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

14 Running title: European beech at the cold margin

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29 **Abstract**

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

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

39 **Location** A large gradient of decreasing winter temperature ($\Delta T > 4$ K along 500 km) from Rostock (Ger-
40 many) to Gdańsk (Poland).

41 **Methods** We analysed climate–growth relationships and the nature of growth reductions of ten beech
42 stands from more central to cold marginal beech populations.

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

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

54

55 Key words: Cold distribution border, cold events, dendroecology, European beech, forest ecology,
56 range margin ecology, winter cold sensitivity, winter ecology

57

58 **Introduction**

59 Tree species distributions are linked to climate through direct effects of climate conditions on tree
60 physiological functioning (Körner *et al.*, 2016). Consequently, potential distribution ranges can be mod-
61 elled by small sets of bioclimatic variables on a regional to global scale (Sykes *et al.*, 1996; Kramer *et*
62 *al.*, 2010; Saltre *et al.*, 2015). Generally, climate envelope models suggest that tree growth and distri-
63 bution range limits are controlled by winter temperature towards the north and by water availability
64 towards the south as well as towards local discontinuities of the distribution range (Sykes *et al.*, 1996).
65 European beech (*Fagus sylvatica* L.), with its high phenotypic plasticity (Meier & Leuschner, 2008;
66 Stojnić *et al.*, 2015) and intra-specific genetic variability (Kreyling *et al.*, 2012; Kreyling *et al.*, 2014), is
67 the dominant forest tree species in Europe, covering an exceptionally broad ecological range of soil
68 types and climates in its distribution range (Leuschner *et al.*, 2006; Bolte *et al.*, 2007). Beech naturally
69 dominates under moderate soil moisture (dry to moist) and moderate soil acidity (acid to alkaline)
70 conditions (Bolte *et al.*, 2007; Leuschner & Ellenberg, 2017). Depending on the region, drought (water
71 availability in summer) and cold (winter temperature threshold, growing season length, late frost) are
72 the main limiting factors of the potential distribution range of European beech (Bolte *et al.*, 2007;
73 Giesecke *et al.*, 2007).

74 Fritts (1966) recognized that one can observe higher climate sensitivity of tree growth to certain limit-
75 ing climatic factors towards the margin of a species' distribution. This may be explained by the assump-
76 tion that climate sensitivity of plants is greater towards both the dry and cold ends of ecological gradi-
77 ents because climate stress there becomes increasingly limiting to the point that potential distribution
78 limits are expressed due to total growth cessation (Fritts, 1966; Brown *et al.*, 1996; Normand *et al.*,
79 2009). Based on multi-site dendroecological studies, drought has emerged as a general driver of
80 growth for beech across Europe (Dittmar *et al.*, 2003; Lebourgeois *et al.*, 2005; Jump *et al.*, 2006;
81 Hacket-Pain *et al.*, 2016; 2017; Knutzen *et al.*, 2017), though drought sensitivity has been indicated to
82 increase towards drier sites along continental or elevational gradients (Jump *et al.*, 2006; Scharnweber
83 *et al.*, 2011; Roibu *et al.*, 2017). However, this observation might be biased due to research focusing
84 on the southern to south-eastern dry parts of the distribution range (Dittmar *et al.*, 2003; Roibu *et al.*,
85 2017), on countries at the southern dry distribution margin (Lebourgeois *et al.*, 2005; Jump *et al.*,
86 2006), and on gradients from the central distribution range to its southern edge (Hacket-Pain *et al.*,
87 2016).

88 The cold north-eastern distribution margin (e.g. northern Poland) has so far been underrepresented in
89 studies on climate sensitivity of European beech. With climate change-induced warming, a range shift
90 of beech across the current north-eastern cold distribution border is projected to buffer range losses
91 from increasing drought stress at the southern distribution margin (Salinger, 2005; Kramer *et al.*, 2010;
92 Saltre *et al.*, 2015). Besides warming, though, climate will additionally become more variable (Salinger,
93 2005). This means that extreme cold events may persist or even increase in frequency in Europe (Pe-
94 toukhov & Semenov, 2010; Kodra *et al.*, 2011; Kodra & Ganguly, 2014). For beech, late frost events
95 and subsequent leaf senescence are often followed by a considerable reduction in growth (Dittmar *et*
96 *al.*, 2006; Príncipe *et al.*, 2017). Although beech populations at colder sites may be locally adapted to

97 cold conditions (Kreyling *et al.*, 2014, 2015), late frost-related growth reductions generally increase
98 towards colder sites where frost severity is greater (Dittmar *et al.*, 2006; Príncipe *et al.*, 2017). Príncipe
99 *et al.* (2017) suggested that impacts of late frost events may become more frequent in the future with
100 warmer and more variable climate conditions, as early spring warm spells and leaf unfolding may in-
101 crease the risk of late frost damage.

102 In contrast to the high sensitivity of young leaves to late frost events, dormant buds and cambium of
103 European beech can acclimate well to cold conditions and are thus particularly resistant to winter frost
104 (Lenz *et al.*, 2016). Consequently, direct damage of winter cold events to above ground tissue may not
105 explain the cold distribution margin of beech (Körner *et al.*, 2016; Lenz *et al.*, 2016). Likewise, the cold
106 distribution is probably not limited by regeneration because beech recruits well at the cold distribution
107 margin and young beech saplings can establish successfully beyond the cold distribution margin of
108 adult trees (Vitasse *et al.*, 2012; Körner *et al.*, 2016; Matisons *et al.*, 2017). Although winter cold events
109 may not explain the cold distribution limit alone, resulting soil frost during winter cold events may still
110 indirectly reduce above ground biomass production (Vitousek *et al.*, 1997; Groffman *et al.*, 2001; Rein-
111 mann & Templer, 2016). Indeed, at forest plantations across the eastern cold distribution margin, Eu-
112 ropean beech was found to be sensitive to multiple stressors across the year: winter cold, cold and dry
113 springs, as well as hot summers (Augustaitis *et al.*, 2012; Matisons *et al.*, 2017). Thus, experiments and
114 dendroecology have indicated that growth reductions and sensitivity to winter temperature may in-
115 crease towards colder sites (Groffman *et al.*, 2001; Augustaitis *et al.*, 2012; Reinmann & Templer,
116 2016). However, the issue remains that too few studies have been conducted at the cold distribution
117 margin to appropriately test the assumption that a future range expansion beyond the current cold
118 margin can compensate for habitat loss at the dry margin. Therefore, studies on gradients of winter
119 cold (i.e. towards the north-eastern cold distribution margin) are urgently needed and will complement
120 climate–growth analyses from the southern, south-eastern, and central distribution range.

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

128

129 **Methods**

130 *Study area*

131 This study was performed in 11 managed mature forest stands with European beech as the dominant
132 tree species. The stands follow a gradient of winter temperature from Billenhagen near Rostock, Ger-
133 many (-0.5 °C mean coldest month temperature) to Kartuzy near Gdańsk, Poland (-4.7 °C mean coldest
134 month temperature, Table 1, Figure 1). During the last few decades, there has been a trend towards

135 slightly increasing annual mean temperatures at the six warmest study sites and slightly warmer win-
136 ters at the moderately cold sites, though there has been no significant warming trend at the coldest
137 sites (Figure S1 in Appendix S1 in Supporting Information). The studied gradient spans from the central
138 to the north-eastern cold margin of the continuous distribution range of European beech (Bolte *et al.*,
139 2007). With a difference in winter temperature of $\Delta T > 4$ K along 500 km, the study gradient covers a
140 relatively large part of the temperature range of beech; in contrast, the precipitation differences are
141 relatively small between the study sites (Figure 1a). We selected sites with similar proximity to the
142 Baltic Sea and thus comparable seasonal climatic patterns and mean annual precipitation sums (540-
143 669 mm). There has been no trend of changing precipitation at the study sites during the last decades
144 (Figure S2 in Appendix S1). Owing to the same glacial history, all sites are characterised by sandy soils
145 of type Cambisol with comparable soil texture of mostly sandy silt to silty sand (Table S1 in Appendix
146 S1). Thus, our selection focus was on all sites having comparable water holding capacity and a compa-
147 rable hydrological setting. Within this framework of broader geographical considerations, we selected
148 individual sites with comparable stand structure (tree height, tree diameter, canopy closure, Table 1).
149 This is a prerequisite for our multi-site gradient analysis because climate–growth relationships can de-
150 pend on the canopy setting (Matisons *et al.*, 2017). To fulfil this major prerequisite of comparable stand
151 structure, tree age varied between sites. We choose typical managed mature beech forest sites, which
152 mostly consist of co-dominant and dominant trees. In doing so, the trees of all sites were similarly
153 linked to soil and atmospheric conditions. Furthermore, intra-specific competition signals, which are
154 typical for suppressed trees and may blur climate–growth relationships, were reduced.

155 *Dendrochronological sampling and sample processing*

156 In the autumn of 2015, two increment cores per tree were extracted at breast height (1.3 m) from at
157 least 20 co-/dominant trees per site. Cores were air-dried, glued on wooden mounts, and sanded with
158 progressively finer sandpaper to highlight annual rings. For each site, scanned cores (‘Mikrotek
159 ScanMaker 1000XL Plus’ at 1200 dpi) were measured and cross-dated with the ‘CooRecorder’ and
160 ‘CDendro’ software (version 8.1, Cybis Electronic & Data, 2015). Individual tree-ring series, built by
161 averaging two cores per tree, were detrended using a cubic smoothing spline with a 50% frequency
162 cut-off at 30 years, followed by autoregressive modelling. Detrending by a smoothing spline accentu-
163 ates climate-induced growth fluctuations while removing longer-term trends that may, for example,
164 reflect tree ageing or effects of forest management activities (Cook & Peters, 1981). We chose to sub-
165 sequently remove the autocorrelation from the data by autoregressive modelling (prewhitening) to
166 further accentuate the high-frequency signal of the tree-ring series, facilitating the detection of cli-
167 matic signals that fluctuate from year-to-year (Piovesan & Schirone, 2000). Detrended tree-ring series
168 were then calculated by dividing the observed by the predicted values. Stand chronologies were con-
169 structed for each site by calculating a bi-weight robust mean of the index series of individual trees, as
170 suggested as a standard dendroecological data preparation step for sound subsequent climate–growth
171 analysis (Cook & Kairiūkštis, 1990; Fritts, 2001). A limited number of cores could not be dated due to
172 rotten segments, and were thus excluded (Table 1).

173 Both *rbar* (Pearson's correlation coefficient indicating the strength of the common signal in growth
174 series from individual trees within a stand) and expressed population signal (*EPS*; a measure of quality
175 of common growth signal within a population, Wigley *et al.*, 1984) were calculated from detrended
176 tree-ring series, whereas the mean sensitivity (indicator for general climate sensitivity of growth) and
177 1st order autocorrelation (indicator for effects of previous-year conditions upon current year's growth)
178 were calculated from index series (raw ring widths of each tree divided by the average ring width of
179 the tree). These measures were calculated for the robust common overlap period from 1940-2009 and
180 used to assess the quality and characteristics of the chronologies. We applied linear regression mod-
181 elling to test if these measures changed along the studied temperature gradient. Here and in all fol-
182 lowing analyses we define a p-value threshold of $p < 0.05$ for accepting statistical significance. Detrend-
183 ing, chronology building, and calculation of chronology statistics was performed using the 'dplR' pack-
184 age 1.6.4 (Bunn, 2008) in R 3.3.1 (R Core Team, 2016).

185 *Climate data*

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

194 *Data analysis*

195 To analyse climate-growth relationships across the winter temperature gradient, we correlated the
196 tree-ring chronologies, which represent site-specific growth signals in annual resolution, with monthly
197 climate variables (temperature, precipitation) from the previous June to the current September over
198 a common observation period. For the sake of robust site chronologies and robust analysis of climate-
199 growth relationships, we further restricted the common observation period for this analysis (1940-
200 2009, robust chronologies with each $N_{Tree} > 15$ per chronology). A 1000-fold bootstrapping correlation
201 procedure (R-package 'treeclim' 2.0.0, Zang & Biondi, 2015) was used to calculate the strength of these
202 relationships (Pearson's *R*). Subsequently, we tested how summer drought and winter cold signals dif-
203 fered over the studied gradient. Therefore, we considered the correlation coefficients for precipitation
204 in June (the time at which most growth occurs according to regional dendrometer monitoring, van der
205 Maaten *et al.*, 2018), as indicative for summer drought. The cold sensitivity of plants is not constant
206 during winter but rather changes persistently depending on complex interactions of physiological and
207 environmental drivers (Malyshev *et al.*, 2018), such that we could not define the month of highest cold
208 sensitivity that represents the winter cold signal *a priori*. Based on an initial analysis of monthly cli-
209 mate-growth relationships from December to March, we chose to consider the correlation coefficients
210 for temperature in February as the winter cold signal (Figure S3 in Appendix S1). We then tested how
211 those summer drought and winter cold signals differed over the studied gradient. We described the

212 changing responses to summer drought or winter cold across sites with two separate regression mod-
213 els. In each model, mean winter temperature of the sites was used as explanatory variable.

214 Superposed epoch analysis (SEA, Chree, 1913) was used to study climate anomalies in negative pointer
215 years (i.e. years with strong, site-wide growth reductions) that occurred in the period 1929–2009. Us-
216 ing the raw individual tree-ring series of each site, pointer years were defined with the ‘normalization
217 in a moving window’ method according to Cropper (1979) as implemented in the R-package ‘pointRes’
218 1.1.2 (van der Maaten-Theunissen *et al.*, 2015). In this method, we first normalized the raw tree-ring
219 series by z-transformation (setting mean to zero and standard deviation to one) to Cropper values (C)
220 within a moving window of five years (Cropper, 1976). Then, we defined three intensity classes (weak:
221 $|C| > 1$, strong: $|C| > 1.28$, and extreme: $|C| > 1.645$) according to Neuwirth *et al.* (2007) for a first
222 descriptive analysis of pointer years. A year was considered a negative pointer year when at least 50%
223 of the trees within a site showed a growth reduction in their previously normalized tree-ring series.
224 For each site, we used SEA to extract the climate data of lag = 0 event years (the previously defined
225 site specific pointer years of at least weak intensity). In this step, all intensity classes of pointer years
226 were treated equally. Afterwards, we applied a 1000-fold bootstrapping procedure to test whether
227 winters were on average abnormally cold or summers abnormally dry in those extracted years. Fur-
228 thermore, we plotted the winter cold and summer drought anomalies of those extracted years against
229 the mean winter temperature of our study sites and assessed the trend significance by regression
230 modelling.

231

232 **Results**

233 *Chronology statistics*

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

240 *Climate–growth relationships*

241 Summer drought (precipitation in June) and winter cold (February temperature) were identified as
242 important drivers of tree growth. For the six warmest sites, years with low precipitation in June showed
243 reduced tree growth (Figure S4 in Appendix S1); years with low February temperature showed reduced
244 growth at the coldest sites (Figure S3 in Appendix S1). With the exception of site DA, a strong summer
245 precipitation or a strong winter cold signal could be detected at every site (Figure 1). The strength of
246 the summer precipitation signal decreased gradually towards the cold distribution margin ($adj. R^2 =$
247 $0.53, p = 0.007$; Figure 2a), whereas the strength of the winter cold signal increased ($adj. R^2 = 0.54, p =$
248 0.006 ; Figure 2b). Sites GD and WE were outliers far outside the confidence interval in both linear

249 regressions. Growth at GD was much more sensitive, and growth at WE was much less sensitive to
250 June precipitation than predicted, whereas the opposite held true for February temperature.

251 *Negative growth anomalies*

252 Negative pointer years occurred at all sites, though only of weak and strong intensity (Figure 3). In
253 1940, 1992, 2000, 2006, and 2011, negative pointer years were observed on multiple sites. SEA re-
254 vealed that negative pointer years coincided with abnormally cold winters at two of the coldest sites
255 (KA and GD, Figure 4a). The relationship of abnormally cold winters and negative pointer years in-
256 creased significantly towards colder sites (*adj. R*² = 0.52, *p* = 0.011).

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

262

263 **Discussion**

264 This study analysed climate–growth relationships for European beech along a gradient from warmer
265 to colder winter climate (from the centre towards the margin of the distribution range). With strong
266 winter temperature differences of $\Delta T > 4$ K across 500 km, the studied temperature gradient covers a
267 substantial part of the winter temperature range of beech (Figure 1a). In accordance with our initial
268 hypothesis, the sensitivity of beech growth to winter cold increased gradually and became significant
269 towards the cold distribution margin of beech. We observed drought stress at the six warmest study
270 sites, substantiating the general drought sensitivity of beech in large parts of its distribution range
271 (Dittmar *et al.*, 2003; Lebourgeois *et al.*, 2005; Jump *et al.*, 2006; Hackett-Pain *et al.*, 2016). As we fur-
272 ther hypothesized, we found that the summer drought signal faded out towards the cold margin, while
273 the winter cold signal became more important. The one exception was the site GR in the middle of the
274 studied temperature gradient. Whereas neighbouring sites were sensitive to drought alone, growth at
275 GR was sensitive to both summer drought and winter cold. Furthermore, the moderately cold site WE
276 was much more sensitive to winter conditions than we had predicted. In contrast to the other, mostly
277 flat study sites, WE was situated in a valley between moraine ridges where a colder microclimate was
278 probably favoured (Vitasse *et al.*, 2017). This highlights, how specific site conditions can pronounce
279 regional winter sensitivity even more locally. The moderately cold site DA was exceptional in that we
280 found neither sensitivity to winter cold, nor to summer precipitation. However, this finding is in line
281 with our regression analysis, which predicted that drought sensitivity alone might be too low and cold
282 sensitivity alone not high enough to be the exclusive driver of growth at locations with mean coldest
283 month temperatures of approximately $T = -2.7$ °C. Another exception was the third-coldest site GD,
284 where we detected a strong drought signal instead of a pronounced winter cold signal. Despite the
285 many possible reasons for growth reductions of beech (e.g. frost events in late spring, Príncipe *et al.*,

286 2017, drought or masting events, Hackett-Pain *et al.*, 2017), we could verify our third hypothesis be-
287 cause we could clearly see a relation of growth reductions (i.e. negative pointer years) to winter cold
288 that increased towards the cold margin of beech in our study area. We also observed this relation for
289 GD, indicating that trees at this site react sensitively to multiple stressors in both summer (general
290 growth signal) and winter (exceptional growth reductions), comparable to sites studied by Augustaitis
291 *et al.* (2012) at the eastern distribution margin of beech. An explanation might be that GD is a cold site
292 more inland from the Baltic (compare Figure 1) with less water availability during summer, but occa-
293 sionally harsh continental winter conditions (Kozłowski & Michalska, 2001). In conclusion, our findings
294 highlight the study area between north-eastern Germany and northern Poland as a transition zone,
295 where summer drought as a general stressor for beech growth fades out towards the colder sites and
296 the response to winter cold becomes gradually more pronounced.

297 Sensitivity of beech growth to winter cold is presently seldom reported in dendroecological research.
298 Some multi-site studies also include montane to subalpine beech populations and locally detected
299 growth sensitivity to winter cold for Central European high altitude sites and the Pyrenees (Dittmar *et al.*,
300 2003), the Eastern Alps (Di Filippo *et al.*, 2007), the Carpathians (Kern & Poppa, 2007; Roibu *et al.*,
301 2017), and the southern Balkans (Fyllas *et al.*, 2017). However, the authors often do not further explore
302 their findings of locally important winter cold sensitivity, but rather focus on the drought sensitivity of
303 beech, which is more important at the regional level (Dittmar *et al.*, 2003; Roibu *et al.*, 2017; Fyllas *et al.*,
304 2017). Moreover, a local winter cold signal could possibly have altogether gone unreported, e.g.
305 for the high-altitude Apennines, due to the prevalence of the regional drought signal in the multivari-
306 ate analysis and the strong differences in precipitation amount between sites (Piovesan *et al.*, 2005)
307 or due to the hypothesis-driven focus on drought as the major driver of beech growth from the start
308 (Piovesan *et al.*, 2008). On a regional level, winter cold sensitivity is generally reported for lowland
309 populations of coniferous and deciduous tree species in northern temperate regions of North America
310 (Pederson *et al.*, 2004; Pearl *et al.*, 2017). In line with our findings on higher winter cold sensitivity
311 towards colder sites, Pearl *et al.* (2017) recognized that the higher latitude populations tended to have
312 higher winter cold sensitivity. However, the authors could not detect a clear spatial trend, probably
313 due to strong differences in local site conditions (Pearl *et al.*, 2017). In conclusion, perspectives on high
314 altitude populations of beech and on other northern temperate tree species clearly show that the
315 spatial understanding of winter cold sensitivity of temperate tree species profits the most from multi-
316 site studies along temperature gradients with comparable precipitation patterns and similar local site
317 conditions.

318 In contrast to the few examples of winter cold sensitivity of high altitude beech populations, impacts
319 of cold events on beech are often reported in relation to growth reductions following damage of young
320 leaves during frost events late in spring (Dittmar *et al.*, 2006; Vanoni *et al.*, 2016; Príncipe *et al.*,
321 2017). Regarding the findings of these authors, the coherence seems clear: the above ground late frost
322 event damages the above ground photoactive, carbon-assimilating organs of a tree, which subse-
323 quently reduces the trunk increment. Our study, in contrast, showed an increasing influence of winter

324 cold during the bud dormancy period on growth of European beech towards the cold distribution mar-
325 gin. However, buds of European beech are hardly damaged even by extreme frost events (Lenz *et al.*,
326 2016). Lenz *et al.* (2016) report -40 °C as critical temperature for 50 % bud damage and -34 °C for 10 %
327 bud damage; temperatures that were never or hardly reached within the observation period of our
328 study area. Namely, the lowest minimum temperature (-36 °C) was recorded in 1969 at site KA (ac-
329 cording to climateEU data). However, we observed a clear relationship of aboveground growth reduc-
330 tions and winter cold. According to the resistance of aboveground biomass to cold events found by
331 Lenz *et al.* (2016), our observed growth reductions are probably only indirectly induced by soil frost
332 damage to fine roots and lower nutrient retention over winter due a disturbed microbial community
333 (Groffman *et al.*, 2001; Yanai *et al.*, 2011; Reinmann & Templer, 2016). With damaged fine roots and
334 lower nutrient availability, less nutrients may be taken up in spring, which can lead to decreased plant
335 growth during the growing season (Campbell *et al.*, 2014; Schuerings *et al.*, 2014; Reinmann & Templer,
336 2016; Gentilesca *et al.*, 2018). Our findings on winter cold sensitivity of adult trees may even be valid
337 for juvenile beech trees in the understory because juvenile and adult conspecifics show similar frost
338 resistance during the same phenological stage (Vitasse *et al.*, 2014) and experience comparable micro-
339 climatic conditions during winter (Vitasse, 2013). In conclusion, our study identified an as of yet largely
340 unnoticed relationship between winter cold and growth reductions. In turn, our study, which revealed
341 this relationship, gives an important motivation for conducting field experiments in forests in combi-
342 nation with extensive ecophysiological and phenological measurements of canopy, trunk, understory,
343 and root compartment to increase the mechanistic understanding of the underlying forest ecosystem
344 processes (Groffman *et al.*, 2001; Lenz *et al.*, 2016).

345 In line with the basic principle of Fritts (1966), which stated that tree growth responds more sensitively
346 to a limiting climatic factor towards the distribution margin, our results suggest that the growth of
347 beech becomes more sensitive to winter cold towards the cold distribution margin. This increased sen-
348 sitivity might explain the potential distribution border of beech in north-eastern Europe, though the
349 realized distribution borders might also be due to anthropogenic influence or competition with other,
350 better locally adapted species (Brown *et al.*, 1996; Giesecke *et al.*, 2007; Kroiss & HilleRisLambers,
351 2015). A possible link between climate sensitivity of tree growth and distribution limits of tree species
352 was further supported by transplantation trials beyond the cold distribution margin of beech and by
353 modelling approaches, showing increased sensitivity of beech growth to winter cold (Augustaitis *et al.*,
354 2012; Matisons *et al.*, 2017; van der Maaten *et al.*, 2017). Towards the dry distribution margin, climate
355 (i.e. drought) sensitivity of beech growth was reported to increase as well (Jump *et al.*, 2006; Roibu *et al.*,
356 2017). In contrast, other studies showed that mean growth rates might be lower towards the dry
357 distribution margin, but that marginal populations may be more adapted and thus less sensitive to
358 drought than core populations (Weber *et al.*, 2013; Thiel *et al.*, 2014; Cavin & Jump, 2017). While ge-
359 netic diversity between dry marginal beech populations is high, our study on the climate sensitivity of
360 beech across a large-scale gradient of decreasing winter temperature was conducted in an area where
361 populations were similar due to anthropogenically influenced migration history (Magri *et al.*, 2006;
362 Bolte *et al.*, 2007). With this low between-population diversity, local adaptations to winter cold either
363 do not exist or are not strong enough to overcome frost damage.

364 As with the relationship between growth sensitivity and distribution margins, the relationship between
365 winter cold and tree distribution limits in Europe is also subject to debate. According to Sykes *et al.*
366 (1996) and van der Maaten *et al.* (2017), the eastern distribution margin of common European tree
367 species is signified by abrupt winter cold thresholds. At their cold margin – and at transplantation sites
368 beyond the cold margin – tree species are predicted to respond to winter cold events with a reduction
369 in growth (Sykes *et al.*, 1996). In contrast, the ability of trees to regenerate at their cold margin and to
370 protect their aboveground tissue from frost indicates that winter temperatures do not limit latitudinal
371 tree species distribution ranges (Körner *et al.*, 2016; Lenz *et al.*, 2016). Still, the findings of our study
372 are in line with Sykes *et al.* (1996) and van der Maaten *et al.* (2017) by showing an increased sensitivity
373 of tree growth to winter cold towards the eastern margin of European beech. On one hand, winter
374 cold could become a more important driver of growth reductions for European beech in the face of a
375 predicted north-eastward range shift in newly colonized habitat. Winter cold events might persist with
376 similar frequency during projected climate change (Petoukhov & Semenov, 2010; Kodra *et al.*, 2011;
377 Kodra & Ganguly, 2014). On the other hand, summer temperatures are predicted to increase while
378 summer precipitation will likely decrease, possibly putting sites that are currently only sensitive to cold
379 events under growth stress of both summer drought and winter cold.

380

381 **Conclusion**

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

392

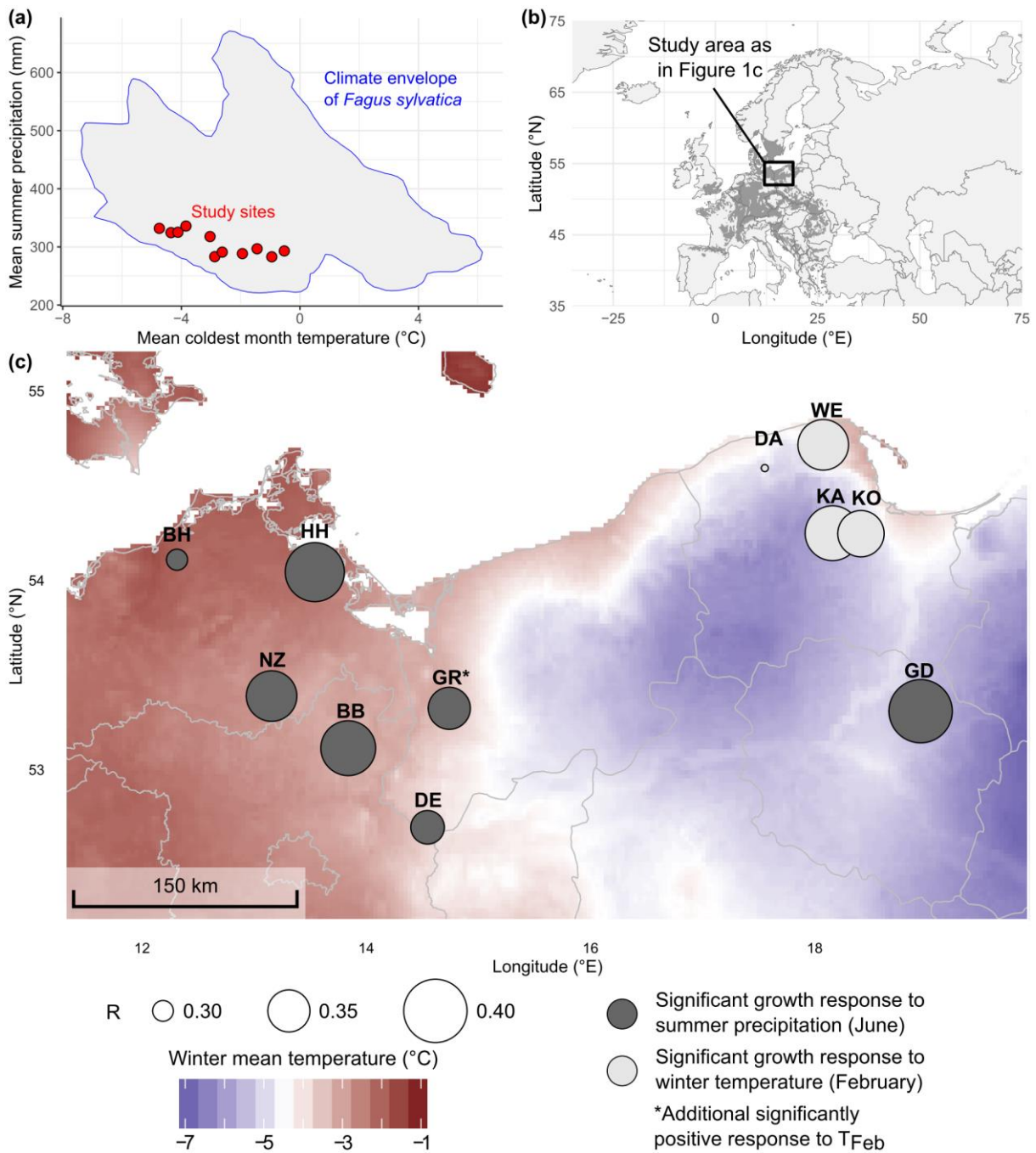
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406 **Figures**

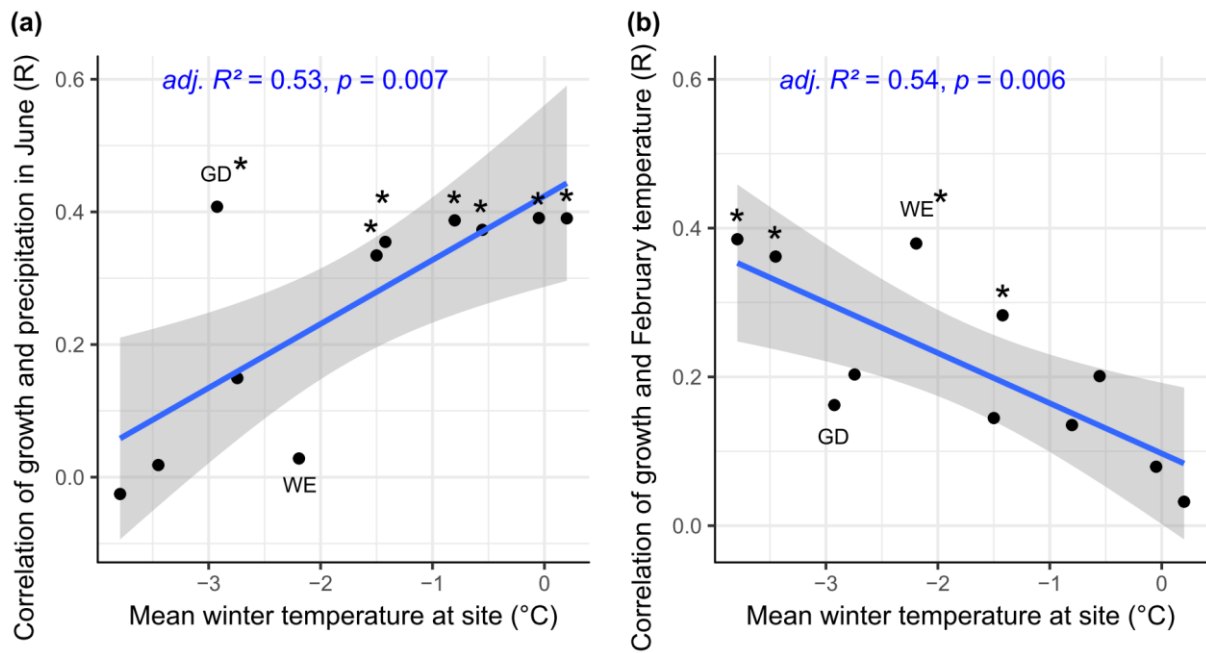
407



408

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

416

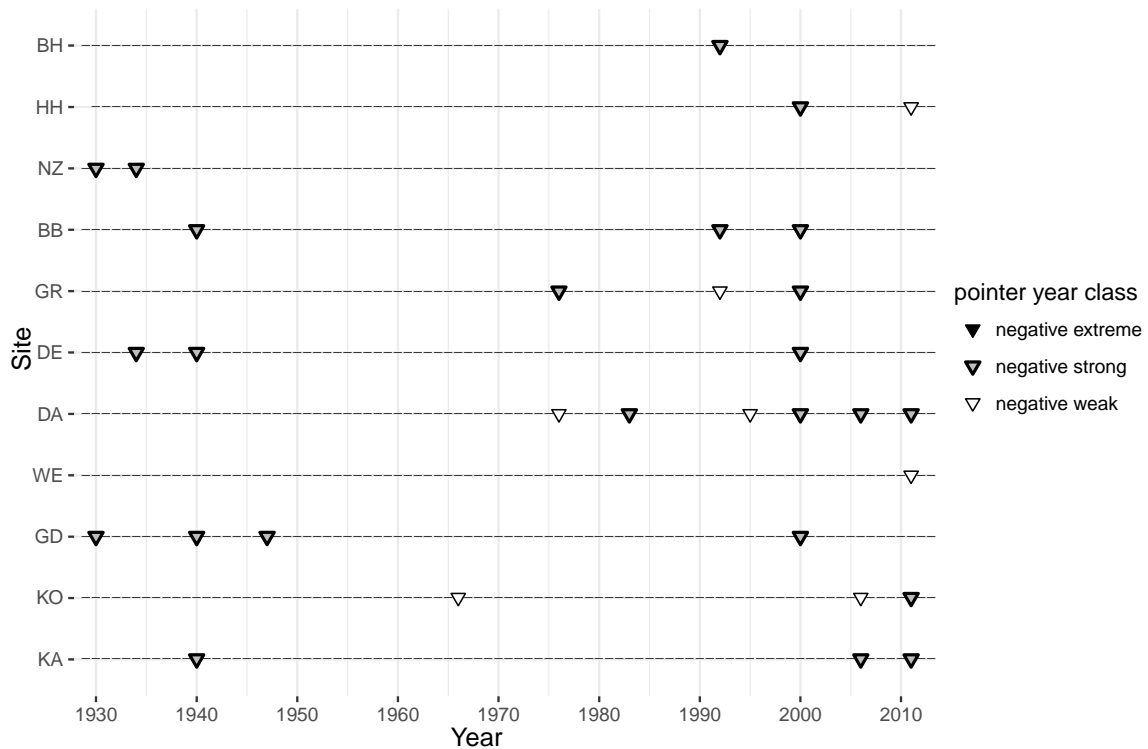


417

418 *Figure 2: Strength of June precipitation signal (a) and February temperature signal (b) in chronologies of tree growth across*
 419 *the spatial gradient of study sites. The correlation between precipitation and growth increases significantly from colder to*
 420 *warmer sites, indicated by a blue line with grey bands representing the 95% confidence intervals of the regression. The cor-*
 421 *relation between winter temperature and growth increases significantly towards the colder sites. Significant correlations for*
 422 *individual sites are indicated by asterisks.*

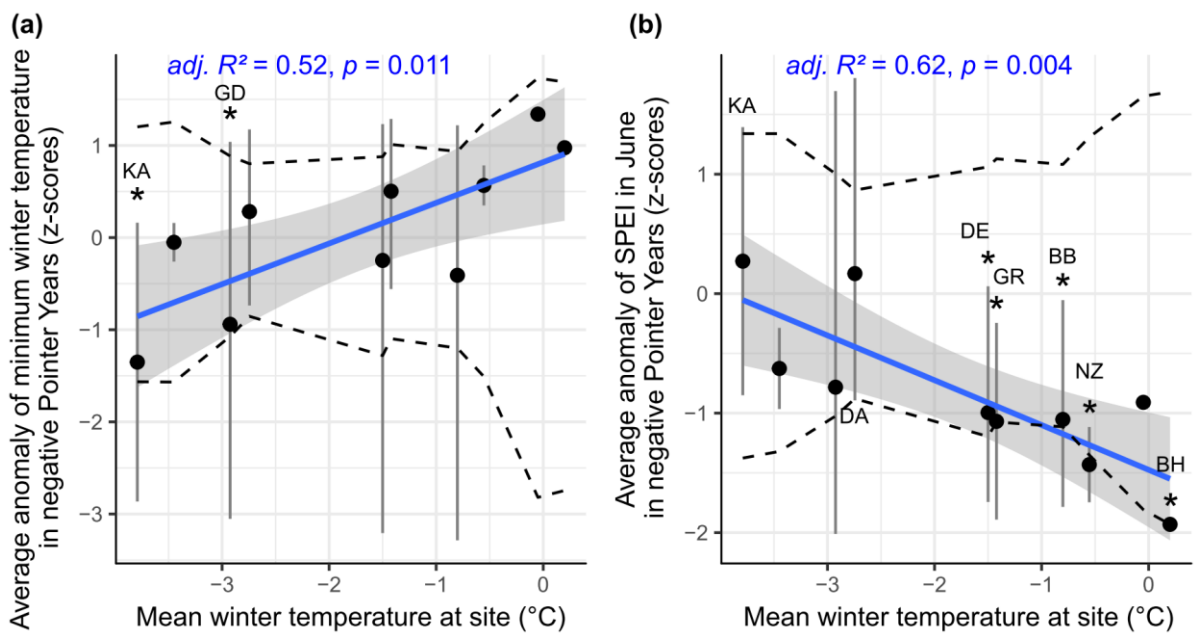
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425

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



430

431 *Figure 4: Superposed Epoch Analysis (standardized climate anomalies in negative pointer years) for the period 1929-2009*
 432 *across the studied gradient of decreasing mean winter temperature. Blue lines with grey bands represent regression lines*
 433 *with 95% confidence intervals. Dashed lines represent the 95% confidence interval for site-specific means of climate param-*
 434 *eters. Asterisks indicate climate anomalies significantly deviating from this mean value. Vertical grey lines represent the*
 435 *range of anomalies at a given site. The site WE is not shown in the regression plots, because no negative growth events occ-*
 436 *urred at this site during the analysed time span of 1929–2009.*

437

438

439 **Tables**

440 *Table 1: Characteristics of the study sites, which are listed in descending order of winter temperature. Geographic position*
 441 *(E: longitude degree, N: latitude degree); mean annual precipitation sum (MAP), mean annual temperature (MAT), and*
 442 *mean coldest month temperature (MCMT) for the climate normal period 1961-1990; Number of dated trees used to build*
 443 *chronologies (N_{Tree}), series length (l_{Series}) as an indicator of approximate tree age, tree height (h) and diameter at breast*
 444 *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

445

446 Table 2: Chronology statistics of tree-ring series. Number of trees (N_{Tree}), correlation between trees (r_{bar}), expressed popula-
 447 tion signal (EPS), mean sensitivity (MS), and mean autocorrelation within trees (AC) in descending order of winter tempera-
 448 ture. r_{bar} and EPS were calculated from detrended series, MS and AC from index series over the common overlap period
 449 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

450

451

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658 **Supporting Information**

659 **Appendix S1** Detailed overview of temporal trends of the climate data that were used to establish
660 climate–growth relationships, correlations of tree growth with monthly (previous June to current
661 September) temperature and precipitation variables, and characterization of soil type at each site.

662

663 **Data availability**

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

666

667 **Biosketch**

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

676 JK and RW conceived the ideas; MK, JK, LM, EM, and RW conducted the field work; MM, LM, EM, and
677 RW prepared the samples in the lab; RW analysed the data with contributions from JK, MM, EM, and
678 MW; EM and RW led the writing with all authors contributing to the text.

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