was expected given the peculiar climatic conditions in equatorial treelines (Körner, 2012), and suggests for these regions the inclusion of nonthermal growth drivers, as precipitation or radiation, in future modeling approaches (Liang et al., 2014; Morales et al., 2004). Second, our statistical models performed well (i.e., featuring a high percentage of explained growth variance) in high-latitude sites, but with regional or local differences. The explanatory power not evenly increasing with elevation suggests the presence of threshold responses to temperature or the additional influences of local factors such as wind or aspect (McIntire et al., 2016). Third, counter to expectations, the abrupt high-latitude *Nothofagus* treelines in the southern Andes seemed more responsive to temperature than diffuse treelines (Harsch & Bader, 2011). This conflicting result highlights the need to include radial growth data in treeline monitoring studies as a main component of treeline dynamics. Fourth, mid-latitude treelines exhibited high variability growth rates. These high (e.g., Pyrenees) to low (e.g., Rocky Mountains) values may be the result of different local and regional climate trends or be conditioned by size and age structures of those treelines (Camarero et al., 2017). More realistic projections of treeline growth

should also consider demographic dynamics, recognizing that reliable, long-term data on recruitment and mortality rates are scarce.

Our study scrutinized tree growth by means of tree rings and age estimations and has an inherent uncertainty in slow-growing treeline trees (Körner, 2012). Understanding whether the temperature-growth coupling of the past century was due to physiological acclimations related to rising temperatures or to CO₂ fertilization and improved water-use efficiency should also be addressed (Camarero et al., 2015). We detected current growth coupling with temperature at treelines, and forecasted a decoupling over the 21st century in almost half of our sites. As the association between temperature and growth fades out, other factors, such as nongrowing season conditions or tree-to-tree interactions, will become crucial. How treeline trees will acclimate to further warming is essential to project forest development in cold biomes. More mechanistic models could also be used to check this acclimation such as the full VS model (Tychkov et al., 2019; Vaganov et al., 2006) to consider the effects of elevated temperatures under rapidly warming climatic scenarios which could constrain growth in cold sites by reducing soil moisture availability (see Sánchez-Salguero et al., 2018). Such a nonlinear association between temperature and growth was not accounted for by the equations used to predict growth as a function of forecasted climate which were based on linear relationships. Since the VS-Lite model deals with the nonlinear growth responses of trees to climate, future studies should implement nonlinear statistical models to forecast growth.

Filtering out the observed growth trends by age, younger trees showed a much stronger increase of basal area increment than older ones. One possible explanation for this is that the younger the trees, the more likely is they established under warm conditions. Genetic selection or acclimation could lead to enhanced growth in such trees, but this should be tested by assessing long-term changes in tree size and biomass to account for any ontogenetic bias (Duchesne et al., 2019). However, we must stress that there were no systematic effects of age on the interpretation of results, that is, younger treeline sites did not shape the growth trend distribution between regions. In treeline sites where temperature-growth couplings were more (e.g., Pyrenees) or less strong (e.g., southern Andes), the overall growth enhancement was maintained even when considering just the old individuals. These results highlight that patterns in treeline growth are complex and depend also on local factors, such as size and age structures, in addition to climate (Camarero et al., 2017). Our results suggest that growth enhancement at treeline was widespread during the 20th century.

5 | CONCLUSIONS

We found that the rapid temperature rise observed during the 20th century was positively associated with tree growth at most treelines excepting subarctic regions showing the aforementioned divergence problem. Rising trends in temperature and growth were globally observed with the exception of tropical treelines where growth seems not as limited by low temperatures as in extratropical regions. However, our predictions suggest that during the 21st century, growth will stop

tracking temperature. This decoupling would suggest that tree growth at treeline will be no longer limited by low temperature. Additional factors, such as nongrowing season conditions and biotic interactions, should be taken into account at regional and local levels. If these novel drivers of growth at treeline will play a pivotal role during the 21st century, global vegetation models should consider these outcomes to fully represent the complexity of future growth responses at treeline.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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