Title: Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests

Author: Jill E. Harvey, M. Smiljanić, T. Scharnweber, A. Buras, A. Cedro, R. Cruz-García, Ryszard Kaczka i in.

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests

Jill E. Harvey[1,2] | Marko Smiljanić[1] | Tobias Scharnweber[1] | Allan Buras[3] |
Anna Cedro[4] | Roberto Cruz-García[1] | Igor Drobyshev[5,6] | Karolina Janecka[1] |
Āris Jansons[7] | Ryszard Kaczka[8] | Marcin Klisz[9] | Alar Läänelaid[10] |
Roberts Matisons[7] | Lena Muffler[1,11] | Kristina Sohar[10] | Barbara Spyt[8] |
Juliane Stolz[12] | Ernst van der Maaten[12] | Marieke van der Maaten-Theunissen[12] |
Adomas Vitas[13] | Robert Weigel[1,11] | Jürgen Kreyling[1] | Martin Wilmking[1]

[1]Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

[2]Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, AB, Canada

[3]Department of Ecology and Ecosystem Management, TUM School of Life Sciences Weihenstephan, Freising, Germany

[4]Faculty of Geosciences, Szczecin University, Szczecin, Poland

[5]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

[6]Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue (UQAT), Val-d'Or, QC, Canada

[7]Latvian State Forest Research Institute, Salaspils, Latvia

[8]Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland

[9]Department of Silviculture and Forest Tree Genetics, Forest Research Institute, Raszyn, Poland

[10]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[11]Albrecht von Haller Institute for Plant Sciences, University of Goettingen, Göttingen, Germany

[12]Chair of Forest Growth and Woody Biomass Production, Dresden, Germany

[13]Centre of Environmental Research, Vytautas Magnus University, Kaunas, Lithuania

Abstract

The role of future forests in global biogeochemical cycles will depend on how different tree species respond to climate. Interpreting the response of forest growth to climate change requires an understanding of the temporal and spatial patterns of seasonal climatic influences on the growth of common tree species. We constructed a new network of 310 tree-ring width chronologies from three common tree species (*Quercus robur*, *Pinus sylvestris* and *Fagus sylvatica*) collected for different ecological, management and climate purposes in the south Baltic Sea region at the border of three bioclimatic zones (temperate continental, oceanic, southern boreal). The major climate factors (temperature, precipitation, drought) affecting tree growth at monthly and seasonal scales were identified. Our analysis documents that 20th century Scots pine and deciduous species growth is generally controlled by different climate parameters, and that summer moisture availability is increasingly important for the growth of deciduous species examined. We report changes in the influence of winter climate variables over the last decades, where a decreasing influence of late winter temperature on deciduous tree growth and an increasing influence of winter temperature on Scots pine growth was found. By comparing climate–growth responses for the 1943–1972 and 1973–2002 periods and characterizing site-level growth response stability, a descriptive application of spatial segregation analysis distinguished sites with stable responses to dominant climate parameters (northeast of the study region), and sites that collectively showed unstable responses to winter climate (southeast of the study region). The findings presented here highlight the temporally unstable and nonuniform responses of tree growth to climate variability, and that there are geographical coherent regions where these changes are similar. Considering continued climate change in the future, our results provide important regional perspectives on

Correspondence
Jill E. Harvey, Natural Resources Canada,
Canadian Forest Service, Northern Forestry
Centre, Edmonton, AB, Canada.
Email: jill.harvey@canada.ca

recent broad-scale climate–growth relationships for trees across the temperate to boreal forest transition around the south Baltic Sea.

1 | INTRODUCTION

The productivity, composition and functional role of future forests in global biogeochemical cycles will depend on how different tree species respond to climate, competition with neighbours, and local environmental conditions. Climate limitations on forest ecosystems are thought to be greatest in high elevation and latitude environments and also in moisture-limited regions where extreme climate events, such as drought, can cause widespread forest mortality (Allen et al., 2010; Anderegg, Kane, & Anderegg, 2013). However, recent research documents considerable climate change effects on temperate forests where reduced timber yield (Lindner et al., 2014), declining resilience (Cavin & Jump, 2017; Gilliam, 2016; Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014), reduced biodiversity (Thom & Seidl, 2016) and increased disturbance activity (Millar & Stephenson, 2015; Senf & Seidl, 2018) have been attributed to warming temperatures and/or reduced moisture availability in the growing season.

Each of the last three decades has been successively warmer than any preceding decade since 1850, with 1983–2012 likely the warmest 30 year period in the last 1,400 years in the Northern Hemisphere (IPCC, 2014). Climate change effects on vegetation have been documented at annual and seasonal scales, with the most research directed at evaluating the effects of climate in summer months. However, climate warming is more pronounced in winter than summer at locations in the mid- to high-latitudes (Xia et al., 2014), where changing winter precipitation patterns (spatial and temporal variability, type; Wu et al., 2019), extreme cold events (magnitude and frequency; Kodra, Steinhaeuser, & Ganguly, 2011) and temperature (variability in extremes and mean) can independently and collectively influence patterns of vegetation growth and distribution, especially in temperate mixed-wood forests (Kreyling, 2010; Kreyling & Henry, 2011). To better identify the effects of these climatic changes on forest productivity, spatially explicit estimations of tree growth (i.e. radial tree-ring growth) responses to seasonal climate are required. Furthermore, analyses assessing the stationarity of these climate–growth responses are necessary to determine changing climate effects on tree growth.

Recent research using broad-scale tree-ring networks have documented changing effects of seasonal climate on temperate and Northern Hemisphere forests (e.g. Babst et al., 2019). The advancement of methods to integrate tree-ring measures into estimates of hemispherical forest productivity (e.g. Seftigen, Frank, Björklund, Babst, & Poulter, 2018), continental vegetation models (e.g. Klesse, Babst, et al., 2018) and future forest growth relies on the development and evaluation of new tree-ring data networks (Babst et al., 2018). Tree-ring networks can be used to characterize the spatial and temporal patterns in the relationship between tree growth and climate and improve our ability to model the impacts of future climate (Charney et al., 2016; Klesse, DeRose, et al., 2018), especially for temperate, complex forests that provide diverse ecosystem services. Given the uncertainty of future climate, an improved understanding of the influence of climate on tree growth in temperate forest ecosystems is needed, especially for winter forest ecology, which has received comparatively less research attention (Weigel et al., 2018).

In this study we developed a multispecies network of tree-ring width data in the temperate oceanic and continental forests surrounding the south Baltic Sea to assess climate–growth relationships at a subcontinental scale. This region includes hemiboreal forests poleward of the study region but is primarily composed of temperate forest ecosystems. Incorporating existing and new tree-ring data, this network is compiled from site-level chronologies, aiming to reduce the individual tree variability that stems from microsite differences, within-population genetic variation and small-scale disturbances. With this composited dataset, we test the assumption that species-specific responses to climate influence tree-growth variability across this generally temperate region, and that this relation is further characterized by different genus-specific responses. The objectives of our study were: (a) to determine the broad species-specific response to climate variables, (b) to investigate the dominant climate factors influencing the growth of common tree species in this region, (c) to explore the temporal stability of climate–growth relationships identified and (d) to assess the spatial pattern of climate–growth responses.

2 | MATERIALS AND METHODS

2.1 | Study region

The south Baltic Sea region includes the postglacial lowland landscapes (~0–400 m above sea level [a.s.l.]) of Denmark, Sweden, Germany, Poland, Kaliningrad region of Russia, Lithuania, Latvia and Estonia surrounding the south Baltic Sea (within ~300 km), south of the gulfs of Bothnia and Finland and east of Skagerrak, lying between ~51–60°N and 9–28°E (Figure 1). Agricultural cropland,
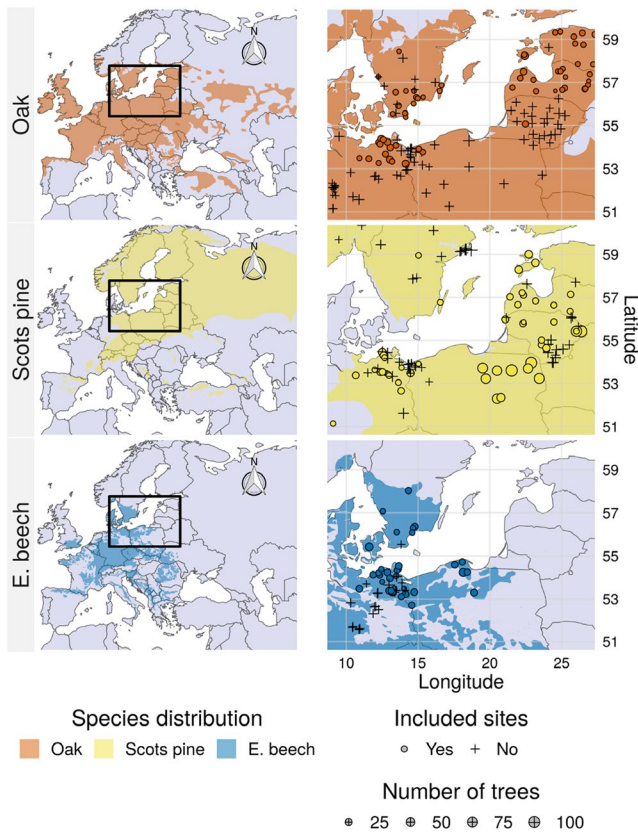
FIGURE 1 The distribution of *Quercus* sp. ('Oak'), *Pinus sylvestris* ('Scots pine') and *Fagus sylvatica* ('E. beech') in Europe (left panels; species distribution: http://www.euforgen.org/species/), and the location of tree-ring width data sites in the network (circle and cross markers) included in the analysis (cross marker) (right panels). Inset black boxes in left panels mark the study region

managed and protected forests and peatland complexes typify the land cover types outside urban and settled areas. Both maritime and continental weather patterns modulate climate across the study region set between the continental interior of Europe and the northern Atlantic Ocean. Cold, moist winters and warm, wet summers characterize the regional climate, with an average 604 mm of annual precipitation and a mean annual temperature of 7.8°C in the southwest of the region (Rostock; 1981–2010 climate normals; CRU TS 4.01) and 704 mm and 5.9°C in the northeast of the region (Tallinn; 1981–2010 climate normals; Estonian Weather Service, 2018). Over the past 100 years, air temperature in the study region has increased in both the warm and cold seasons (Figure S1). Winter precipitation in some poleward areas of the study region have experience increased precipitation, and summer precipitation at some equatorward areas record less precipitation in the late 20th and early 21st centuries (Figure S1).

2.2 | Common forest tree species

Common tree species that characterize the contemporary forests in the south Baltic Sea region include: pedunculate oak (*Quercus*

robur L.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) Karst), black alder (*Alnus glutinosa*), common ash (*Fraxinus excelsior*), silver birch (*Betula pendula*) and Eurasian aspen (*Populus tremula*). From these common species, pedunculate oak, Scots pine and European beech are the primary species used in dendrochronological studies based in the south Baltic Sea region (e.g. Balanzategui et al., 2017; Drobyshev, Niklasson, Eggertsson, Linderson, & Sonesson, 2008; Scharnweber et al., 2011; Sohar, Läänelaid, Eckstein, Helama, & Jaagus, 2014; van der Maaten-Theunissen et al., 2016) and are the target species for this study.

Pedunculate oak (hereafter referred to as 'oak') is the most widely dispersed oak species in the south Baltic Sea region. Oak trees generally tolerate a wide range of edaphic conditions with optimal growth most frequently observed on fertile and well-watered sites (Arend, Kuster, Günthardt-Goerg, & Dobbertin, 2011; van der Maaten et al., 2018). Scots pine is the most broadly distributed pine species found throughout Eurasia. A high tolerance to poor soils, drought and frost events permits Scots pine trees to grow in a wide variety of environments ranging from 0 to 2,600 m a.s.l., and also commonly occurring as an early seral species in disturbed settings (Durrant, De Rigo, & Caudullo, 2016). European beech is found growing from southern Italy to southern Norway and Sweden, occurring in various habitats from mountainous regions to lowlands (Seynave, Gégout, Hervé, & Dhôte, 2008), with cold winter temperatures and low moisture availability restricting beech from more northern and/or drier locations (Peters, 1997).

2.3 | Tree-ring data

We compiled tree-ring width data from three species growing at 310 sites ranging from 2 to 550 m a.s.l into a dataset covering much of the south Baltic Sea region (Figure 1). Network sites cover different portions of the distribution range of each species (Figure 1). We relied on chronologies that were previously developed for dendroclimatological (Cedro, 2004; Cedro & Cedro, 2018; Helama, Sohar, Läänelaid, Bijak, & Jaagus, 2018; Jansons, Matisons, Šēnhofa, Katrevičs, & Jansons, 2016; Läänelaid, Sohar, & Meikar, 2008; Matisons, Elferts, & Brūmelis, 2013; Sohar, Vitas, & Läänelaid, 2012; Vitas, 2004, 2006, 2011) and dendroecological analyses (Scharnweber et al., 2011; Scharnweber, Manthey, & Wilmking, 2013; van der Maaten, Mehl, Wilmking, & van der Maaten-Theunissen, 2017; van der Maaten-Theunissen et al., 2016; Vitas & Zunde, 2019; Weigel et al., 2018), as well as chronologies from the International Tree-Ring Database (ITRDB; *n* = 42 sites) and chronologies not previously published (*n* = 42 sites; Table S1).

At all sites, including those not previously published (Table S2), one or two increment cores were collected ~1.3 m above the base of ≥10 trees with an increment borer. Tree cores were dried and fixed to wooden mounting boards and sanded with progressively finer sand paper or cut with a sharp blade so the ring boundaries could be clearly identified. Ring widths were measured to the nearest 0.01 or 0.001 mm using either digital measuring software

(e.g. WinDENDRO, CooRecorder) or a measuring table system (e.g. Lintab, Velmex).

To assign each ring to a calendar year, ring widths were visually crossdated and statistically verified using COFECHA (Holmes, 1983) or CDendro (Cybis Electronik & Data, Sweden). In the case of two cores per tree, annual ring measurements were averaged between cores to yield one series per tree. All raw, crossdated ring-width series were detrended to remove age-related trends and other nonclimatic influences on growth (e.g. growth releases). The variance in each ring-width series was stabilized by adaptive power transformation to produce homoscedastic indices (Cook & Peters, 1997), and then a spline function with a 50% frequency cut-off at 32 years was fit to each time series using ARSTAN (Cook, 1985). Residuals from the detrending functions were computed via subtraction (Helama, Lindholm, Timonen, & Eronen, 2004). For each site, individual, detrended ring-width series for each species were combined into an annual chronology using a biweight robust mean (Cook, 1985). To form a representative sample suitable for climate–growth analysis, site chronologies were selected from the network that included at least six individuals and exhibited a subsample signal strength (SSS; Buras, 2017; Wigley, Briffa, & Jones, 1984) of 0.84 or higher over the 1943–2002 period (Table S1). This period was the longest interval we could select that included the most chronologies.

The complete Baltic Sea tree-ring network presented here includes 136 oak, 119 Scots pine and 55 beech sites (Table S1), including series from 6,121 individual trees. Detrended standardized chronologies for each site are presented in Table S2. In this study, we present 42 new and previously unpublished chronologies that include five oak, 18 Scots pine and 19 European beech new tree-ring width datasets that span intervals within 1647–2016 (Table S1). From the complete network, 61 oak, 56 Scots pine and 35 European beech chronologies captured the 1943–2002 interval and were included in the climate–growth correlation analysis.

2.4 | Climate data

We obtained site-specific climate data using the software package ClimateEU 4.63 (Hamann, Wang, Spittlehouse, & Murdock, 2013). Interpolated climate datasets are calculated by this frontend software using the Parameter-elevation Regressions on Independent Slopes Model (Daly et al., 2008) for precipitation and ANUSplin for temperature, and are based on the CRU TS 3.1 climate dataset (Mitchell & Jones, 2005). Monthly precipitation sums and monthly mean, maximum and minimum temperature for each month from January to September in the growth year and June to December in the previous year were obtained. Seasonal temperature and precipitation variables were also computed by averaging monthly values (summer: June–August; autumn: September–November; winter: December–February; spring: March–May). We calculated the standardized precipitation–evapotranspiration index (SPEI; Beguería, Vicente-Serrano, Reig, & Latorre, 2014) from the monthly temperature and precipitation datasets. SPEI is a multiscalar climatic drought

index that can be computed for multiple temporal scales and considers precipitation and the effect of temperature on drought severity by including evapotranspiration (Vicente-Serrano, Beguería, & López-Moreno, 2010). In this study, we used the Thornthwaite equation to estimate potential evapotranspiration (Thornthwaite, 1948) and calculated SPEI integrated over 1-, 3- and 6 month periods (SPEI1, SPEI3 and SPEI6; Beguería & Vicente-Serrano, 2017). Both precipitation and SPEI climate variables are used to describe 'moisture availability'.

2.5 | Tree growth responses to climate

To identify the climate-response patterns across sites and species in the study region, the response of the ARSTAN standard chronologies to monthly climate variables was calculated over the 16 month time window (i.e. from the previous June to current September) and for seasonal climate variables. We performed bootstrapped Pearson's correlation analysis with 5,000 replicates to identify the predominant factors contributing to the observed growth variability. Climate–growth relationships were calculated over the common periods of 1943–2002 (60 years), 1943–1972 (30 years) and 1973–2002 (30 years). We then focused on two climate–growth relationships for each tree species (oak, Scots pine and European beech): (a) the dominant climate variable influencing the regional growth of a species across the study region ('dominant climate response'), and (b) the climate–growth relationship that exhibited the greatest change in strength and/or direction when we compared the response for the two 30 year periods ('greatest change climate response'). The strongest average response among sites for each species and climate variable was used to determine these relationships. We then assessed the temporal stability of these two climate–growth relationships for each tree species in more detail by employing bootstrapped correlation analysis with 5,000 replicates in 31 year moving windows lagged by 1 year over the 1943–2002 period. To assess the effect of autocorrelation in these analyses, we conducted the same climate–growth analyses described above using the ARSTAN residual chronologies that were processed using autoregressive modelling to remove autocorrelation (Cook & Holmes, 1986).

2.6 | Spatial patterns of changing climate–growth responses

We employed spatial segregation analysis to describe any broad spatial patterns in the stability of the growth responses for the two types of climate–growth relationships (see (a) and (b) in previous section). More commonly applied in epidemiological research of infectious disease outbreaks (e.g. Diggle, Zheng, & Durr, 2005; Tarr et al., 2018), spatial segregation analysis can be used to describe structure in spatial point patterns over space. First, for each site we classified the climate response as 'stable' or 'unstable' by comparing the significance of the correlation coefficients at the 0.95 confidence level for the 1943–1972

and 1973–2002 periods for both of the climate–growth relationships. An 'unstable' change in climate response between the two periods was determined if one of the following criteria was met: (a) the sign (positive, negative) of a significant response changed while responses remained significant, (b) the response changed from statistically insignificant to significant in either direction, (c) the response changed from statistically significant to insignificant. If any one of those criteria were not met, a 'stable' classification was assigned. Considering the site-level stability estimates were based on bootstrapped correlations, and in order to prevent spurious correlations that we could possibly expect at eight of the 152 sites per each bootstrap iteration (95% confidence level) from affecting the further analysis, we iterated the entire bootstrap procedure 999 times. Sites were finally classified if a consistent classification was assigned in at least 65% of the bootstrapped iterations. This threshold was selected to include as many sites as possible, while excluding the sites that classified inconsistently—most likely due to spurious correlations. Sites that did not meet this criterion were excluded from this analysis. Two sites from dominant climate response and five sites from the greatest change climate response were excluded.

The site-level classifications of the climate correlation stability were pooled into two datasets (regardless of species) representing the two climate–growth relationships (dominant and largest change climate responses). For each of the datasets we evaluated if spatial synchrony in 'stable' and 'unstable' changes in the climate responses was present using spatial segregation analysis with 1,000 Monte Carlo iterations (Zheng & Diggle, 2013). For any point in space, spatial segregation analysis determines the probability that a point is 'stable' or 'unstable' based on the stability classification of the sites. The probability that a point will be stable was estimated by averaging the probability distributions obtained by kernel smoothing estimations of each site (Diggle et al., 2005), where 1 is a 'stable' site and 0 is 'unstable'. Finally, the p-values of the Monte Carlo spatial segregation test were mapped across the study region highlighting the probability of similar changes in climate–growth responses for both the dominant and greatest change climate responses.

Statistical analyses were completed in R (R Development Core Team, 2018). Tree-ring datasets were processed using the *dplR* package (Bunn, 2008), climate–growth analysis conducted with the *boot* package (Canty & Ripley, 2015; Davison & Hinkley, 1997), and spatial data analyses were computed using the packages *spatialkernel* (Gómez-Rubio et al., 2017) and *spatstat* (Baddeley & Turner, 2005).

3 | RESULTS

3.1 | Monthly and seasonal climate responses

Over the period 1943–2002, correlations between climate variables and tree growth varied among the species examined (Figure S2). Although variability in correlation strength and direction was detected among sites for each climate variable and for each tree species, we report here (a) the broadly dominant relationship between tree growth and climate, and (b) the climate–growth relationship exhibiting the greatest change (strength and/or direction in correlation value) over the 1943–2002 period. Overall, the climate–growth relationships reported are generally weak to moderate ($r = -0.4 < 0 < 0.4$; Figure S2), which is consistent with other tree-ring width studies in this generally temperate region (cf. Babst et al., 2013; Scharnweber et al., 2011; Sohar et al., 2014).

Across the oak sites, growth was most strongly and significantly related to June and summer precipitation, as well as monthly measures of previous summer/autumn SPEI1 from 1943 to 2002 (Figure 2; Figure S2). June precipitation in the growth year was most consistently and positively related to oak ring width across the study region and this relationship remained generally stable for many sites over the 60 year period when the 1943–1972 and 1973–2002 intervals are compared (Figures 2 and 3), and in moving window correlation analysis (Figure 4). When correlation values for each climate variable are compared between the two 30 year periods, the greatest change in growth response is with average February temperature (Figures 2 and 3). From 1943 to 1972, oak growth was positively related to average February temperature at many sites (Figure 2), however, this sensitivity of oak growth to average February temperature collectively declines at most sites in the more recent decades (Figure 4).

Across the Scots pine sites, growth was most strongly and significantly related to mean March temperature in the growth year from 1943 to 2002 (Figure 2; Figure S2). Variables representing winter and spring mean temperature, and mean February temperature, were also often significantly related to Scots pine growth (Figure 2; Figure S2). When the climate correlation values for these related variables are compared between the two 30 year periods (Figures 2 and 3), and for March temperature in the moving window correlations (Figure 4), these relationships remain generally stable through time. However, a notable change in climate response is detected between pine growth and average January temperature at many sites (Figures 2, 3 and 4). Between 1943 and 1972 pine growth at many sites was not significantly related to January temperature, however, during the interval of 1973 and 2002 a stronger positive relationship is observed (Figures 2 and 3).

Across the European beech sites, growth was most strongly and significantly related to June precipitation in the growth year from 1943 to 2002 (Figure 2; Figure S2). Over the 60 year period, beech growth exhibits a slight increase in the positive response to June precipitation at many sites (Figures 2, 3 and 4). Despite this increase, we considered June precipitation to have the most consistent and strong effect on beech growth. When the climate–growth responses for intervals 1943–1972 and 1973–2002 are compared, the greatest change was detected for average February temperature (Figures 2 and 3). At many sites from 1943 to 1972, tree growth was positively related to February temperature suggesting a growth sensitivity to winter cold; however, from 1973 to 2002 this relationship declines (Figure 2). A further notable change in climate–growth response of beech trees was detected for SPEI variables and previous summer temperature for the two 30 year periods, where the growth of beech trees at many sites exhibits an enhanced positive response to SPEI variables
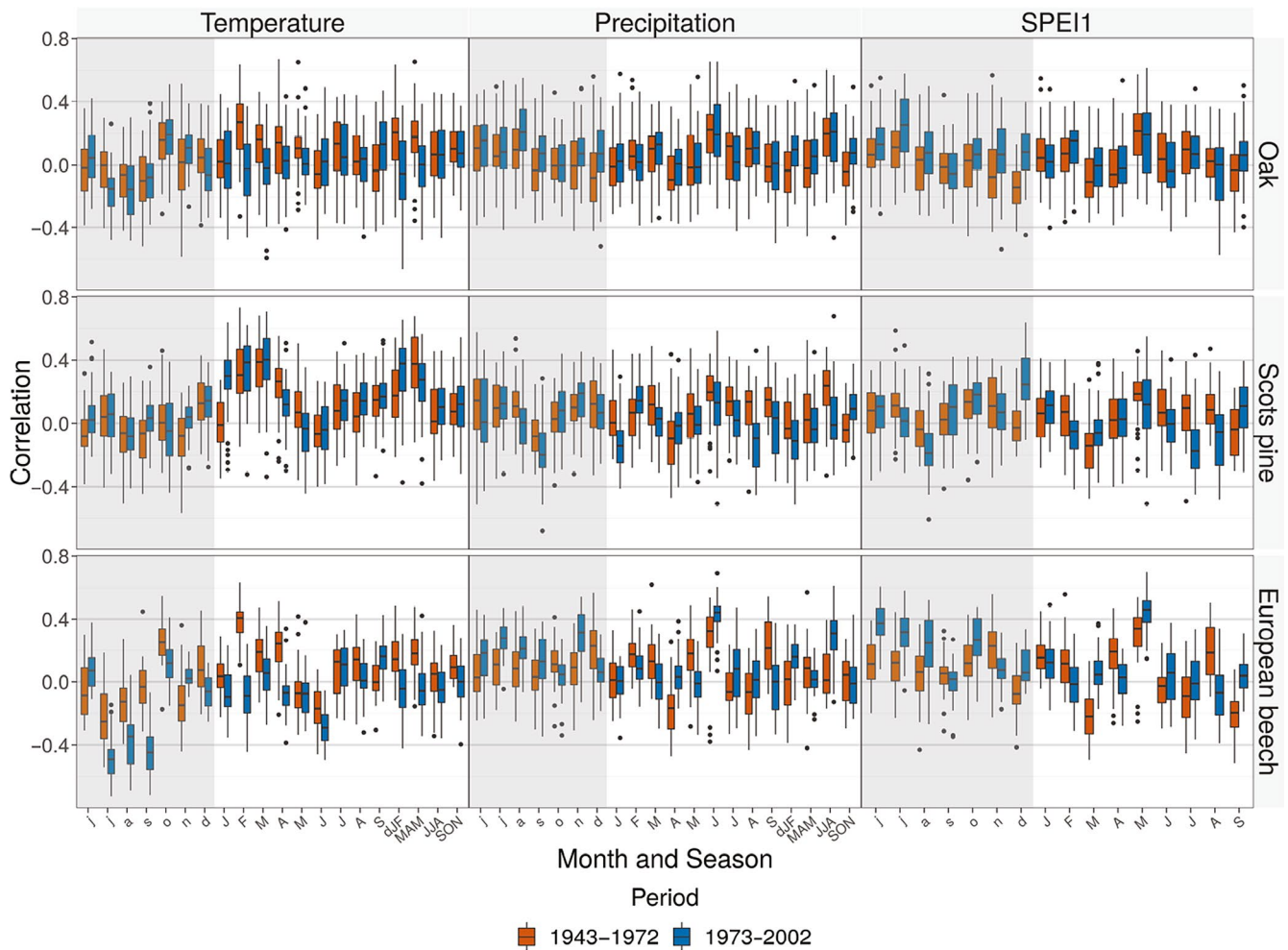
FIGURE 2 Distributions of the median bootstrapped correlations between tree-ring width chronologies and mean monthly (average monthly temperature; precipitation; SPEI1, monthly standardized precipitation–evapotranspiration index) and seasonal (summer ('JJA'): June, July and August; autumn ('SON'): September, October and November; winter ('dJF'): December, January and February; spring ('MAM'): March, April and May) climate variables for oak, Scots pine and European beech for the periods 1943–1972 and 1973–2002. Months are labelled with the first letter of the month, with lower letter case indicating previous year and upper letter case indicating current year (e.g. current year January = 'J', previous year August = 'a'). Box plots show median, lower and upper quartiles (25% and 75%) of bootstrapped correlations. Black dots are outlier correlation values that fall outside these quartiles

in the previous growing season in the more recent 30 year interval, and an increasing negative response to previous summer temperature (Figure 2; Figure S3).

Here we focus on growth responses to mean temperature; similar responses are found with minimum and maximum temperature (Figure S4). For all studied tree species and all climatic drivers, very similar relationships between growth and climate parameters were found using the residual chronologies (where autocorrelation is removed; Figure S5).

3.2 | Spatial patterns in changing climate–growth responses

Stability classification of sites for both the dominant and greatest change climate responses appear spatially segregated over the

1943–2002 interval. For the dominant climate–growth responses, the probability surface shows two 'peaks' (Figure 5). Oak and pine sites in the northeast of the study region were primarily determined to exhibit 'stable' responses to the dominant climate factor influencing tree growth. This finding suggests that this region contains a spatially contiguous arrangement of sites exhibiting similar responses to the dominant climate factor over time. A significant aggregation of 'unstable' sites was found in northeastern Germany (southwest of the study region; Figure 5). This finding indicates that at these sites the correlation strength and/or direction changed between the two 30 year periods for the dominant climate response using our classification criteria.

For the greatest change climate response 'unstable' Scots pine sites in eastern Poland, Lithuania and Latvia and some oak sites in western Latvia and Lithuania are significantly segregated in the east of the study region (Figure 5). Over southern Sweden a collection of

FIGURE 3 Spatial distribution of the correlations between tree growth and the dominant monthly climate variable influencing tree growth (a), and the climate–growth relationship that exhibited the greatest change (b) when the two subperiods of 1943–1972 and 1973–2002 were compared for each species. The average monthly climate variables correlated to tree growth at the sites in each panel are given in the inset text boxes. Triangles mark significant correlations between site chronologies and the climate parameter, while circles mark insignificant correlations
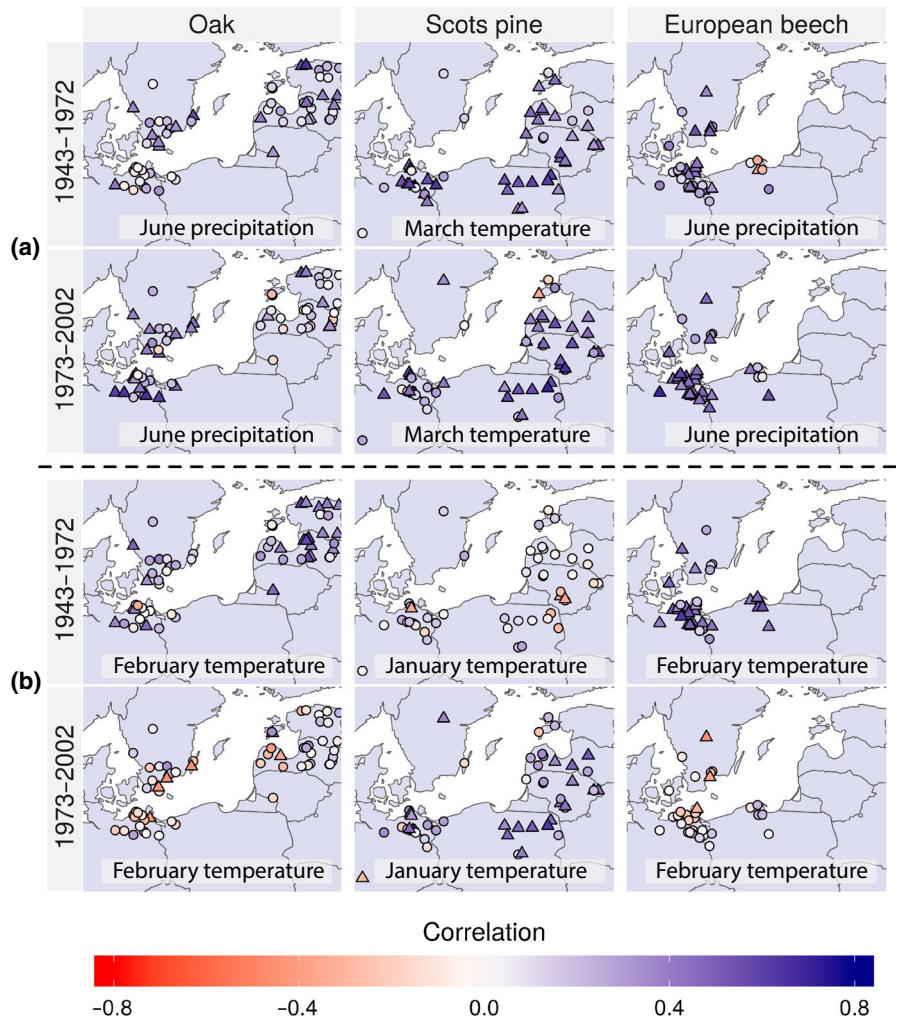

FIGURE 4 Results of moving correlation analysis estimating bootstrapped correlation values in 31 year moving windows offset by 1 year for each site included in the climate–growth analysis. Bootstrapped correlations for each site and each window are reported. The x-axis reports the last year of each 31 year window of analysis ('Period'). Colour shades were assigned based on the site longitude with dark (light) shades representing sites further west (east). Black lines represent mean bootstrapped correlation coefficients. The climate variables correlated to tree growth for each site are given in the inset text boxes
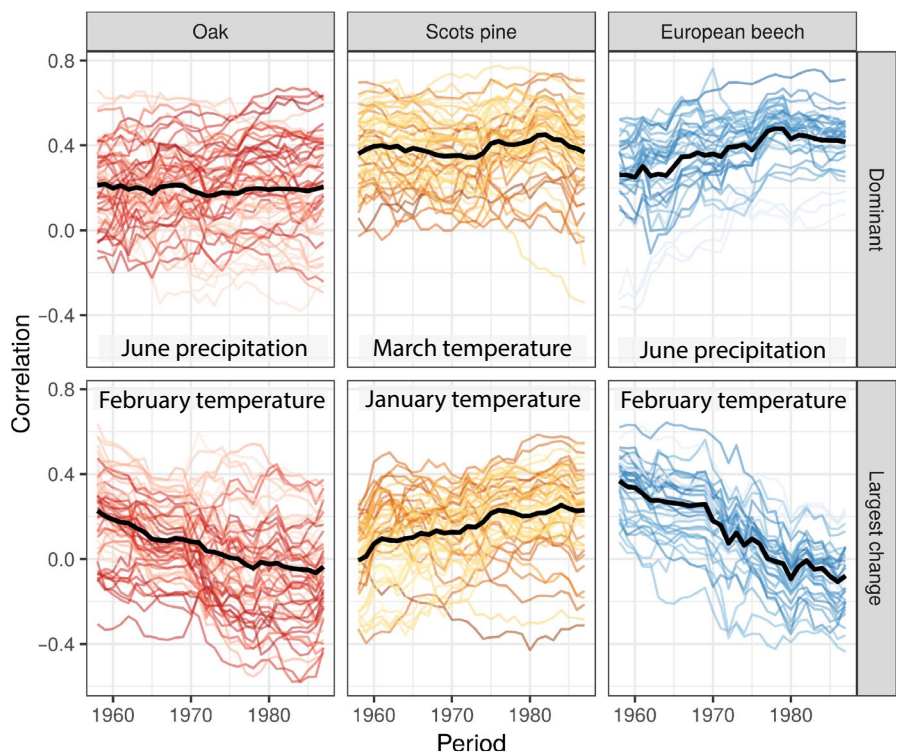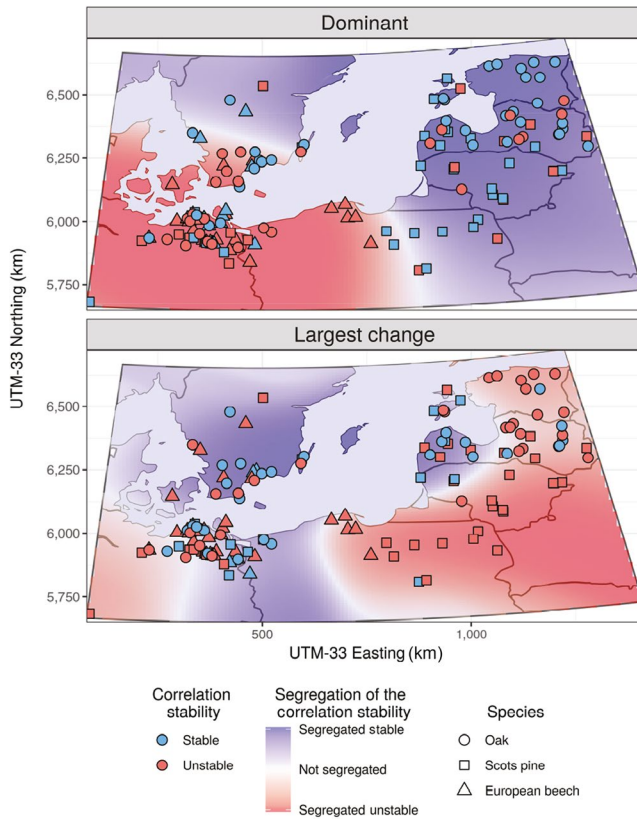
FIGURE 5 Results of spatial segregation analysis for the dominant climate–growth relationship and the climate–growth relationship that exhibited the greatest change in strength and/or direction over the 1943–2002 interval. In this analysis, a probability surface was determined by kernel-based estimation of spatial segregation. Dark red shading marks areas with a significantly higher probability of similar unstable growth change responses (segregated unstable), while dark blue shading suggests regions with a significantly higher probability of stable responses (segregated stable). See Section 2 for criteria used to classify correlation stability

'stable' sites is significantly segregated driven by the greater number and location of 'stable' responses found at oak and European beech sites (Figure 5). The high density of sites and variability in 'stable' and 'unstable' classifications in northeastern Germany resulted in no significant segregation of sites in that area of the study region (Figure 5).

4 | DISCUSSION

This tree-ring network is the largest tree-ring dataset for the south Baltic Sea region and presents a balanced perspective of tree growth by relying on site-level, tree-ring measurements collected for different purposes including ecological, climatological and management applications. Our interpretations focus on broad climatic species-specific controls on tree growth across the study region. Across the species examined, growth responses to early spring and summer climate were identified as regionally dominant, while responses to

some winter climate variables exhibited the greatest change. We focus our interpretations on these two broad patterns.

4.1 | Dominant climate–growth relationships

June precipitation had the greatest overall influence on the growth of deciduous species (albeit weakly for oak) suggesting that moisture variability broadly influences the growth of oak and European beech in the study region from 1943 to 2002 (Figure 2; Figure S2). The absence of a stronger and more spatially coherent relationship between oak growth and a dominant climate factor is consistent with previous studies near the study region that report an influence of site conditions on tree growth (e.g. Friedrichs, Trouet, et al., 2009; Rybníček et al., 2016). Furthermore, Haneca, Čufar, and Beeckman (2009) summarize the diverse climate–growth associations made between oak growth and climate variables in European studies, which include growth sensitivities to both temperature and precipitation. Despite the variability in the growth response of oak to climate and site conditions, prior studies indicate that summer moisture availability broadly controls oak tree growth in Europe (Friedrichs, Büntgen, et al., 2009; Haneca et al., 2009; Neuwirth, Schweingruber, & Winiger, 2007). In our study, there is some evidence for an increasing sensitivity of oak growth to moisture availability in more recent decades in northeastern Germany, with the strength of the correlated relationship between growth and June precipitation increasing at some sites in the latter 30 year period (Figure 3; Figure S10). This result lends support to the findings presented in Babst et al. (2019) providing further evidence that recent reduced moisture availability has influenced deciduous tree growth. Notably in our study, this finding is based on a representative network of sites collected for different tree-ring applications. In summary, our findings support the conclusions that moisture availability primarily controls oak growth and that site conditions may contribute to the absence of a spatially consistent and strong growth response of oak to climate in our study region.

Among the species examined, the growth of European beech trees showed the greatest similarity in responses to a dominant climate variable over the 60 year period from 1943 to 2002 (Figure S2). The limited distribution of beech forests in the study region and the close proximity of site locations included in the correlation analyses are likely determinants in the similarity detected. Nonetheless, our results show that in northeastern Germany, northwestern Poland and southern Sweden a positive relationship between growth and June precipitation in the growth year exists (Figures 2, 3 and 4). This result indicates that similar to oak, moisture availability in the growing season predominantly influences annual incremental growth of beech (Babst et al., 2019) and is further supported by studies conducted elsewhere throughout the range of beech (e.g. Cavin & Jump, 2017; Hacket-Pain, Cavin, Friend, & Jump, 2016; Jump, Hunt, & Penuelas, 2006). Variability in the growth responses to precipitation in the early part of the common period appears to decrease over time (Figure 4). This could be attributed to the early-life growth associated

with the late-20th and early 21st century start dates of some beech chronologies (Table S1) and the response change to environmental variability with age. Our results also indicate stronger positive responses of beech growth to June precipitation and monthly SPEI1 (Figure 2) in recent decades, suggesting that the role of moisture availability in the growing season is becoming increasingly important for growth. Recent studies on the sensitivity of European beech trees to drought events in Europe have documented an increasing response in recent decades (Latte, Lebourgeois, & Claessens, 2015), especially in the central range of the species (Cavin & Jump, 2017) and lowland settings (Latte et al., 2015).

The positive and significant correlations between Scots pine growth and February and March temperature were consistent among nearly all sites when we compared the 1943–1972 and 1973–2002 periods (Figure 2), which suggests a synchronous and stable response to late winter/early spring climate variability across the south Baltic Sea region. Previous dendrochronological studies at sites in northern Europe and at high elevation sites, document a positive relationship between annual ring width and summer temperature (Briffa, Jones, Pilcher, & Hughes, 1988; Düthorn, Holzkämper, Timonen, & Esper, 2013; Grudd et al., 2002), indicating that warmer summer temperatures promote Scots pine tree growth. Contrarily, in the European Lowlands of Germany and Poland late winter/ early spring temperature has been frequently reported to promote growth of Scots pine (Balanzategui et al., 2017; Hordo, Metslaid, & Kiviste, 2009; Koprowski, Przybylak, Zielski, & Pospieszyńska, 2012; Läänelaid & Eckstein, 2003; Pärn, 2009; Vitas, 2006), indicating warm late winter/early spring temperature conditions are important for Scots pine growth in these regions. The spatial transitions separating the disparate climate–growth responses of Scots pine growth in central and northern Europe, and the ecophysiological causal mechanisms, are not well understood or documented. Perhaps warming temperatures in the early spring extend the growing season in the south Baltic Sea region (Vitas, 2011), promoting productivity and growth. Scots pine, as an evergreen species, can capitalize on the early onset of these winter climate conditions conducive to growth (Antonova & Stasova, 1993; Gruber, Strobl, Veit, & Oberhuber, 2010). At sites further north (i.e. northern Norway) late winter and early spring climate conditions likely remain too harsh to support growth and summer temperature remains the primary factor limiting growth (Rossi et al., 2008). In North America, warmer winter and early spring temperatures are positively related to conifer growth in boreal forests, where lagged effects such as earlier snow melt and soil warming are thought to lengthen the growing season and promote early growth (D'Orangeville et al., 2016).

4.2 | Unstable growth responses to winter climate

In many of the European beech and oak populations we studied, the relationship between tree growth and late winter temperature weakens in recent decades (Figures 2 and 3). We suggest that in the early portion of the study interval (1943–1972), winter cold may

have caused reduced growth due to occurrence of winter xylem embolism (Cochard, Lemoine, Améglio, & Grainier, 2001; Pederson, Cook, Jacoby, Peteet, & Griffin, 2004; Sperry & Sullivan, 1992) and frost events (Kollas, Körner, & Randin, 2014). WInter embolisms disrupt the conductance of water in the stem of a tree leading to xylem dysfunction, a process documented in beech and oak trees in Europe including temperate and 'warm' regions (e.g. Cavender-Bares et al., 2005). Pederson et al. (2004) postulated that in anomalously cold years with more frequent or severe embolism occurrence, resources that could be used for early growth would instead be used for recovery. A recent study by Weigel et al. (2018) reports a relationship of beech growth reductions and winter cold that was enhanced towards cold-marginal populations. Furthermore, Weigel (2019) conducted a winter manipulation experiment in beech forests in northern Germany and Poland that shows winter cold, through sublethal root damage or reduced root nutrient uptake, affects beech growth negatively, a finding that is also supported by results presented in Reinmann, Susser, Demaria, and Templer (2019). In the context of our study, this finding could indicate that winter soil warming was more important in the early period (1943–1972) and is becoming less important with recent climate warming (Figure S6). Not all previous research supports a positive relationship between deciduous tree growth and late winter temperatures, with some studies documenting fast acclimation to freezing, positing that winter temperature plays a small role in shaping the cold range limit of beech (e.g. Lenz, Hoch, & Vitasse, 2016; Matisons, Purina, Adamovičs, Robalte, & Jansons, 2017).

A notable change in climate–growth sensitivity was found when the response of Scots pine growth to January temperature was compared between the 1943–1972 and 1973–2002 periods (Figures 2 and 3), and in the moving windows correlation analysis (Figure 4). The number of sites exhibiting a significant positive relationship to January temperature increases, and overall stronger positive correlations are found when testing 30 year intervals after 1973 (Figure 4). The average cold season temperatures from 1918 to 2017 (Figure S1) and over the interval of analysis (Figure S6) show a generally increasing trend that is consistent with recorded climate warming for this region (IPCC, 2014). Therefore, we suggest an increasing influence of January temperature as a factor affecting the growth of Scots pine trees in this region, a finding supported by conifer growth responses to winter climate by Babst et al. (2013). The physiological rationale for a late winter growth relationship has been discussed for some tree species (Pederson et al., 2004), however, the biological processes underpinning this persistent growth response of Scots pine trees are not well explained. The winter growth sensitivity of Scots pine could be driven by winter photosynthesis (positive carbon gain when needles are not frozen; Havranek & Tranquillini, 1995) and/or frost damage to green foliage during winter (Ensminger et al., 2004; Pederson et al., 2004). Winter photosynthesis in this region is probable provided that the freezing depth of soils in the winter is shallow (Ensminger, Schmidt, & Lloyd, 2008). Additionally, warm early-growth season temperatures (i.e. warmer January temperatures in recent decades) likely advance the onset of the vegetation period

influencing the overall length of the growing season (Vaganov, Hughes, Kirdyanov, Schweingruber, & Silkin, 1999), where shorter cold seasons result in increased productivity (wider tree-ring) and conversely, longer cold seasons would lead to decreased productivity (narrower tree-ring). Therefore, we postulate that enhanced winter photosynthetic activity driven by warmer late winter/early spring conditions coupled with possible longer growing seasons as plausible explanations for this climate–growth response.

4.3 | Spatial segregation of climate–growth responses

Significant segregation of 'stable' sites in the northeast of the study region indicates the dominant climate growth responses have remained stable between the two 30 year periods (Figure 5). This finding suggests that the growth of Scots pine trees in the northeast of the region has been consistently influenced by mean March temperature and the growth of oak by June precipitation. Furthermore, it could be considered that the influence of recent climate change on the dominant climate factors influencing tree growth in forests in the northeast of the study area is lower, at least for the climate variables considered here. A unit of segregated 'unstable' sites centred mainly in northeastern Germany was detected, and we suggest that the slightly increasing sensitivity of deciduous tree sites to June precipitation over the interval of analysis (Figure 3) resulted in many sites being classified as 'unstable' prior to the segregation analysis.

For the greatest change climate response, sites classified as 'unstable' in eastern Poland, Lithuania, and eastern Latvia aggregate to form an eastern unit of primarily Scots pine and some oak sites, which suggests a high probability for changing winter climate drivers of growth (Figure 5). We suggest that as winter climate conditions have warmed (Figures S1 and S6), trees previously limited by cold winter or spring conditions in this unit have responded similarly. This finding suggests that within the south Baltic Sea region, tree-ring sites in the eastern part of the study region may exhibit a higher probability of unstable climate–growth relationships to the winter climate variables examined in this study. In southern Sweden, most sites were classified as 'stable', indicating the effects of winter climate have remained spatially and temporally consistent, although the spatial distribution of sites is notably lower here (Figure 5).

Our application of spatial segregation analysis combines species responses to different climate variables for the two types of climate–growth responses, and applies generalized rules to classify climate–growth correlation stability. A partitioning of the network and subsequent runs of this analysis with (a) only Scots pine sites and (b) beech and oak sites combined (Figures S7 and S8), supported the interpretations from the multispecies-based spatial analysis. In order to gain a more precise estimation of spatial segregation patterns, more work is needed to buffer edge effects by increasing the spatial distribution of sites and adapt the analysis for a discontinuous spatial domain (i.e. remove the small-scale nonterrestrial landscape elements) for the kernel estimation. Therefore we present this descriptive analysis as a system-level perspective of the forest response to 20th century climate. It also represents a new approach in linking temporal variability in biological responses, represented as tree-ring chronologies, in the spatial domain.

4.4 | Possible age effects in tree-ring networks

In large-scale tree-ring network analyses, recent research has indicated that the relationships between climate and tree-ring chronologies could be inflated ('climate sensitivity bias'; Babst et al., 2018), caused by including preferentially sampled datasets that targeted older, bigger trees and/or at sites to maximize their sensitivity to a single climate parameter. Unlike recent network studies that rely heavily on sites from the ITRDB and dendroclimatological studies sampled for specific climate purposes (e.g. Babst et al., 2019), the network presented here includes sites that were collected for ecological and stand management projects in addition to dendroclimatological investigations. Furthermore, the age distribution of individual trees (inferred from site-level mean tree series length) was generally similar among sites classified as 'stable' and 'unstable' in the spatial segregation analysis for the greatest change climate variable (Figure S9). A possible exception to this interpretation includes 14 beech sites with average series lengths between 240 and 295 years that were all classified as 'unstable' (Figure S9) when the climate responses of growth to February temperatures were compared for 1943–1972 and 1973–2002. Previous research has documented an increasing sensitivity of larger trees to climate reflected in growth responses (Mérian & Lebourgeois, 2011; Trouillier et al., 2019), therefore this finding could suggest that bigger, and inherently older, trees at these 14 sites exhibit a more pronounced response to recent winter warming, or simply that smaller trees are more sensitive to frost damage. Nonetheless, due to the generally similar age-structure of our chronologies we consider the size- and/or age-related effects on climate responses to be reasonably small with a minimal influence on the broad interpretations presented from this network.

4.5 | Summary and outlook

The role of tree growth sensitivity to climate in forest carbon dynamics and changing community composition has been highlighted in many types of forests (e.g. Anderegg et al., 2015; Babst et al., 2013; Charney et al., 2016; Clark et al., 2016), including ecosystems that contain species (and populations) that are not typically considered climatically limited (e.g. Cavin & Jump, 2017). In this study we sought to provide insights on tree growth responses to recent climate change in the south Baltic Sea region. Our findings indicate summer moisture availability limits oak and European beech trees, with an enhanced effect in the latter 20th century, and considering the projected climatic drying in sub-boreal and temperate forest ecosystems, a strong influence of moisture availability in the current and previous growing seasons will likely persist. The stationary

response of Scots pine growth to February and March temperature over time, and increasing positive response to January temperature likely points to critical early season photosynthetic gains. The documented unstable growth responses to winter temperature for all species examined suggest winter climate change might release some forest trees from cold season climatic limitations in the future. How the responses we documented will contribute to ecosystem level changes in composition and patterns of distribution remains unclear at this point. However, insights from this study can provide valuable information, especially for winter climate responses, to guide the selection of tolerant provenances and refine projections of the expected changes in forest growth and terrestrial carbon budget models needed to support climate change mitigation practices.

ACKNOWLEDGEMENTS

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

ORCID

Jill E. Harvey https://orcid.org/0000-0002-6041-5852
Allan Buras https://orcid.org/0000-0003-2179-0681
Juliane Stolz https://orcid.org/0000-0002-5098-4090
Robert Weigel https://orcid.org/0000-0001-9685-6783
Jürgen Kreyling https://orcid.org/0000-0001-8489-7289
Martin Wilmking https://orcid.org/0000-0003-4964-2402

REFERENCES

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Anderegg, W. R., Kane, J. M., & Anderegg, L. D. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30. https://doi.org/10.1038/nclimate1635

Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., … Pacala, S. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528–532. https://doi.org/10.1126/science.aab1833

Antonova, G. F., & Stasova, V. V. (1993). Effects of environmental factors on wood formation in Scots pine stems. *Trees*, 7, 214–219.

Arend, M., Kuster, T., Günthardt-Goerg, M. S., & Dobbertin, M. (2011). Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiology*, 31, 287–297. https://doi.org/10.1093/treephys/tpr004

Babst, F., Bodesheim, P., Charney, N., Friend, A. D., Girardin, M. P., Klesse, S., … Evans, M. E. K. (2018). When tree rings go global: Challenges and opportunities for retro- and prospective insight. *Quaternary Science Reviews*, 197, 1–20. https://doi.org/10.1016/j.quascirev.2018.07.009

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M. P., & Frank, D. C. (2019). Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5, 1–9. https://doi.org/10.1126/sciadv.aat4313

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., … Frank, D. (2013). Site-and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, 22, 706–717. https://doi.org/10.1111/geb.12023

Baddeley, A., & Turner, R. (2005). Spatstat: An R package for analyzing spatial point patterns. *Journal of Statistical Software*, 12, 1–42.

Balanzategui, D., Knorr, A., Heussner, K. U., Wazny, T., Beck, W., Słowiński, M., … Heinrich, I. (2017). An 810-year history of cold season temperature variability for northern Poland. *Boreas*, 47, 443–453.

Beguería, S., & Vicente-Serrano, S. M. (2017). SPEI: Calculation of the standardised precipitation-evapotranspiration index. R Package Version, 1.7. Retrieved from https://CRAN.R-project.org/package=SPEI

Beguería, S., Vicente-Serrano, S. M., Reig, F., & Latorre, B. (2014). Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology*, 34, 3001–3023. https://doi.org/10.1002/joc.3887

Briffa, K. R., Jones, P. D., Pilcher, J. R., & Hughes, M. K. (1988). Reconstructing summer temperatures in northern Fennoscandinavia back to AD 1700 using tree-ring data from Scots pine. *Arctic and Alpine Research*, 20, 385–394. https://doi.org/10.2307/1551336

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, 26, 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Buras, A. (2017). A comment on the expressed population signal. *Dendrochronologia*, 44, 130–132. https://doi.org/10.1016/j.dendro.2017.03.005

Canty, A., & Ripley, B. (2015). R Package 'boot'. Retrieved from https://cran.r-project.org/web/packages/boot/

Cavender-Bares, J., Cortes, P., Rambal, S., Joffre, R., Miles, B., & Rocheteau, A. (2005). Summer and winter sensitivity of leaves and xylem to minimum freezing temperatures: A comparison of co-occurring Mediterranean oaks that differ in leaf lifespan. *New Phytologist*, 168, 597–612. https://doi.org/10.1111/j.1469-8137.2005.01555.x

Cavin, L., & Jump, A. S. (2017). Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*, 23, 362–379. https://doi.org/10.1111/gcb.13366

Cedro, A. (2004). Zmiany klimatyczne na Pomorzu Zachodnim w świetle analizy przyrostów rocznych sosny zwyczajnej, daglezji zielonej i rodzimych gatunków dębów [Climatic changes in Western Pomerania in the light of analysis of tree-ring sequences of Scots Pine, Douglas Fir, and native species of Oak]. PhD Dissertation, Wydawnictwo In Plus, Szczecin, Poland, pp. 1–149.

Cedro, A., & Cedro, B. (2018). Wpływ warunków klimatycznych i zanieczyszczenia powietrza na reakcję przyrostową sosny zwyczajnej (*Pinus sylvestris* L.) rosnącej w Lasach Miejskich Szczecina. *Leśne Prace Badawcze*, 79, 105–112.

Charney, N. D., Babst, F., Poulter, B., Record, S., Trouet, V. M., Frank, D., … Evans, M. E. K. (2016). Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecology Letters*, 19, 1119–1128. https://doi.org/10.1111/ele.12650

Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., … Zimmermann, N. E. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, 22, 2329–2352. https://doi.org/10.1111/gcb.13160

Cochard, H., Lemoine, D., Améglio, T., & Granier, A. (2001). Mechanisms of xylem recovery from winter embolism in *Fagus sylvatica*. *Tree Physiology*, 21, 27–33. https://doi.org/10.1093/treephys/21.1.27

Cook, E. R. (1985). A time-series analysis approach to tree-ring standardization. PhD dissertation, University of Arizona, Tucson, Arizona, USA.

Cook, E. R., & Holmes, R. L. (1986). *Guide for computer program ARSTAN*. Tucson, AZ: University of Arizona.

Cook, E. R., & Peters, K. (1997). Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene*, 7, 361–370. https://doi.org/10.1177/095968369700700314

D'Orangeville, L., Duchesne, L., Houle, D., Kneeshaw, D., Côté, B., & Pederson, N. (2016). Northeastern North America as a potential refugium for boreal forests in a warming climate. *Science*, 352, 1452–1455. https://doi.org/10.1126/science.aaf4951

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., … Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, 28, 2031–2064. https://doi.org/10.1002/joc.1688

Davison, A. C., & Hinkley, D. V. (1997). *Bootstrap methods and their application*. New York, NY: Cambridge University Press.

Diggle, P., Zheng, P., & Durr, P. (2005). Nonparametric estimation of spatial segregation in a multivariate point process: Bovine tuberculosis in Cornwall, UK. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 54, 645–658. https://doi.org/10.1111/j.1467-9876.2005.05373.x

Drobyshev, I., Niklasson, M., Eggertsson, O., Linderson, H., & Sonesson, K. (2008). Influence of annual weather on growth of pedunculate oak in southern Sweden. *Annals of Forest Science*, 65, 512. https://doi.org/10.1051/forest:2008033

Durrant, T. H., De Rigo, D., & Caudullo, G. (2016). *Pinus sylvestris* in Europe: distribution, habitat, usage and threats. European Atlas of Forest Tree Species, Luxembourg: Publication Office of the European Union (pp. 132–133).

Düthorn, E., Holzkämper, S., Timonen, M., & Esper, J. (2013). Influence of micro-site conditions on tree-ring climate signals and trends in central and northern Sweden. *Trees*, 27, 1395–1404. https://doi.org/10.1007/s00468-013-0887-8

Ensminger, I., Schmidt, L., & Lloyd, J. (2008). Soil temperature and intermittent frost modulate the rate of recovery of photosynthesis in Scots pine under simulated spring conditions. *New Phytologist*, 177, 428–442. https://doi.org/10.1111/j.1469-8137.2007.02273.x

Ensminger, I., Sveshnikov, D., Campbell, D. A., Funk, C., Jansson, S., Lloyd, J., … Äquist, G. (2004). Intermittent low temperatures constrain spring recovery of photosynthesis in boreal Scots pine forests. *Global Change Biology*, 10, 995–1008. https://doi.org/10.1111/j.1365-2486.2004.00781.x

Estonian Weather Service. (2018). Climate normals. Retrieved from http://www.ilmateenistus.ee/kliima/kliimanormid/ohutemperatuur/?xml:lang=en

Friedrichs, D. A., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B., & Löffler, J. (2009). Complex climate controls on 20th century oak growth in Central-West Germany. *Tree Physiology*, 29, 39–51. https://doi.org/10.1093/treephys/tpn003

Friedrichs, D. A., Trouet, V., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B., & Löffler, J. (2009). Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*, 23, 729–739. https://doi.org/10.1007/s00468-009-0315-2

Gilliam, F. S. (2016). Forest ecosystems of temperate climatic regions: From ancient use to climate change. *New Phytologist*, 212, 871–887. https://doi.org/10.1111/nph.14255

Gómez-Rubio, V., Zheng, P., Diggle, P., Cotton, R., Murta, A., Shewchuk, J. R., …Rowlingson, B. (2017). spatialkernel: Non-parametric estimation of spatial segregation in a multivariate point process. Retrieved from https://cran.r-project.org/web/packages/spatialkernel/index.html

Gruber, A., Strobl, S., Veit, B., & Oberhuber, W. (2010). Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiology*, 30, 490–501. https://doi.org/10.1093/treephys/tpq003

Grudd, H., Briffa, K. R., Karlén, W., Bartholin, T. S., Jones, P. D., & Kromer, B. (2002). A 7400-year tree-ring chronology in northern Swedish Lapland: Natural climatic variability expressed on annual to millennial timescales. *The Holocene*, 12, 657–665. https://doi.org/10.1191/0959683602hl578rp

Hacket-Pain, A. J., Cavin, L., Friend, A. D., & Jump, A. S. (2016). Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research*, 135, 897–909. https://doi.org/10.1007/s10342-016-0982-7

Hamann, A., Wang, T., Spittlehouse, D. L., & Murdock, T. Q. (2013). A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. *Bulletin of the American Meteorological Society*, 94, 1307–1309. https://doi.org/10.1175/BAMS-D-12-00145.1

Haneca, K., Čufar, K., & Beeckman, H. (2009). Oaks, tree-rings and wooden cultural heritage: A review of the main characteristics and applications of oak dendrochronology in Europe. *Journal of Archaeological Science*, 36, 1–11. https://doi.org/10.1016/j.jas.2008.07.005

Havranek, W. M., & Tranquillini, W. (1995). Physiological processes during winter dormancy and their ecological significance. In W. K. Smith & T. M. Hinckley (Eds.), *Ecophysiology of coniferous forests* (pp. 95–124). London, UK: Academic Press.

Helama, S., Lindholm, M., Timonen, M., & Eronen, M. (2004). Detection of climate signal in dendrochronological data analysis: A comparison of tree-ring standardization methods. *Theoretical and Applied Climatology*, 79, 239–254. https://doi.org/10.1007/s00704-004-0077-0

Helama, S., Sohar, K., Läänelaid, A., Bijak, S., & Jaagus, J. (2018). Reconstruction of precipitation variability in Estonia since the eighteenth century, inferred from oak and spruce tree rings. *Climate Dynamics*, 50, 4083–4101. https://doi.org/10.1007/s00382-017-3862-z

Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 73, 69–78.

Hordo, M., Metslaid, S., & Kiviste, A. (2009). Response of Scots pine (*Pinus sylvestris* L.) radial growth to climate factors in Estonia. *Baltic Forestry*, 15, 195–205.

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. In Core Writing Team, R. K. Pachauri & L. A. Meyer (Eds.). Geneva, Switzerland: Author, 151 pp.

Jansons, Ā., Matisons, R., Šēnhofa, S., Katrevičs, J., & Jansons, J. (2016). High-frequency variation of tree-ring width of some native and alien tree species in Latvia during the period 1965–2009. *Dendrochronologia*, 40, 151–158.

Jump, A. S., Hunt, J. M., & Penuelas, J. (2006). Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, 12, 2163–2174. https://doi.org/10.1111/j.1365-2486.2006.01250.x

Klesse, S., Babst, F., Lienert, S., Spahni, R., Joos, F., Bouriaud, O., … Frank, D. C. (2018). A combined tree ring and vegetation model assessment of European forest growth sensitivity to interannual climate

variability. *Global Biogeochemical Cycles*, 32, 1226–1240. https://doi.org/10.1029/2017GB005856

Klesse, S., DeRose, R. J., Guiterman, C. H., Lynch, A. M., O'Connor, C. D., Shaw, J. D., & Evans, M. E. (2018). Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. *Nature Communications*, 9, 5336. https://doi.org/10.1038/s41467-018-07800-y

Kodra, E., Steinhaeuser, K., & Ganguly, A. R. (2011). Persisting cold extremes under 21st-century warming scenarios. *Geophysical Research Letters*, 38(8). https://doi.org/10.1029/2011GL047103

Kollas, C., Körner, C., & Randin, C. F. (2014). Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *Journal of Biogeography*, 41, 773–783. https://doi.org/10.1111/jbi.12238

Koprowski, M., Przybylak, R., Zielski, A., & Pospieszyńska, A. (2012). Tree rings of Scots pine (*Pinus sylvestris* L.) as a source of information about past climate in northern Poland. *International Journal of Biometeorology*, 56, 1–10.

Kreyling, J. (2010). Winter climate change: A critical factor for temperate vegetation performance. *Ecology*, 91, 1939–1948. https://doi.org/10.1890/09-1160.1

Kreyling, J., & Henry, H. A. (2011). Vanishing winters in Germany: Soil frost dynamics and snow cover trends, and ecological implications. *Climate Research*, 46, 269–276. https://doi.org/10.3354/cr00996

Läänelaid, A., & Eckstein, D. (2003). Development of a tree-ring chronology of Scots pine (*Pinus sylvestris* L.) for Estonia as a dating tool and climatic proxy. *Baltic Forestry*, 9, 76–82.

Läänelaid, A., Sohar, K., & Meikar, T. (2008). Present state and chronology of oaks in an oak forest in Saaremaa Island, Estonia. *Baltic Forestry*, 14, 34–43.

Latte, N., Lebourgeois, F., & Claessens, H. (2015). Increased tree-growth synchronization of beech (*Fagus sylvatica* L.) in response to climate change in northwestern Europe. *Dendrochronologia*, 33, 69–77. https://doi.org/10.1016/j.dendro.2015.01.002

Lenz, A., Hoch, G., & Vitasse, Y. (2016). Fast acclimation of freezing resistance suggests no influence of winter minimum temperature on the range limit of European beech. *Tree Physiology*, 36, 490–501. https://doi.org/10.1093/treephys/tpv147

Lindner, M., Fitzgerald, J. B., Zimmermann, N. E., Reyer, C., Delzon, S., van der Maaten, E., … Hanewinkel, M. (2014). Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *Journal of Environmental Management*, 146, 69–83. https://doi.org/10.1016/j.jenvman.2014.07.030

Matisons, R., Elferts, D., & Brūmelis, G. (2013). Possible signs of growth decline of pedunculate oak in Latvia during 1980–2009 in treering width and vessel size. *Baltic Forestry*, 19, 137–142.

Matisons, R., Puriņa, L., Adamovičs, A., Robalte, L., & Jansons, Ā. (2017). European beech in its northeasternmost stands in Europe: Varying climate–growth relationships among generations and diameter classes. *Dendrochronologia*, 45, 123–131. https://doi.org/10.1016/j.dendro.2017.08.004

Mérian, P., & Lebourgeois, F. (2011). Size-mediated climate–growth relationships in temperate forests: A multi-species analysis. *Forest Ecology and Management*, 261, 1382–1391. https://doi.org/10.1016/j.foreco.2011.01.019

Millar, C. I., & Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, 349, 823–826. https://doi.org/10.1126/science.aaa9933

Mitchell, T. D., & Jones, P. D. (2005). An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, 25, 693–712. https://doi.org/10.1002/joc.1181

Neuwirth, B., Schweingruber, F. H., & Winiger, M. (2007). Spatial patterns of central European pointer years from 1901 to 1971. *Dendrochronologia*, 24, 79–89. https://doi.org/10.1016/j.dendro.2006.05.004

Pärn, H. (2009). Temporal history of relationships between Scots pine (*Pinus sylvestris* L.) radial growth and mean monthly temperatures. *Baltic Forestry*, 15, 48–57.

Pederson, N., Cook, E. R., Jacoby, G. C., Peteet, D. M., & Griffin, K. L. (2004). The influence of winter temperatures on the annual radial growth of six northern range margin tree species. *Dendrochronologia*, 22, 7–29. https://doi.org/10.1016/j.dendro.2004.09.005

Peters, R. (1997). *Beech forests* (Vol. 24). Dordrecht, The Netherlands: Springer Science+Business Media.

R Development Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reinmann, A. B., Susser, J. R., Demaria, E. M. C., & Templer, P. H. (2019). Declines in northern forest tree growth following snowpack decline and soil freezing. *Global Change Biology*, 25, 420–430. https://doi.org/10.1111/gcb.14420

Rossi, S., Deslauriers, A., Griçar, J., Seo, J. W., Rathgeber, C. B. K., Anfodillo, T., … Jalkanen, R. (2008). Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography*, 17, 696–707. https://doi.org/10.1111/j.1466-8238.2008.00417.x

Rybníček, M., Cermak, P., Prokop, O., Zid, T., Trnka, M., & Kolar, T. (2016). Oak (*Quercus* spp.) response to climate differs more among sites than among species in central Czech Republic. *Dendrobiology*, 75, 55–65.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., & Wilmking, M. (2011). Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, 262, 947–961.

Scharnweber, T., Manthey, M., & Wilmking, M. (2013). Differential radial growth patterns between beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on periodically waterlogged soils. *Tree Physiology*, 33, 425–437.

Seftigen, K., Frank, D. C., Björklund, J., Babst, F., & Poulter, B. (2018). The climatic drivers of normalized difference vegetation index and tree-ring-based estimates of forest productivity are spatially coherent but temporally decoupled in Northern Hemispheric forests. *Global Ecology and Biogeography*, 27, 1352–1365. https://doi.org/10.1111/geb.12802

Senf, C., & Seidl, R. (2018). Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Global Change Biology*, 24(3), 1201–1211. https://doi.org/10.1111/gcb.13897

Seynave, I., Gégout, J. C., Hervé, J. C., & Dhôte, J. F. (2008). Is the spatial distribution of European beech (*Fagus sylvatica* L.) limited by its potential height growth? *Journal of Biogeography*, 35, 1851–1862.

Sohar, K., Läänelaid, A., Eckstein, D., Helama, S., & Jaagus, J. (2014). Dendroclimatic signals of pedunculate oak (*Quercus robur* L.) in Estonia. *European Journal of Forest Research*, 133, 535–549. https://doi.org/10.1007/s10342-014-0783-9

Sohar, K., Vitas, A., & Läänelaid, A. (2012). Sapwood estimates of pedunculate oak (*Quercus robur* L.) in eastern Baltic. *Dendrochronologia*, 30, 49–56. https://doi.org/10.1016/j.dendro.2011.08.001

Sperry, J. S., & Sullivan, J. E. (1992). Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology*, 100, 605–613. https://doi.org/10.1104/pp.100.2.605

Tarr, G. A., Shringi, S., Phipps, A. I., Besser, T. E., Mayer, J., Oltean, H. N., … Rabinowitz, P. (2018). Geogenomic segregation and temporal trends of human pathogenic *Escherichia coli* O157: H7, Washington, USA, 2005–2014. *Emerging Infectious Diseases*, 24, 32.

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, 91, 760–781. https://doi.org/10.1111/brv.12193

Thornthwaite, C. W. (1948). An approach toward a rational classification of climate. *Geographical Review*, 38, 55–94. https://doi.org/10.2307/210739

Trouillier, M., van der Maaten-Theunissen, M., Scharnweber, T., Würth, D., Burger, A., Schnittler, M., & Wilmking, M. (2019). Size matters – A comparison of three methods to assess age- and size-dependent climate sensitivity of trees. *Trees*, *33*, 183–192. https://doi.org/10.1007/s00468-018-1767-z

Vaganov, E. A., Hughes, M. K., Kirdyanov, A. V., Schweingruber, F. H., & Silkin, P. P. (1999). Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, *400*, 149. https://doi.org/10.1038/22087

van der Maaten, E., Mehl, A., Wilmking, M., & van der Maaten-Theunissen, M. (2017). Tapping the tree-ring archive for studying effects of resin extraction on the growth and climate sensitivity of Scots pine. *Forest Ecosystems*, *4*, 7. https://doi.org/10.1186/s40663-017-0096-9

van der Maaten, E., Pape, J., van der Maaten-Theunissen, M., Scharnweber, T., Smiljanić, M., Cruz-García, R., & Wilmking, M. (2018). Distinct growth phenology but similar daily stem dynamics in three co-occurring broadleaved tree species. *Tree Physiology*, *38*, 1820–1828. https://doi.org/10.1093/treephys/tpy042

van der Maaten-Theunissen, M., Bümmerstede, H., Iwanowski, J., Scharnweber, T., Wilmking, M., & van der Maaten, E. (2016). Drought sensitivity of beech on a shallow chalk soil in northeastern Germany – a comparative study. *Forest Ecosystems*, *3*, 24. https://doi.org/10.1186/s40663-016-0083-6

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, *23*, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vitas, A. (2004). Dendroclimatological research of Scots pine (*Pinus sylvestris* L.) in the Baltic coastal zone of Lithuania. *Baltic Forestry*, *10*, 65–71.

Vitas, A. (2006). Sensitivity of Scots pine trees to winter colds and summer droughts: Dendroclimatological investigation. *Baltic Forestry*, *12*, 220–226.

Vitas, A. (2011). Seasonal growth variations of pine, spruce, and birch recorded by band dendrometers in NE Lithuania. *Baltic Forestry*, *17*, 197–204.

Vitas, A., & Zunde, M. (2019). Sapwood rings estimation for *Pinus sylvestris* L. in Lithuania and Latvia. *Tree-Ring Research*, *75*, 1–13. https://doi.org/10.3959/1536-1098-75.1.1

Weigel, R. (2019). *Temperate deciduous forests in Europe under climate change: Impacts across spatial scales and sensitivity to winter soil temperature variation* (Doctoral dissertation, University of Greifswald). Retrieved from https://nbn-resolving.org/urn:nbn:de:gbv:9-opus-26780

Weigel, R., Muffler, L., Klisz, M., Kreyling, J., van der Maaten-Theunissen, M., Wilmking, M., & van der Maaten, E. (2018). Winter matters: Sensitivity to winter climate and cold events increases towards the cold distribution margin of European beech (*Fagus sylvatica* L.). *Journal of Biogeography*, *45*, 2779–2790.

Wigley, T. M., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, *23*, 201–213. https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Wu, X., Li, X., Liu, H., Ciais, P., Li, Y., Xu, C., ... Zhang, C. (2019). Uneven winter snow influence on tree growth across temperate China. *Global Change Biology*, *25*(1), 144–154. https://doi.org/10.1111/gcb.14464

Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y., & Wan, S. (2014). Terrestrial carbon cycle affected by non-uniform climate warming. *Nature Geoscience*, *7*, 173. https://doi.org/10.1038/ngeo2093

Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., & Menzel, A. (2014). Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. *Global Change Biology*, *20*, 3767–3779. https://doi.org/10.1111/gcb.12637

Zheng, P. P., & Diggle, P. (2013). Spatialkernel: Nonparameteric estimation of spatial segregation in a multivariate point process. R package version 0.4-19.

SUPPORTING INFORMATION

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