

RESEARCH PAPER

Winter matters: Sensitivity to winter climate and cold events increases towards the cold distribution margin of European beech (*Fagus sylvatica* L.)

Robert Weigel¹  | Lena Muffler¹ | Marcin Klisz²  | Juergen Kreyling¹  |
 Marieke van der Maaten-Theunissen³ | Martin Wilmking⁴ | Ernst van der Maaten³

¹Experimental Plant Ecology, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

²Department of Silviculture and Genetics of Forest Trees, Forest Research Institute, Raszyn, Poland

³Forest Growth and Woody Biomass Production, Institute of Forest Growth and Forest Computer Sciences, TU Dresden, Tharandt, Germany

⁴Landscape Ecology and Ecosystem Dynamics, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

Correspondence

Robert Weigel, Experimental Plant Ecology, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany.
 Email: robert.weigel@uni-greifswald.de

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Abstract

Aim: The dominant forest tree in Europe, European beech (*Fagus sylvatica* L.), covers large areas of continental Europe and thus experiences diverse climatic conditions. In the face of predicted climate change and shifts of distribution ranges, it is important to understand the diverse climate–growth relationships towards distribution margins. Beech is generally reported to be sensitive to summer drought towards dry and continental regions; yet, few studies have investigated climate sensitivity towards the cold distribution margin of beech. We hypothesized that at colder sites (a) growth of beech is more sensitive to winter cold, (b) growth is less influenced by summer drought, and (c) stand-wide growth reductions (negative pointer years) are related to extreme winter cold events.

Taxon: European beech (*Fagus sylvatica* L.).

Location: A large gradient of decreasing winter temperature ($\Delta T > 4$ K along 500 km) from Rostock (Germany) to Gdańsk (Poland).

Methods: We analysed climate–growth relationships and the nature of growth reductions of 11 beech stands from more central to cold marginal beech populations.

Results: Towards the cold marginal populations, growth became increasingly sensitive to winter cold (February temperature) and less sensitive to summer water availability (June precipitation). Likewise, negative pointer years coincided with winter cold anomalies at the colder sites and with summer drought anomalies at the warmer sites. Thus, over the studied gradient, the general sensitivity of beech to summer drought transitions into sensitivity to winter cold.

Main conclusions: A range shift of beech across the current cold distribution margin is often assumed to compensate for habitat and productivity losses of drought-prone southern and central populations. With respect to the winter cold sensitivity found in our study, such assumptions should be taken with caution. Since winter cold events are predicted to persist with similar frequency and magnitude even during predicted climate warming, beech populations in the newly colonized habitat might be significantly sensitive to winter cold.



KEYWORDS

cold distribution border, cold events, dendroecology, European beech, forest ecology, range margin ecology, winter cold sensitivity, winter ecology

1 | INTRODUCTION

Tree species distributions are linked to climate through direct effects of climate conditions on tree physiological functioning (Körner et al., 2016). Consequently, potential distribution ranges can be modelled by small sets of bioclimatic variables on a regional to global scale (Kramer et al., 2010; Salter, Duputie, Gaucherel, & Chuine, 2015; Sykes, Prentice, & Cramer, 1996). Generally, climate envelope models suggest that tree growth and distribution range limits are controlled by winter temperature towards the north and by water availability towards the south as well as towards local discontinuities of the distribution range (Sykes et al., 1996). European beech (*Fagus sylvatica* L.), with its high phenotypic plasticity (Meier & Leuschner, 2008; Stojnić et al., 2015) and intraspecific genetic variability (Kreyling et al., 2012, 2014), is the dominant forest tree species in Europe, covering an exceptionally broad ecological range of soil types and climates in its distribution range (Bolte, Czajkowski, & Kompa, 2007; Leuschner, Meier, & Hertel, 2006). Beech naturally dominates under moderate soil moisture (dry to moist) and moderate soil acidity (acid to alkaline) conditions (Bolte et al., 2007; Leuschner & Ellenberg, 2017). Depending on the region, drought (water availability in summer) and cold (winter temperature threshold, growing season length, late frost) are the main limiting factors of the potential distribution range of European beech (Bolte et al., 2007; Giesecke, Hickler, Kunkel, Sykes, & Bradshaw, 2007).

Fritts (1966) recognized that one can observe higher climate sensitivity of tree growth to certain limiting climatic factors towards the margin of a species' distribution. This may be explained by the assumption that climate sensitivity of plants is greater towards both the dry and cold ends of ecological gradients because climate stress there becomes increasingly limiting to the point that potential distribution limits are expressed due to total growth cessation (Brown, Stevens, & Kaufman, 1996; Fritts, 1966; Normand et al., 2009). Based on multisite dendroecological studies, drought has emerged as a general driver of growth for beech across Europe (Dittmar, Zech, & Elling, 2003; Hacket-Pain, Cavin, Friend, & Jump, 2016; Hacket-Pain, Lageard, & Thomas, 2017; Jump, Hunt, & Peñuelas, 2006; Knutzen, Dulamsuren, Meier, & Leuschner, 2017; Lebourgeois, Bréda, Ulrich, & Granier, 2005), though drought sensitivity has been indicated to increase towards drier sites along continental or elevational gradients (Jump et al., 2006; Roibu, Popa, Kirchhefer, & Palaghianu, 2017; Scharnweber et al., 2011). However, this observation might be biased due to research focusing on the southern to south-eastern dry parts of the distribution range (Dittmar et al., 2003; Roibu et al., 2017), on countries at the southern dry distribution margin (Jump et al., 2006; Lebourgeois et al., 2005), and on gradients from the central distribution range to its southern edge (Hacket-Pain et al., 2016).

The cold north-eastern distribution margin (e.g., northern Poland) has so far been underrepresented in studies on climate sensitivity of European beech. With climate change-induced warming, a range shift of beech across the current north-eastern cold distribution border is projected to buffer range losses from increasing drought stress at the southern distribution margin (Kramer et al., 2010; Salinger, 2005; Salter et al., 2015). Besides warming, though, climate will additionally become more variable (Salinger, 2005). This means that extreme cold events may persist or even increase in frequency in Europe (Kodra & Ganguly, 2014; Kodra, Steinhäuser, & Ganguly, 2011; Petoukhov & Semenov, 2010). For beech, late frost events and subsequent leaf senescence are often followed by a considerable reduction in growth (Dittmar, Fricke, & Elling, 2006; Príncipe et al., 2017). Although beech populations at colder sites may be locally adapted to cold conditions (Kreyling, Schmid, Aas, & Higgins, 2015; Kreyling et al., 2014), late frost-related growth reductions generally increase towards colder sites where frost severity is greater (Dittmar et al., 2006; Príncipe et al., 2017). Príncipe et al. (2017) suggested that impacts of late frost events may become more frequent in the future with warmer and more variable climate conditions, as early spring warm spells and leaf unfolding may increase the risk of late frost damage.

In contrast to the high sensitivity of young leaves to late frost events, dormant buds and cambium of European beech can acclimate well to cold conditions and are thus particularly resistant to winter frost (Lenz, Hoch, & Vitasse, 2016). Consequently, direct damage of winter cold events to above ground tissue may not explain the cold distribution margin of beech (Körner et al., 2016; Lenz et al., 2016). Likewise, the cold distribution is probably not limited by regeneration because beech recruits well at the cold distribution margin and young beech saplings can establish successfully beyond the cold distribution margin of adult trees (Körner et al., 2016; Matisons, Puriņa, Adamovičs, Robalte, & Jansons, 2017; Vitasse et al., 2012). Although winter cold events may not explain the cold distribution limit alone, resulting soil frost during winter cold events may still indirectly reduce above ground biomass production (Groffman et al., 2001; Reinmann & Templer, 2016; Vitousek et al., 1997). Indeed, at forest plantations across the eastern cold distribution margin, European beech was found to be sensitive to multiple stressors across the year: winter cold, cold and dry springs, as well as hot summers (Augustaitis, Jasineviciene, Girgzdiene, Kliucius, & Marozas, 2012; Matisons et al., 2017). Thus, experiments and dendroecology have indicated that growth reductions and sensitivity to winter temperature may increase towards colder sites (Augustaitis et al., 2012; Groffman et al., 2001; Reinmann & Templer, 2016). However, the issue remains that too few studies have been conducted at the cold distribution margin to appropriately test the assumption



that a future range expansion beyond the current cold margin can compensate for habitat loss at the dry margin. Therefore, studies on gradients of winter cold (i.e., towards the north-eastern cold distribution margin) are urgently needed and will complement climate–growth analyses from the southern, south-eastern and central distribution range.

This study analysed the climate sensitivity of European beech along a gradient from the central distribution area of European beech in northern Germany towards the natural cold distribution margin in northern Poland. The focus of our study was winter temperature signals. We hypothesized that (a) the growth response to winter temperature is more pronounced at colder sites, (b) with increasing cold stress, responses to summer drought (water availability) are less pronounced, and (c) relatedness of negative growth anomalies to cold events, rather than to drought events, increases towards the cold distribution margin.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was performed in 11 managed mature forest stands with European beech as the dominant tree species. The stands follow a gradient of winter temperature from Billenhagen near Rostock, Germany (-0.5°C mean coldest month temperature) to Kartuzy near Gdańsk, Poland (-4.7°C mean coldest month temperature, Table 1, Figure 1). During the last few decades, there has been a trend towards slightly increasing annual mean temperatures at the six warmest study sites and slightly warmer winters at the moderately cold sites, though there has been no significant warming trend at the coldest sites (Figure S1 in Appendix S1 in Supporting Information). The studied gradient spans from the central to the north-eastern cold margin of the continuous distribution range of European beech (Bolte et al., 2007). With a difference in winter temperature of $\Delta T > 4\text{ K}$ along 500 km, the study gradient covers a relatively large part of the temperature range of beech; in contrast, the precipitation differences are relatively small between the study sites (Figure 1a). We selected sites with similar proximity to the Baltic Sea and thus comparable seasonal climatic patterns and mean annual precipitation sums (540–669 mm). There has been no trend of changing precipitation at the study sites during the last decades (Figure S2 in Appendix S1). Owing to the same glacial history, all sites are characterized by sandy soils of type Cambisol with comparable soil texture of mostly sandy silt to silty sand (Table S1 in Appendix S1). Thus, our selection focus was on all sites having comparable water holding capacity and a comparable hydrological setting. Within this framework of broader geographical considerations, we selected individual sites with comparable stand structure (tree height, tree diameter, canopy closure, Table 1). This is a prerequisite for our multisite gradient analysis because climate–growth relationships can depend on the canopy setting (Matisons et al., 2017). To fulfil this major prerequisite of comparable stand structure, tree age varied between sites. We choose typical managed mature beech

forest sites, which mostly consist of co-dominant and dominant trees. In doing so, the trees of all sites were similarly linked to soil and atmospheric conditions. Furthermore, intraspecific competition signals, which are typical for suppressed trees and may blur climate–growth relationships, were reduced.

2.2 | Dendrochronological sampling and sample processing

In the autumn of 2015, two increment cores per tree were extracted at breast height (1.3 m) from at least 20 co-/dominant trees per site. Cores were air-dried, glued on wooden mounts and sanded with progressively finer sandpaper to highlight annual rings. For each site, scanned cores ('Mikrotek ScanMaker 1000XL Plus' at 1,200 dpi) were measured and cross-dated with the 'CooRecorder' and 'CDendro' software (8.1, Cybis Electronic & Data, 2015). Individual tree-ring series, built by averaging two cores per tree, were detrended using a cubic smoothing spline with a 50% frequency cut-off at 30 years, followed by autoregressive modelling. Detrending by a smoothing spline accentuates climate-induced growth fluctuations while removing longer-term trends that may, for example, reflect tree ageing or effects of forest management activities (Cook & Peters, 1981). We chose to subsequently remove the autocorrelation from the data by autoregressive modelling (prewhitening) to further accentuate the high-frequency signal of the tree-ring series, facilitating the detection of climatic signals that fluctuate from year-to-year (Piovesan & Schirone, 2000). Detrended tree-ring series were then calculated by dividing the observed by the predicted values. Stand chronologies were constructed for each site by calculating a bi-weight robust mean of the index series of individual trees, as suggested as a standard dendroecological data preparation step for sound subsequent climate–growth analysis (Cook & Kairiūkštis, 1990; Fritts, 2001). A limited number of cores could not be dated due to rotten segments, and were thus excluded (Table 1).

Both r_{bar} (Pearson's correlation coefficient indicating the strength of the common signal in growth series from individual trees within a stand) and expressed population signal (EPS; a measure of quality of common growth signal within a population, Wigley, Briffa, & Jones, 1984) were calculated from detrended tree-ring series, whereas the mean sensitivity (indicator for general climate sensitivity of growth) and 1st order autocorrelation (indicator for effects of previous-year conditions upon current year's growth) were calculated from index series (raw ring widths of each tree divided by the average ring width of the tree). These measures were calculated for the robust common overlap period from 1940–2009 and used to assess the quality and characteristics of the chronologies. We applied linear regression modelling to test if these measures changed along the studied temperature gradient. Here and in all following analyses we define a p -value threshold of $p < 0.05$ for accepting statistical significance. Detrending, chronology building and calculation of chronology statistics was performed using the 'dplR' package 1.6.4 (Bunn, 2008) in R 3.3.1 (R Core Team, 2016).

TABLE 1 Characteristics of the study sites, which are listed in descending order of winter temperature. Geographic position (°E: longitude degree, °N: latitude degree); mean annual precipitation sum (MAP), mean annual temperature (MAT) and mean coldest month temperature (MCMT) for the climate normal period 1961–1990; number of dated trees used to build chronologies (N_{Tree}), series length (l_{Series}) as an indicator of approximate tree age, tree height (h) and diameter at breast height (DBH)

Site ID	Site	°E	°N	MAP (mm)	MAT (°C)	MCMT (°C)	N_{Tree}	l_{Series} (years)	h (m)	DBH (cm)
BH	Billenhagen	12.32	54.12	587	8.0	−0.5	18	83 ± 4	27.1 ± 4.2	43.0 ± 4.6
HH	Hanshagen	13.51	54.05	569	8.2	−0.9	27	76 ± 5	31.7 ± 2.3	43.2 ± 5.9
NZ	Neustrelitz	13.14	53.39	579	7.9	−1.5	20	141 ± 14	35.6 ± 2.8	44.7 ± 2.9
BB	Afrika in Brandenburg	13.83	53.11	567	8.4	−1.9	18	91 ± 5	32.2 ± 1.5	45.6 ± 3.2
GR	Gryfino	14.73	53.32	567	8.2	−2.6	25	167 ± 35	39.7 ± 2.5	52.8 ± 11.0
DE	Debno	14.56	52.71	540	8.8	−2.9	20	91 ± 3	32.6 ± 2.4	42.0 ± 3.9
WE	Wejherowo	18.08	54.72	622	7.0	−3.0	20	106 ± 8	33.5 ± 2.3	40.9 ± 5.4
DA	Damnica	17.55	54.59	669	7.3	−3.8	22	112 ± 5	35.9 ± 2.9	44.6 ± 4.9
GD	Golub-Dobrzyn	18.90	53.30	558	7.4	−4.1	22	115 ± 14	32.3 ± 2.9	55.6 ± 8.1
KO	Kolbudy	18.43	54.25	592	5.6	−4.4	20	130 ± 8	34.5 ± 1.9	38.6 ± 4.4
KA	Kartuzy	18.15	54.24	620	5.8	−4.7	39	102 ± 8	34.5 ± 3.4	37.0 ± 4.3

2.3 | Climate data

Climate data for the studied sites was obtained using the software package ‘ClimateEU’ 4.63 (Wang, Hamann, Spittlehouse, & Murdock, 2012; Hamann, Wang, Spittlehouse, & Murdock, 2013; available for download at <http://tinyurl.com/ClimateEU>). Using this software, generated with the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 2008), we queried Europe-wide monthly, seasonal and annual historical climate data for the years 1929 (restricted by common observation period in our tree-ring series) to 2009 (restricted by availability of climate data). Here, we extracted monthly temperature and precipitation data. The Standardized Precipitation-Evaporation Index (SPEI) was calculated from temperature and precipitation data (R-package ‘SPEI’ 1.6, Beguería & Vicente-Serrano, 2013).

2.4 | Data analysis

To analyse climate–growth relationships across the winter temperature gradient, we correlated the tree-ring chronologies, which represent site-specific growth signals in annual resolution, with monthly climate variables (temperature, precipitation) from the previous June to the current September over a common observation period. For the sake of robust site chronologies and robust analysis of climate–growth relationships, we further restricted the common observation period for this analysis (1940–2009, robust chronologies with each $N_{\text{Tree}} > 15$ per chronology). A 1,000-fold bootstrapping correlation procedure (R-package ‘treeclim’ 2.0.0, Zang & Biondi, 2015) was used to calculate the strength of these relationships (Pearson's R). Subsequently, we tested how summer drought and winter cold signals differed over the studied gradient. Therefore, we considered the correlation coefficients for precipitation in June (the time at which most growth occurs according to regional dendrometer monitoring,

van der Maaten et al., 2018), as indicative for summer drought. The cold sensitivity of plants is not constant during winter but rather changes persistently depending on complex interactions of physiological and environmental drivers (Malyshev, Henry, Bolte, Arfin Khan, & Kreyling, 2018), such that we could not define the month of highest cold sensitivity that represents the winter cold signal a priori. Based on an initial analysis of monthly climate–growth relationships from December to March, we chose to consider the correlation coefficients for temperature in February as the winter cold signal (Figure S3 in Appendix S1). We then tested how those summer drought and winter cold signals differed over the studied gradient. We described the changing responses to summer drought or winter cold across sites with two separate regression models. In each model, mean winter temperature of the sites was used as explanatory variable.

Superposed epoch analysis (SEA, Chree, 1913) was used to study climate anomalies in negative pointer years (i.e., years with strong, site-wide growth reductions) that occurred in the period 1929–2009. Using the raw individual tree-ring series of each site, pointer years were defined with the ‘normalization in a moving window’ method according to Cropper (1976) as implemented in the R-package ‘pointRes’ 1.1.2 (van der Maaten-Theunissen, van der Maaten, & Bouriaud, 2015). In this method, we first normalized the raw tree-ring series by z-transformation (setting mean to zero and standard deviation to one) to Cropper values (C) within a moving window of 5 years (Cropper, 1976). Then, we defined three intensity classes (weak: $|C| > 1$, strong: $|C| > 1.28$, and extreme: $|C| > 1.645$) according to Neuwirth, Schweingruber, and Winiger (2007) for a first descriptive analysis of pointer years. A year was considered a negative pointer year when at least 50% of the trees within a site showed a growth reduction in their previously normalized tree-ring series. For each site, we used SEA to extract the climate data of lag = 0 event years (the previously defined site specific

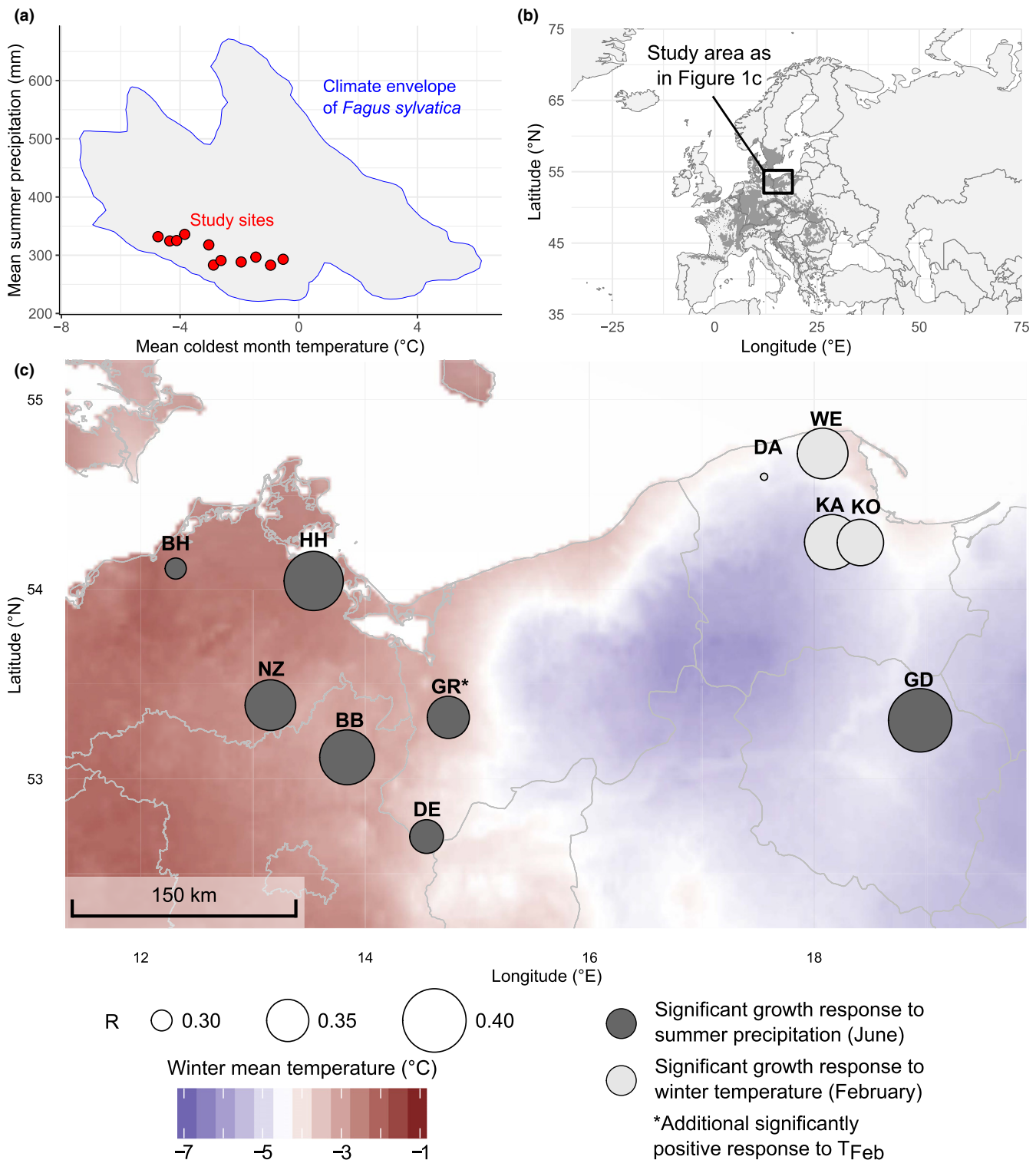


FIGURE 1 Position of the sample sites in climate envelope of *Fagus sylvatica* (a), location of the study area in Europe with distribution range of beech (EUFORGEN, 2009) represented by shading (b), and site-specific climate-growth relationships (c). Strength of climatic signal (Pearson's R) is represented by the size of the circles; grey-tone fillings indicate summer precipitation and winter temperature signals. At site DA, tree growth was not significantly correlated with any of the shown parameters (respective point in map is not to scale). Climate-envelope according to Kölling (2007) from species occurrences data (EUFORGEN, 2009) and climate data (climateEU data, Wang et al., 2012; Hamann et al., 2013). Map data by South (2011). Winter mean temperature was calculated as mean of monthly temperatures December–February [Colour figure can be viewed at wileyonlinelibrary.com]

pointer years of at least weak intensity). In this step, all intensity classes of pointer years were treated equally. Afterwards, we applied a 1,000-fold bootstrapping procedure to test whether

winters were on average abnormally cold or summers abnormally dry in those extracted years. Furthermore, we plotted the winter cold and summer drought anomalies of those extracted years

against the mean winter temperature of our study sites and assessed the trend significance by regression modelling.

3 | RESULTS

3.1 | Chronology statistics

As shown by the chronology statistics (Table 2), the highest r_{bar} values (share of common growth signal) were found among the coldest sites (KO: $r_{bar} = 0.52$; GD: $r_{bar} = 0.54$); the lowest r_{bar} values were found at the warmest sites (NZ: $r_{bar} = 0.28$; BH: $r_{bar} = 0.39$). However, the tendency of increasing synchronicity towards colder sites was not significant (adj. $R^2 = 0.26$, $p = 0.061$). General climate sensitivity (MS) and the 1st order autocorrelation (AC) were not found to be related to the winter temperature gradient and varied strongly from site to site.

3.2 | Climate–growth relationships

Summer drought (precipitation in June) and winter cold (February temperature) were identified as important drivers of tree growth. For the six warmest sites, years with low precipitation in June showed reduced tree growth (Figure S4 in Appendix S1); years with low February temperature showed reduced growth at the coldest sites (Figure S3 in Appendix S1). With the exception of site DA, a strong summer precipitation or a strong winter cold signal could be detected at every site (Figure 1). The strength of the summer precipitation signal decreased gradually towards the cold distribution margin (adj. $R^2 = 0.53$, $p = 0.007$; Figure 2a), whereas the strength of the winter cold signal increased (adj. $R^2 = 0.54$, $p = 0.006$; Figure 2b). Sites GD and WE were outliers far outside the confidence interval in both linear regressions. Growth at GD was much more sensitive, and

growth at WE was much less sensitive to June precipitation than predicted, whereas the opposite held true for February temperature.

3.3 | Negative growth anomalies

Negative pointer years occurred at all sites, though only of weak and strong intensity (Figure 3). In 1940, 1992, 2000, 2006 and 2011, negative pointer years were observed on multiple sites. SEA revealed that negative pointer years coincided with abnormally cold winters at two of the coldest sites (KA and GD, Figure 4a). The relationship of abnormally cold winters and negative pointer years increased significantly towards colder sites (adj. $R^2 = 0.52$, $p = 0.011$).

Abnormally dry summers (negative z-scores of SPEI) during negative pointer years significantly increased towards the warmer sites (adj. $R^2 = 0.62$, $p = 0.004$, Figure 4b). At five (DE, GR, BB, NZ, BH) of the six warmest sites, negative pointer years coincided with summer drought events (significantly negative SPEI anomalies in June). Pointer years on sites with a mean winter temperature below -2°C , however, did not coincide with significant summer drought events.

4 | DISCUSSION

This study analysed climate–growth relationships for European beech along a gradient from warmer to colder winter climate (from the centre towards the margin of the distribution range). With strong winter temperature differences of $\Delta T > 4\text{ K}$ across 500 km, the studied temperature gradient covers a substantial part of the winter temperature range of beech (Figure 1a). In accordance with our initial hypothesis, the sensitivity of beech growth to winter cold increased gradually and became significant towards the cold distribution margin of beech. We observed drought stress at the six warmest study sites, substantiating the general drought sensitivity of beech in large parts of its distribution range (Dittmar et al., 2003; Hackett-Pain et al., 2016; Jump et al., 2006; Lebourgeois et al., 2005). As we further hypothesized, we found that the summer drought signal faded out towards the cold margin, while the winter cold signal became more important. The one exception was the site GR in the middle of the studied temperature gradient. Whereas neighbouring sites were sensitive to drought alone, growth at GR was sensitive to both summer drought and winter cold. Furthermore, the moderately cold site WE was much more sensitive to winter conditions than we had predicted. In contrast to the other, mostly flat study sites, WE was situated in a valley between moraine ridges where a colder microclimate was probably favoured (Vitaske, Klein, Kirchner, & Rebetez, 2017). This highlights, how specific site conditions can pronounce regional winter sensitivity even more locally. The moderately cold site DA was exceptional in that we found neither sensitivity to winter cold, nor to summer precipitation. However, this finding is in line with our regression analysis, which predicted that drought sensitivity alone might be too low and cold sensitivity alone not high enough to be the exclusive driver of growth at locations with mean coldest month

TABLE 2 Chronology statistics of tree-ring series. Number of trees (N_{Tree}), correlation between trees (r_{bar}), expressed population signal (EPS), mean sensitivity (MS) and mean autocorrelation within trees (AC) in descending order of winter temperature. r_{bar} and EPS were calculated from detrended series, MS and AC from index series over the common overlap period 1940–2009 (also used for climate–growth relationships)

Site ID	N_{Tree}	r_{bar}	EPS	MS	AC
BH	18	0.39	0.92	0.21 ± 0.04	0.72 ± 0.12
HH	27	0.45	0.95	0.25 ± 0.03	0.69 ± 0.12
NZ	20	0.28	0.89	0.32 ± 0.05	0.66 ± 0.16
BB	18	0.48	0.94	0.29 ± 0.05	0.74 ± 0.10
GR	25	0.47	0.96	0.30 ± 0.05	0.61 ± 0.14
DE	20	0.51	0.95	0.28 ± 0.04	0.70 ± 0.10
WE	20	0.39	0.93	0.23 ± 0.04	0.72 ± 0.09
DA	22	0.48	0.95	0.28 ± 0.07	0.72 ± 0.11
GD	22	0.54	0.96	0.31 ± 0.06	0.50 ± 0.16
KO	20	0.52	0.96	0.23 ± 0.04	0.65 ± 0.13
KA	39	0.46	0.97	0.21 ± 0.04	0.63 ± 0.15



FIGURE 2 Strength of June precipitation signal (a) and February temperature signal (b) in chronologies of tree growth across the spatial gradient of study sites. The correlation between precipitation and growth increases significantly from colder to warmer sites, indicated by a blue line with grey bands representing the 95% confidence intervals of the regression. The correlation between winter temperature and growth increases significantly towards the colder sites. Significant correlations for individual sites are indicated by asterisks [Colour figure can be viewed at wileyonlinelibrary.com]

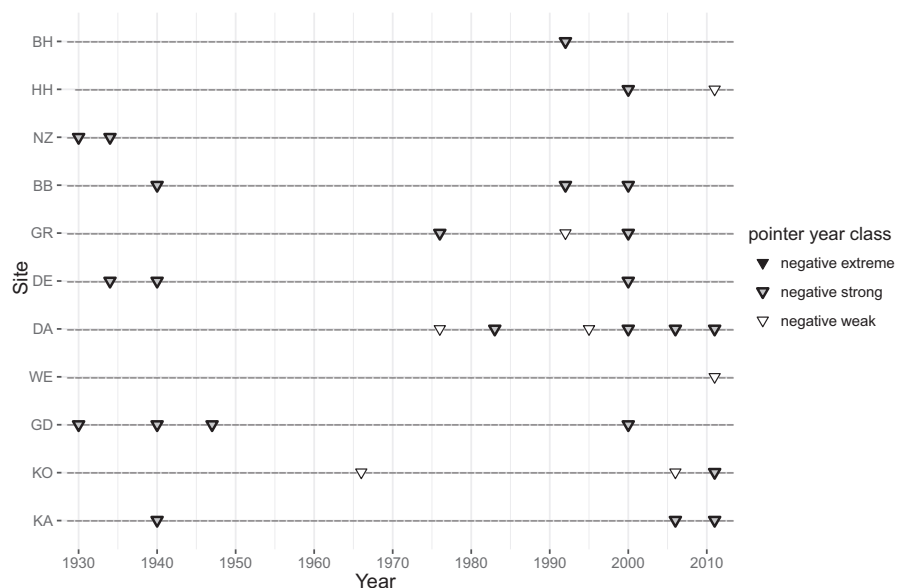
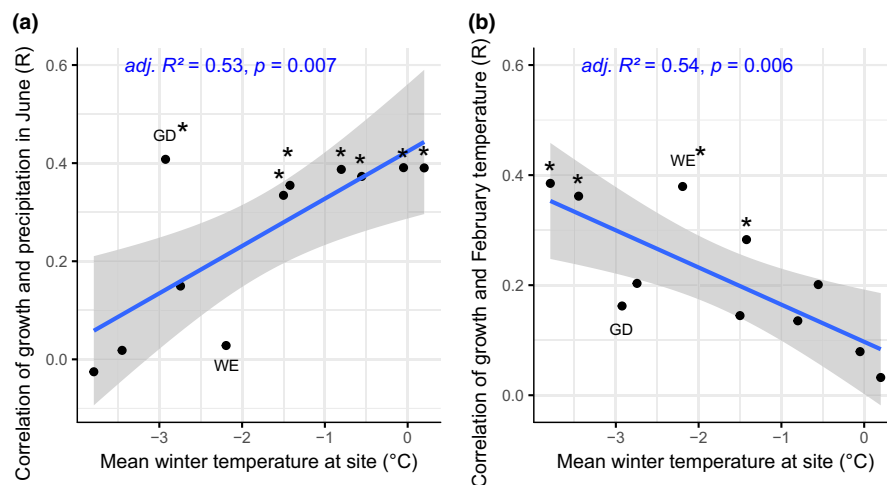


FIGURE 3 Negative pointer years (negative growth anomalies at site level) for the study sites. Growth deviations were detected within a moving window of 5 years. On the y-axis, the sites are ordered from warmer to colder winter conditions (top to bottom)

temperatures of approximately $T = -2.7^{\circ}\text{C}$. Another exception was the third-coldest site GD, where we detected a strong drought signal instead of a pronounced winter cold signal. Despite the many possible reasons for growth reductions of beech (e.g., frost events in late spring, Príncipe et al., 2017; drought or masting events, Hacket-Pain et al., 2017), we could verify our third hypothesis because we could clearly see a relation of growth reductions (i.e., negative pointer years) to winter cold that increased towards the cold margin of beech in our study area. We also observed this relation for GD, indicating that trees at this site react sensitively to multiple stressors in both summer (general growth signal) and winter (exceptional growth reductions), comparable to sites studied by Augustaitis et al. (2012) at the eastern distribution margin of beech. An explanation might be that GD is a cold site more inland from the Baltic (compare Figure 1) with less water availability during summer, but occasionally harsh continental winter conditions (Kozłowski & Michalska, 2001). In conclusion, our findings highlight the study area between north-eastern

Germany and northern Poland as a transition zone, where summer drought as a general stressor for beech growth fades out towards the colder sites and the response to winter cold becomes gradually more pronounced.

Sensitivity of beech growth to winter cold is presently seldom reported in dendroecological research. Some multisite studies also include montane to subalpine beech populations and locally detected growth sensitivity to winter cold for Central European high altitude sites and the Pyrenees (Dittmar et al., 2003), the Eastern Alps (Di Filippo et al., 2007), the Carpathians (Kern & Popa, 2007; Roibu et al., 2017) and the southern Balkans (Fyllas et al., 2017). However, the authors often do not further explore their findings of locally important winter cold sensitivity, but rather focus on the drought sensitivity of beech, which is more important at the regional level (Dittmar et al., 2003; Fyllas et al., 2017; Roibu et al., 2017). Moreover, a local winter cold signal could possibly have altogether gone unreported, e.g., for the high-altitude Apennines, due to the

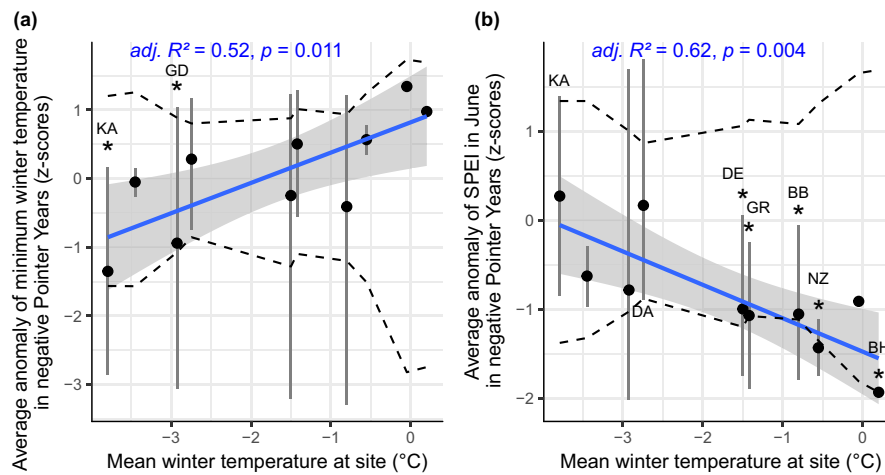


FIGURE 4 Superposed Epoch Analysis (standardized climate anomalies in negative pointer years) for the period 1929–2009 across the studied gradient of decreasing mean winter temperature. Blue lines with grey bands represent regression lines with 95% confidence intervals. Dashed lines represent the 95% confidence interval for site-specific means of climate parameters. Asterisks indicate climate anomalies significantly deviating from this mean value. Vertical grey lines represent the range of anomalies at a given site. The site WE is not shown in the regression plots, because no negative growth events occurred at this site during the analysed time span of 1929–2009 [Colour figure can be viewed at wileyonlinelibrary.com]

prevalence of the regional drought signal in the multivariate analysis and the strong differences in precipitation amount between sites (Piovesan, Biondi, Bernabei, Di Filippo, & Schirone, 2005) or due to the hypothesis-driven focus on drought as the major driver of beech growth from the start (Piovesan, Biondi, Di Filippo, Alessandrini, & Maugeri, 2008). On a regional level, winter cold sensitivity is generally reported for lowland populations of coniferous and deciduous tree species in northern temperate regions of North America (Pearl, Anchukaitis, Pederson, & Donnelly, 2017; Pederson, Cook, Jacoby, Peteet, & Griffin, 2004). In line with our findings on higher winter cold sensitivity towards colder sites, Pearl et al. (2017) recognized that the higher latitude populations tended to have higher winter cold sensitivity. However, the authors could not detect a clear spatial trend, probably due to strong differences in local site conditions (Pearl et al., 2017). In conclusion, perspectives on high altitude populations of beech and on other northern temperate tree species clearly show that the spatial understanding of winter cold sensitivity of temperate tree species profits the most from multisite studies along temperature gradients with comparable precipitation patterns and similar local site conditions.

In contrast with the few examples of winter cold sensitivity of high altitude beech populations, impacts of cold events on beech are often reported in relation to growth reductions following damage of young leaves during frost events late in spring (Dittmar et al., 2006; Príncipe et al., 2017; Vanoni, Bugmann, Nötzli, & Bigler, 2016). Regarding the findings of these authors, the coherence seems clear: the above ground late frost event damages the above ground photoactive, carbon-assimilating organs of a tree, which subsequently reduces the trunk increment. Our study, in contrast, showed an increasing influence of winter cold during the bud dormancy period on growth of European beech towards the cold distribution margin. However, buds of European beech are hardly damaged even by

extreme frost events (Lenz et al., 2016). Lenz et al. (2016) report -40°C as critical temperature for 50% bud damage and -34°C for 10% bud damage; temperatures that were never or hardly reached within the observation period of our study area. Namely, the lowest minimum temperature (-36°C) was recorded in 1969 at site KA (according to climateEU data). However, we observed a clear relationship of aboveground growth reductions and winter cold. According to the resistance of aboveground biomass to cold events found by Lenz et al. (2016), our observed growth reductions are probably only indirectly induced by soil frost damage to fine roots and lower nutrient retention over winter due to a disturbed microbial community (Groffman et al., 2001; Reinmann & Templer, 2016; Yanai, Toyota, & Okazaki, 2011). With damaged fine roots and lower nutrient availability, less nutrients may be taken up in spring, which can lead to decreased plant growth during the growing season (Campbell, Socci, & Templer, 2014; Gentilesca et al., 2018; Reinmann & Templer, 2016; Schuerings, Jentsch, Walter, & Kreyling, 2014). Our findings on winter cold sensitivity of adult trees may even be valid for juvenile beech trees in the understorey because juvenile and adult conspecifics show similar frost resistance during the same phenological stage (Vitasse, Lenz, Hoch, Körner, & Piper, 2014) and experience comparable microclimatic conditions during winter (Vitasse, 2013). In conclusion, our study identified an as of yet largely unnoticed relationship between winter cold and growth reductions. In turn, our study, which revealed this relationship, gives an important motivation for conducting field experiments in forests in combination with extensive ecophysiological and phenological measurements of canopy, trunk, understorey and root compartment to increase the mechanistic understanding of the underlying forest ecosystem processes (Groffman et al., 2001; Lenz et al., 2016).

In line with the basic principle of Fritts (1966), which stated that tree growth responds more sensitively to a limiting climatic



factor towards the distribution margin, our results suggest that the growth of beech becomes more sensitive to winter cold towards the cold distribution margin. This increased sensitivity might explain the potential distribution border of beech in north-eastern Europe, though the realized distribution borders might also be due to anthropogenic influence or competition with other, better locally adapted species (Brown et al., 1996; Giesecke et al., 2007; Kroiss & HilleRisLambers, 2015). A possible link between climate sensitivity of tree growth and distribution limits of tree species was further supported by transplantation trials beyond the cold distribution margin of beech and by modelling approaches, showing increased sensitivity of beech growth to winter cold (Augustaitis et al., 2012; van der Maaten et al., 2017; Matisons et al., 2017). Towards the dry distribution margin, climate (i.e., drought) sensitivity of beech growth was reported to increase as well (Jump et al., 2006; Roibu et al., 2017). In contrast, other studies showed that mean growth rates might be lower towards the dry distribution margin, but that marginal populations may be more adapted and thus less sensitive to drought than core populations (Cavin & Jump, 2017; Thiel et al., 2014; Weber, Bugmann, Pluess, Walther, & Rigling, 2013). While genetic diversity between dry marginal beech populations is high, our study on the climate sensitivity of beech across a large-scale gradient of decreasing winter temperature was conducted in an area where populations were similar due to anthropogenically influenced migration history (Bolte et al., 2007; Magri et al., 2006). With this low between-population diversity, local adaptations to winter cold either do not exist or are not strong enough to overcome frost damage.

As with the relationship between growth sensitivity and distribution margins, the relationship between winter cold and tree distribution limits in Europe is also subject to debate. According to Sykes et al. (1996) and van der Maaten et al. (2017), the eastern distribution margin of common European tree species is signified by abrupt winter cold thresholds. At their cold margin—and at transplantation sites beyond the cold margin—tree species are predicted to respond to winter cold events with a reduction in growth (Sykes et al., 1996). In contrast, the ability of trees to regenerate at their cold margin and to protect their aboveground tissue from frost indicates that winter temperatures do not limit latitudinal tree species distribution ranges (Körner et al., 2016; Lenz et al., 2016). Still, the findings of our study are in line with Sykes et al. (1996) and van der Maaten et al. (2017) by showing an increased sensitivity of tree growth to winter cold towards the eastern margin of European beech. On one hand, winter cold could become a more important driver of growth reductions for European beech in the face of a predicted north-eastward range shift in newly colonized habitat. Winter cold events might persist with similar frequency during projected climate change (Kodra & Ganguly, 2014; Kodra et al., 2011; Petoukhov & Semenov, 2010). On the other hand, summer temperatures are predicted to increase while summer precipitation will likely decrease, possibly putting sites that are currently only sensitive to cold events under growth stress of both summer drought and winter cold.

5 | CONCLUSION

Studies on the growth and climate sensitivity of European beech towards its eastern cold distribution margin have so far been under-represented. Here, we showed that winter cold increasingly influences growth of beech and that exceptionally cold winters are related to exceptional growth reductions at colder eastern sites. A north-eastward range shift of European beech is often assumed to compensate for habitat and productivity losses of drought-prone southern and central populations. With respect to the winter cold sensitivity found in the present study, such assumptions should be taken with care. Sensitivity to winter cold might become increasingly important for expansion of beech into colder areas under climate change. Since dendroecological methods can only show retrospective climate–growth relationships, temperature manipulation experiments could further contribute to a deeper mechanistic understanding that can then be used to update model predictions.

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DATA AVAILABILITY

All chronologies of tree-ring series used to establish climate–growth relationships in this manuscript are publicly available from www.dendrobox.org.

ORCID

Robert Weigel  <http://orcid.org/0000-0001-9685-6783>

Marcin Klisz  <http://orcid.org/0000-0001-9486-6988>

Juergen Kreyling  <http://orcid.org/0000-0001-8489-7289>

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BIOSKETCH

Robert Weigel uses a variety of methodological approaches (dendroecology, experimental plant ecology, vegetation analysis) to increase the understanding of ecological processes in forest ecosystems and how those processes change in time and space. In his PhD studies at the University of Greifswald (Germany) he focuses on the influence of winter climate and winter extreme events on beech forest ecosystems towards the cold distribution margin of European beech (*Fagus sylvatica* L.). All authors collaborate by combining their methodological assets of dendroecology and experimental plant ecology to explore environment–plant interactions—with special regard to changing climatic trends and climatic extreme events—in various ecosystems.

Author contributions: J.K. and R.W. conceived the ideas; M.K., J.K., L.M., E.M., and R.W. conducted the fieldwork; M.M., L.M., E.M., and R.W. prepared the samples in the lab; R.W. analysed the data with contributions from J.K., M.M., E.M., and M.W.; E.M. and R.W. led the writing with all authors contributing to the text.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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