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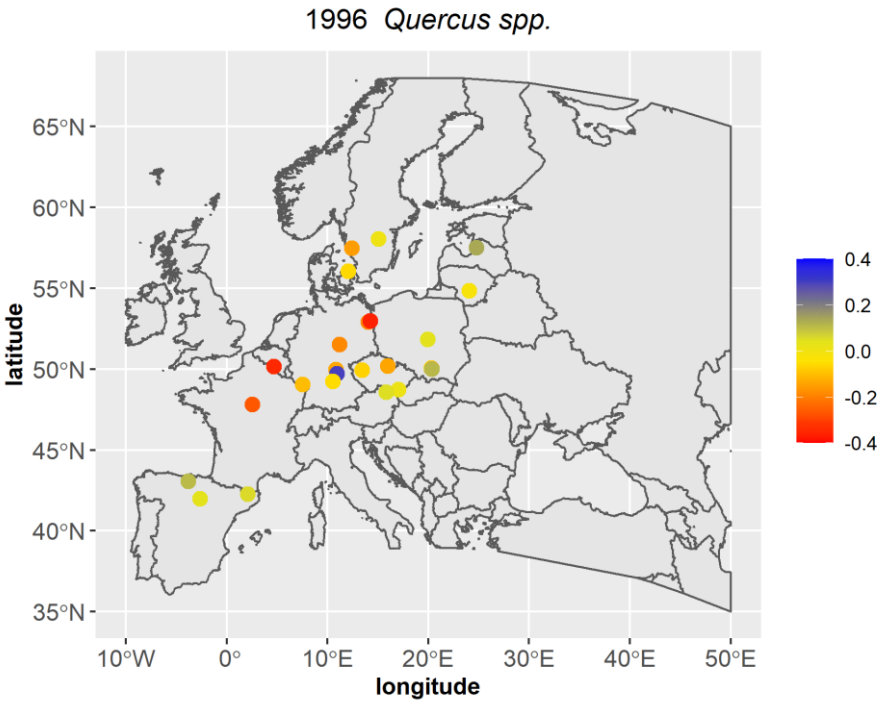
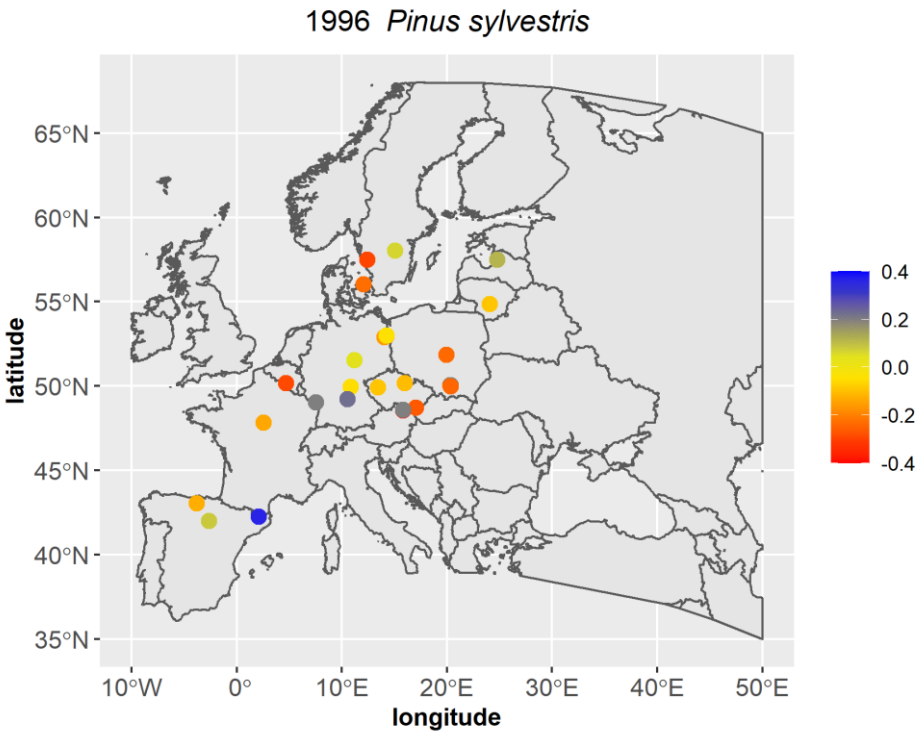
Abstract

Quercus robur/*Quercus petraea* and *Pinus sylvestris* are widely distributed and economically important tree species in Europe co-occurring on mesotrophic, xeric and mesic sites. Increasing dry conditions may reduce their growth, but growth reductions may be modified by mixture, competition and site conditions. The annual diameter growth in monospecific and mixed stands along an ecological gradient with mean annual temperatures ranging from 5.5°C to 11.5°C was investigated in this study. On 36 triplets (108 plots), trees were cored and the year-ring series were cross-dated, resulting in year-ring series of 785 and 804 trees for *Q. spp.* and *P. sylvestris*, respectively. A generalized additive model with a logarithmic link was fit to the data with random effects for the intercept at the triplet, year and tree level and a random slope for the covariate age for each tree; the Tweedie-distribution was used. The final model explained 87 % of the total variation in diameter increment for both tree species. Significant covariates were age, climate variables (long-term mean, monthly), local competition variables, relative dbh, mixture, stand structure and interactions thereof. Tree growth declined with age and local density and increased with social position. It was positively influenced by mixture and structural diversity (Gini coefficient); mixture effects were significant for *P. sylvestris* only. The influence of potential evapotranspiration (PET) in spring and autumn on tree growth was positive and non-linear, whereas tree growth sharply decreased with increasing PET in June, which proved to be the most influential month on tree growth along the whole ecological gradient. Interactions of PET with tree social position (relative dbh) were significant in July and September for *Q. spp.* and in April for *P. sylvestris*. Interactions of climate with density or mixture were not significant. Climatic effects found agree well with previous results from intra-annual growth studies and indicate that the model captures the causal factors for tree growth well. Furthermore, the interaction between climate and relative dbh might indicate a longer growth duration for trees of higher social classes. Analysis of

81 random effects across time and space showed highly dynamic patterns, with competitive
82 advantages changing annually between species and spatial patterns showing no large-scale
83 trends but pointing to the prevalence of local site factors. In mixed-species stands, the tree
84 species have the same competitivity in the long-term, which is modified by climate each year.
85 Climate warming will shift the competitive advantages, but the direction will be highly site-
86 specific.

Graphical abstract





A random intercept for each triplet and year for *Quercus robur* and *Quercus petraea* (top) and *Pinus sylvestris* (bottom) showing the inter-annual variation in diameter increment on different sites at the logarithmic scale in mm

1. Introduction

Quercus robur/*Quercus petraea (Q. spp.* hereafter*)* and *Pinus sylvestris* are economically important tree species constituting a considerable proportion of the forest cover in Europe (Eaton et al. 2016, Durrant et al. 2016). All three species range from southern Europe (Iberian peninsula, Greece) to Scandinavia, but *P. sylvestris* grows on a wider latitudinal and longitudinal range (Eaton et al. 2016, Durrant et al. 2016) than *Q. spp.*. The two *Quercus* species naturally hybridize, forming fertile offspring, so that they are viewed as sub-species by some_authors (e.g. Roloff und Bärtels 2006). Because of their considerable range overlap, frequent hybridization and similar ecology, the two species are often investigated jointly.

Q. spp. and *P. sylvestris* are light-demanding tree species growing in a mixture on xeric and mesic, acidophilous sites where they represent the climatic climax (Muller 1992, Eaton et al. 2016, Durrant et al. 2016). The exigency for nutrients is lower for *P. sylvestris* than for *Q. spp.* (Mellert et al. 2012). *Q. spp.* are thermophilic, and they grow on sites with a minimum of 8.4°C during the growing season, while the temperature range of the pioneer species *P. sylvestris* is considerably larger (Vospernik 2021). All three tree species have been recognized as drought tolerant and with an efficient protection against high irradiance (*Q. spp.*: Epron and Dreyer 1993, Arend et al. 2011, Bose et al. 2021, Vitasse et al. 2019, *P. sylvestris:* Eilmann et al. 2006, Rigling et al. 2001). *Q. spp.* have deep penetrating tap roots and are an-isohydric tree species, known to keep their stomata open under drought conditions, showing a good resistance and resilience to drought and consequently a small decrease in tree growth in drought years (Trouvé et al. 2017, Leuzinger et al. 2005). Comparative studies on *Q. robur* and *Q. petraea*. reported only slight differences between the two species, with *Q. petraea* being more drought tolerant because of its higher intrinsic water-use efficiency (Epron and Dreyer 1993, Arend et al. 2011).

P. sylvestris is also well adapted to a dry climate, but as conifer species, has a more conservative water use strategy. It can be classified as an iso-hydric species, closing its stomata earlier under drought conditions (Martín-Gómez et al. 2017, Zweifel 2009), which leads to carbon starvation and a long-term reduction of the needle mass (Rigling et al. 2001, Zweifel 2009). Subsequently, carbon starvation is thought to result in mortality, and higher mortality rates under drought were observed for *P. sylvestris* than for both *Q. spp.* (Bigler et al. 2006, Eilmann et al. 2006). In the last years, *P. sylvestris* has suffered tremendously from heat waves (Salomon et al. 2022), which may result in a species shift in favor of *Q. spp.* on dry sites with increasing climate warming (Eilmann et al. 2006).

While tree growth in the South of Europe is limited by summer drought, imposed by the Mediterranean climate, tree growth in Central regions, exhibiting mesic growing conditions, is more dependent on the competitive potential (Ramírez-Valiente et al. 2020). In the Mediterranean climate, however, both *P. sylvestris* and *Q. spp.* show unimodal growth patterns. Tree growth starts in spring, showing a maximum around the summer solstice and a decline in late summer and autumn with the growing season being shorter on the more drought prone sites (Strieder and Vospernik 2021). As a consequence of this tree growth pattern, drought effects vary with season (Merlin et al. 2015), and spring or early summer droughts have a more substantial impact on tree growth (Bose et al. 2021). *P. sylvestris* is an evergreen conifer, which starts to grow when the temperature rises above 5 °C. As ring-porous trees, *Q. spp.* do not come into leaf until late April-May (Eaton et al. 2016), although their growth starts before budburst (Suzuki et al. 1996).

Tree ring analysis is an important and frequently used way to investigate climate-growth relationships (Linderholm 2001, Mérian et al. 2013). Since the tree species studied here are widespread, many tree ring studies have been carried out to analyse their growth (e.g. Barsoum et al. 2015, Trouvé et al. 2017). Previous studies reported that *Q. spp.* and *P. sylvestris* respond to drought with reduced ring width, but fluctuations in ring width are less

pronounced for *Q. spp.* because of its an-isohydric nature (Zweifel 2009) and tree growth at high elevations was reported to show less between year variation (Vospernik and Nothdurft 2018) than tree growth at lower ones; Similarly, a response to long-term drought was reported for higher elevations, whereas a response to short-term drought was observed at lower elevation sites (Bhuyan et al. 2017). These previous studies, however, focus on a specific area and do not encompass the whole climatic gradient where both *Q. spp*. and *P. sylvestris* co-occur, nor do they explicitly include mixture or competition effects, which may be prevalent in a temperate climate.

Growth related mixture effects for *Q. spp./P. sylvestris*, which occupy a similar ecological niche, are reported to be positive on average, with a range between 6-14 % and considerable variation between sites (Steckel et al. 2019, Steckel et al. 2020a, Pretzsch et al. 2020). The competitive advantage for *P. sylvestris* in the mixture increases with site index and water supply, while it decreases with site index for *Q. spp.* (Pretzsch et al. 2020). Differences in productivity between monospecific and mixed stands at the stand level may result from higher stand densities, higher inequality of tree size distribution and growth-size relationships with stronger size asymmetry and emergent properties derived from effects at the tree level (Pretzsch and Schütze 2016). In contrast, at the individual tree level possible reasons for positive mixture effects are tree specific differences in the crown and root morphology, water and nutrient use strategy, different leaf and litter composition and tree phenology (Kelty et al. 1992, Pretzsch and Schütze 2016, Ammer 2019). At the individual tree level *Q. spp*. profited on average from the admixture of *P. sylvestris* (Toïgo et al. 2018) or behaved indifferently (Barsoum et al. 2015) or negative mixture effects were observed (Nothdurft and Engel 2020). However, interactions between a given pair of species are often dynamic, changing as resource availability and climate conditions change. It is not unusual for net complementary interactions between a given species pair to transform into net competitive interactions, or vice versa (Forrester 2014, Jacobs et al. 2022).

At the individual tree level, species coexistence is driven by fine-scale spatial patterns and the competitive ability of species (Collet et al. 2017). Even if species are mixed at the stand scale, species may be segregated at the local scale. Such fine-scaled spatial patterns may be captured by local competition indices and describe the physiological response of trees in the interspecific and intraspecific neighbourhood (Höwler et al. 2019). Local heterogeneity may also result from small-scale spatial heterogeneity of environmental factors (micro-site) or interactions between species. Such local competition effects are rarely included in tree-ring studies.

Hypothesis

In this study we analyse the climate-growth relationship of *Quercus spp*. and *P. sylvestris* along a gradient across Europe in monospecific and mixed stands. We hypothesize that:

(1) Tree growth reactions are site-specific. (i) Trees within the same bio-climatic regions show analogous tree growth patterns while patterns between different bio-climatic regions differ.

(2) Tree growth reactions to drought are species, mixture and season specific (i) *Q. spp.* is more drought resistant (ii) *P. sylvestris* is more tolerant to cold, (iii) both species react more sensitively to drought on drought prone sites (iv) both species react less sensitive to drought in mixture compared to monocultures

(3) Tree growth is influenced by mixture (i) mixture effects are positive for both tree species, (ii) mixture effects depend on local competition

2. Material and Methods

2.1 Material

2.1.1 Study area and research sites

This study builds on a comprehensive transect of 36 *Q. spp.* - *P. sylvestris* triplets located along an ecological gradient through Europe, reaching from nutrient-poorer and xeric to nutrient-richer and mesic sites (Fig. 1). The transect was initially established as part of the ERA-Net SUMFOREST project REFORM ("Resilience of FORest Mixtures", reform-mixing.eu) and is described in detail in previous studies focusing on stand productivity and tree drought resilience (Steckel et al. 2019, Pretzsch et al. 2020, Steckel et al. 2020a). Long-term mean temperature on triplets ranged between 5.5 °C and 11.5 °C, with long-term mean precipitation ranging from 456-929 mm (Table 1). By design, each triplet contains three sub-plots, representing one mixed *P. sylvestris* - *Q. spp.* stand and two monospecific stands of each species, respectively. In the sampling protocol stands were required to be even-aged, at maximum density and unthinned for at least 20 years and exhibit a more or less pronounced mono-layered structure. Stand age and stand density are given in Table 1.

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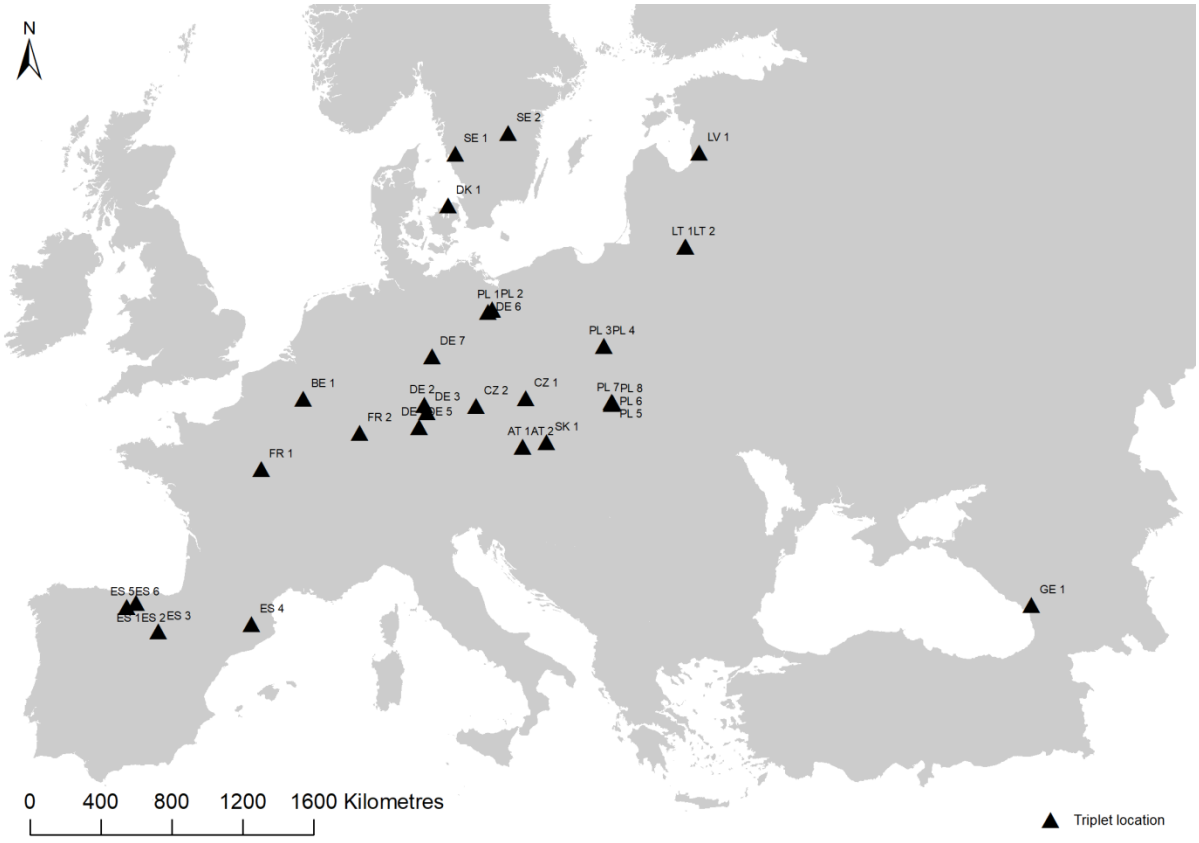

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209 **Figure 1** Triplets (*Q. spp.-P. sylvestris*) distribution along European ecological gradient

Table 1 Summary statistics of triplets. Tri = Triplet code; Lat = Latitude (degree); Long = Longitude (degree); Incl=Inclination (degree); Asp=Aspect (degree); P = long-term mean (1976-2015) annual precipitation (mm); T = long-term mean (1976-2015) annual temperature (Celsius degree); n = number of year rings observed on each plot; Age = Mean age of cored trees; QMD = quadratic mean diameter (cm); SDI = Stand density index for pure *Quercus spp. (Q.)* plots, pure *Pinus sylvestris (P.)* plots and mixed (M.) plots; id = average yearly diameter increment (mm) for *Quercus spp. (Q.)* and *Pinus sylvestris (P.)* in pure and mixed stands in the 20 years analysed; Note that one triplet was not included because no trees were available, were local competition variables could be calculated without edge effect

Tri	Lat	Long	Incl	Asp	P	T	n	Age	QMD	SDI			id			
													Pure		Mixed	
										Q.	*P.*	M.	*Q.*	*P.*	*Q.*	*P.*
AT 1	48.6	15.8	0.0	180	658	8.7	1452	103	30.5	556	1024	785	0.266	0.150	0.177	0.161
AT 2	48.6	15.8	0.0	180	658	8.7	1249	56	26.3	643	1152	876	0.222	0.229	0.209	0.207
BE 1	50.2	4.7	0.0	180	929	9.3	1298	69	26.0	413	477	534	0.265	0.459	0.318	0.332
CZ 1	50.2	16.0	0.0	180	620	9.2	1012	95	26.2	632	900	962	0.225	0.176	0.207	0.195
CZ 2	49.9	13.5	0.0	180	573	8.7	726	76	21.2	937	1327	1053	0.235	0.250	0.178	0.327
DE 1	49.9	10.8	28.8	225	615	8.5	1122	108	27.5	1049	1034	1045	0.217	0.200	0.206	0.221
DE 2	49.9	10.8	27.6	225	615	8.5	858	108	26.4	1007	1060	1168	0.179	0.215	0.257	0.163
DE 3	49.7	11.0	23.6	315	663	8.4	22	110	29.7	836			0.092			
DE 4	49.2	10.6	6.4	180	718	8.1	748	48	20.0		1144	921		0.219	0.541	0.440
DE 5	49.2	10.6	4.8	180	718	8.1	1078	46	20.7	864	1076	879	0.470	0.325	0.525	0.510
DE 6	52.9	14.1	0.0	180	558	9.4	1496	82	30.0	765	897	816	0.336	0.306	0.301	0.396
DE 7	51.5	11.2	53.2	202	503	9.5	946	80	21.0	1459	1715	1429	0.251	0.114	0.187	0.191
DK 1	56.0	12.1	0.0	180	667	8.0	462	50	27.1	833	1014	795	0.330	0.321	0.409	0.550
ES 1	43.0	3.8	45.3	236	819	11.4	503	45	20.6	1210	1517	1526	0.114	0.343	0.243	0.273
ES 2	43.0	3.8	41.9	259	819	11.4	374	45	21.5	1126	1461	1513	0.214	0.451	0.288	0.199
ES 3	42.0	2.0	27.0	180	586	10.0	660	61	24.9	911	1158		0.152	0.503		
ES 4	42.3	2.1	60.7	22	846	10.9	861	53	17.9	637	395		0.143	0.312		
ES 5	42.9	4.2	26.4	45	793	9.9	902	55	25.4	1258	1444	1412	0.206	0.373	0.259	0.310
FR 1	47.8	2.5	0.0	180	724	11.0	1332	64	28.7	651	867	705	0.288	0.361	0.246	0.319
FR 2	49.0	7.5	25.4	45	893	9.8	1496	112	37.3	413	792	519	0.296	0.190	0.255	0.185
GE 1	43.0	41.6	15.1	79	456	11.5	532	83	21.0	608	694	1419	0.130	0.189	0.174	0.333
LT 1	54.8	24.1	0.0	180	614	6.6	792	59	26.7	1093	632	871	0.349	0.290	0.242	0.298
LT 2	54.8	24.1	0.0	180	614	6.6	968	86	31.3	811	927	864	0.270	0.254	0.295	0.367
LV 1	57.5	24.8	0.0	180	657	5.5	1254	70	28.9	565	835	801	0.196	0.304	0.181	0.430
PL 1	53.0	14.3	10.4	180	604	9.1	946	55	23.1	863	1071	1054	0.240	0.333	0.254	0.374
PL 2	53.0	14.3	7.4	180	604	9.1	1034	56	24.2	899	1086	901	0.230	0.301	0.237	0.397
PL 3	51.8	19.9	0.0	180	554	8.1	1100	74	29.7	893	905	880	0.211	0.362	0.355	0.354
PL 4	51.8	19.9	0.0	180	554	8.1	1144	75	31.3	808	944	750	0.304	0.329	0.419	0.404
PL 5	50.1	20.3	0.0	180	671	8.4	1716	65	29.0	845	1020	999	0.287	0.352	0.421	0.323
PL 6	50.1	20.3	0.0	180	671	8.4	1606	65	29.5	854	1155	907	0.291	0.378	0.327	0.340
PL 7	50.0	20.4	0.0	180	680	8.4	1705	75	36.2	747	1218	804	0.452	0.282	0.357	0.298
PL 8	50.0	20.4	0.0	180	680	8.4	858	85	39.2	763	868		0.260	0.266		
SE 1	57.5	12.4	6.0	202	891	7.2	962	86	26.2	505	883	568	0.336	0.199	0.380	0.322
SE 2	58.0	15.6	38.1	169	598	6.0	738	127	27.4	876	1149	876	0.147	0.088	0.155	0.096
SK 1	48.7	17.1	0.0	180	580	9.8	814	66	27.6	678	1051	728	0.166	0.202	0.182	0.220

220 2.1.2 Data collection and preparation

221 Field sampling was carried out in late 2017 at the end of the growing season,
222 following a comprehensive standardized sampling protocol (Pretzsch et al. 2020). All trees on
223 each plot of the triplets were assessed and for each tree coordinates, dbh, height and height to
224 the crown base were recorded. On a sub-sample of trees, two increment cores were extracted
225 at breast height (1.3 m) from north and east cardinal directions, covering the entire diameter
226 distribution. A minimum of 20 dominant and 10 sub-dominant trees per species were sampled
227 on each plot, after removing damaged cores and trees sampled close to plot boundary, to
228 avoid edge effects in the calculation of local competition (see section 2.2.1 neighborhood
229 analysis), the resulting number of cores was 785 and 804 trees for *Q. spp.* and *P. sylvestris*,
230 respectively for the total gradient. The diameter at breast height (dbh) was also measured with
231 an accuracy of 0.1 cm, using a girth tape.

232 Annual ring-widths were measured from each increment core, using standardized
233 dendrochronological techniques (Speer 2010). Cross-dating was performed for the individual
234 plots of each triplet, guided by narrow ring widths in species-specific pointer years
235 (Schweingruber et al. 1990). Inter-series correlation ranged between 0.34-0.77 for *Q. spp.* and
236 0.39-0.74 for *P. sylvestris*. The expressed population signal, estimating how well the
237 particular sample of cores at hand represents the theoretical population chronology from
238 which it is drawn based on the inter-series correlation (Wigley et al. 1984), ranged from 0.61-
239 0.96 and 0.84-0.99 for *Q. spp.* and *P. sylvestris*, respectively. Thus, it was above the
240 recommended threshold value of 0.85 for *P. sylvestris* on all sites, but below this threshold on
241 some sites for *Q. spp.*. To reflect the current competitive status, only year-ring series from
242 1996-2017, a period with no silvicultural interventions, were used in this analysis.

243

244 2.1.3 Climate data

Meteorological information (monthly mean temperature (T) and monthly precipitation total (P)) was obtained from local meteorological stations. It was assumed that the observations from meteorological stations reflect local site conditions as well as possible. Meteorological stations used were located in close proximity to the research sites in question. Such sites did not exhibit any regional topographical peculiarities that would prohibit such an approach.

In cases where no suitable local station data was available (no coverage at all or distance to site considered too far), interpolated observations as gridded data sets as provided by national meteorological services or the CRU (Climatic Research Unit) 0.5° (Harris et al. 2020). In general, such modelled data used was cross-checked with station measurements (where possible) to evaluate the comparability of data sources. Monthly meteorological data were subsequently further aggregated to annual values or multi-annual means. From the gridded temperature and precipitation data, the potential evapotranspiration (PET) according to Thornthwaite (1948) and the climatic water balance (P-PET) were derived for each month. In addition, different drought indices were calculated: the De Martonne aridity index (DMI) (Martonne 1926), the standardized precipitation index (SPI) (McKee et al. 1993), and the standardized precipitation and evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010). The climate growth relationship was analyzed from August of the previous year to September of the year of tree-ring formation based on previous dendroecological and intra-annual growth studies (e.g. Sánchez-Salguero et al. 2013).

2.2 Methods

2.2.1 Neighbourhood analysis

We analyzed the competitive constellation of every cored tree on the plot to reveal how the local inter- and intra-specific environment modify tree growth. First, a circle with the

recommended radius of r = 7 m (Biging and Dobbertin 1992, Biging and Dobbertin 1995) around the stem coordinate of each cored tree was constructed and all trees within the circle were used in the neighbourhood analyses. Circles of this size include 8-9 trees on average and at least the 5–6 most impactful neighbors (Prodan 1968a, Prodan 1968b).

For the neighbourhood analysis, we calculated the tree's specific competition index according to Hegyi (1974), with $ci_j = \sum_{\substack{i=1 \\ i \neq j}}^{n} \left(\frac{d_i}{d_j} \times \frac{1}{dst_{ij}} \right)$, which quantifies the competition of central tree j based on its stem diameter (d_j), the stem diameters of its neighbours (n) $d_{i,i=1\ldots n}$, and the distance $\left(dst_{ij}\right)$ between the central tree j and the respective neighbors and the local Stand Density Index, SDI, (Reineke 1933): $SDI = N \times \left(\frac{25}{d_g}\right)^{\alpha}$, where N is the stem number within the 7 m radius, dg is the quadratic mean diameter within the radius and α is the species-specific allometric exponent derived by Pretzsch and Biber (2010). We used the same approach to calculate the tree's specific density, but did not include the tree of interest (central tree).

The trees sampled in the circle were also used to calculate the local mixing proportions using all admixed tree species. The mixing proportions $m_1 \ldots m_n$ should reflect the area proportions of the two or more species in the observed mixed stands (Dirnberger et al. 2017, Pretzsch and Del Río 2020). Tree number, basal area or volume proportions are only appropriate for this purpose if the mixed species have similar growing area requirements (Pretzsch et al. 2017, pp. 137-140). The considered tree species vary per se in the growing area requirement and maximum stand density in fully stocked stands. In order to standardize the density and to calculate unbiased area related to mixing proportions we applied the equivalence factors by Pretzsch and Biber (2016). The potential edge effect was considered by simply removing all trees with search radii reaching beyond the edge of the plots.

To describe forest structure, the Gini coefficient by basal area was calculated in the local neighborhood with a radius of 7 m as suggested by Binkley et al. (2006). Furthermore,

295 the relative dbh was calculated by dividing individual tree dbh by quadratic mean diameter
296 (dg) averaged over all species in the stand to characterize each tree's social position at the
297 stand level.
298
299 2.2.1 Modeling

300 Diameter increment was modeled using the generalized additive models (GAMs).
301 originally developed by Hastie and Tabshirani (1990) blending properties of additive models
302 with generalized linear models. In generalized additive models, the expected value depends
303 on unknown smooth functions of the predictor variables and the observed values are assumed
304 to be of some exponential family distribution (Wood 2011, 2017).
305 GAMs were estimated using the mgcv-package (Wood 2011, 2017) in R (R Core
306 Team 2018); Within the GAM-framework of mgcv, model-covariates may be specified: (a) in
307 parametric form or (b) non-parametrically, as smooth functions. The smooth functions are
308 made of basis functions, that added together compose the smooth terms, hence the name
309 (Wood 2011, 2017). Each smooth f_j is represented by a sum of k simpler, fixed basis
310 functions ($b_{j,k}$). multiplied by corresponding coefficients $\beta_{j,k}$ which need to be estimated.

311 $$f_j(x_j) = \sum_{k=1}^{k} (\beta_{j,k} \cdot b_{j,k}(x_k)) \quad (1)$$

312 Numerous different basis functions, such as cubic splines, circular splines or thin plate
313 regression splines, are provided by the mgcv-package, and the type and number of basis
314 functions can be set.
315 Given a matrix of known coefficients S, we can formally note a penalized likelihood function:

$$l_p(\beta) = l(\beta) - \frac{1}{2}\sum_j \lambda_j \beta^T S_j \beta$$

316 Where $l(\beta)$ is the usual GLM likelihood function and $\lambda_j$are the smoothing parameters. The
317 part of the function including λ penalizes curvature in the function and
318 controls the degree to which the model fits the data. As $\lambda \to \infty$, the estimator for f_j becomes
319 linear while $\lambda = 0$ would allow any $f$that interpolates the data (Wood, 2006). Technically, it
320 can be set, but it is usually determined programmatically by minimizing the least squares
321 criterion subject to a roughness penalty based on second derivatives, i.e. if the second
322 derivatives are zero, the function is linear and these departures from linearity (smoothness)
323 are penalized, which avoids overfitting The final complexity of the smooth is given by the
324 effective degree of freedom (edf) and an edf of 1 is equivalent to a linear function. The model
325 degrees of freedom are obtained by summing the effective degrees of freedom (Wood 2011,
326 2017).
327
328 In addition, the mgcv-package also allows for the inclusion of random terms.Since the
329 data set used in this study is a hierarchical data set with trees at the same plot and
330 measurements at the same tree being correlated, random effects at the tree, triplet and year
331 level for both intercept and slope were included, where necessary. Diameter increment was
332 linked to the covariates with a logarithmic link function and as exponential family
333 distribution, the Tweedie distribution was used, which allows for fitting the type of
334 exponential distribution from the data via a parameter p, encompassing different exponential
335 distributions such as the normal (p=0), Gamma (p=2) and inverse Gaussian distribution.
336 Parametric terms were used for categorical covariates, whereas smooth functions were used
337 for continuous covariates, with thin plate regression splines as basis functions. The number of
338 basis functions used in model fitting was 10 The mgcv option “select” was set to TRUE,
339 enabling shrinkage. Shrinkage adds an extra penalty and if the smoothing parameter λ, is
340 large enough, the coefficients will shrink to zero. In this manner it can be assessed whether a
341 predictor is adding anything to the model and it can be used as variable selection technique.

342 Enabling shrinkage helps to deal with concurvity of the covariates (Marra and Wood 2011).
343 Concurvity refers to the non-linear dependence of covariates in the GAM-framework, causing
344 unstable estimates similar to collinearity in the linear case. Interactions were included as
345 tensor product interactions, which can be used for variables that operate on different scales.
346 The specification "ti-interaction", i.e. a tensor product interaction where variable 1, variable 2
347 and their combination are separate, was used. All covariates described in the data section were
348 included in model fitting and the best fitting model was selected based on Akaike's
349 information criterion (AIC) (Akaike 1973). From the fitted model variance components for
350 smoothing parameters and random effects were extracted. Note the two variance components
351 for the tensor product smooth indicated by "ti". The first is the variance component of the
352 tensor product smooth for the marginal basis of the first variable; the second is the variance
353 component of the tensor product smooth for the marginal basis of the second variable.
354

355 # 3. Results

356 ## 3.1 Overall model results

357 The final fitted models for diameter increment for *P. sylvestris* and *Q. spp.* included
358 mixture effects at the plot level, age, relative dbh, local SDI, tree species specific Gini
359 coefficient, long-term mean temperature, evapotranspiration of the month of September of the
360 previous year and for each month from April-July (PET 4-7) of the current year and the
361 interaction thereof with relative dbh as fixed effects and triplet and tree specific random
362 effects (Equation 2). The climatic drivers differed slightly between species; PET in April
363 (PET 4) was significant for *P. sylvestris* only, PET in May (PET 5) for *Q. spp.*. The
364 interactions between climate and stand density index and climate and mixture were not
365 significant.

$$\ln(id_{ijk}) = \beta_o + \beta_1 \cdot mixture + f(age) + f(local\ SDI) + f(gini\ ba) + + f(relative\ dbh) + f(LTMT) + f(PET\ previous\ 9) + f(PET\ 4-7) + f(PET\ previous\ 9,\ relative\ dbh) + f(PET\ 4-7,\ relative\ dbh) + \gamma_{1i} \cdot Triplet\ \cdot t_{ij} + \gamma_k \cdot Tree_k + y_k \cdot Tree_k \cdot f(age) + e_{ijk} \quad (2)$$

id_{ijkl}	observed diameter increment for tree k, in season j, on triplet i
β_o	population mean of diameter increment
$\beta_1 \cdot mixture$	parametric mixture effect
f(age)	smooth function for age
$f(local\ SDI)$	smooth function for local SDI
$f(gini\ ba)$	smooth function for species specific Gini coefficient
$f(relative\ dbh)$	smooth function for relative dbh
$f(LTMT)$	smooth function for long-term mean temperatures
$f(PET\ previous\ 9)$	smooth function for monthly potential evapotranspiration for September of the previous year
$f(PET4\text{-}7)$	smooth function for monthly potential evapotranspiration for each month from April - July
$\gamma_{1i} \cdot Triplet\ \cdot t_{ij}$	triplet and year specific random effect
$\gamma_k \cdot Tree_k$	tree specific random intercept
$y_k \cdot Tree_k \cdot f(age)$	tree specific random slope, random effect of age within each level of tree
ϵ_{ijk}	random error

Overall, the model explained 87.4 % and 87.0 % of the total variation for each of the two models (Table 2). Thereof, 41.9 % and 38.2 % were explained by the fixed part of the model for *Q. spp.* and *P. sylvestris*, respectively. The most important variables in the fixed part of the model were relative dbh, species-specific Gini coefficient, and long-term mean temperature for *Q. spp.* and relative dbh as indicated by the variance components (Table 3). In the random part of the model, tree-specific random effects explained more variation, than triplet- and year-specific random effects (Table 3).

For the parametric mixture effects the coefficient and the p-value are given; Table 2 contains the effective degrees of freedom and the p-value for the smooth terms. A high degree of non-linearity for the fixed part of the model was found for age, relative dbh, and local SDI whereas a linear decrease, as is indicated by effective degrees of freedom of 1, was found for other variables, in particular for PET in various month for *P. sylvestris*.

Table 2: Coefficients for parametric effects (Estimate) and effective degrees of freedom for smooth terms (edf) for *Quercus spp*. and *Pinus sylvestris*. The p-value indicates significance of terms. R^2, Akaike's information criterion and the number of observations are given in the bottom lines. Tweedie p gives the estimate for the

shape parameter p of the Tweedie distribution. Note that mixture and LTM are not significant in the *Quercus spp.* model and PET in May is not significant in the *Pinus sylvestris* model as is indicated by the italic font. Variables modelled as random effects are indicated in bold letters

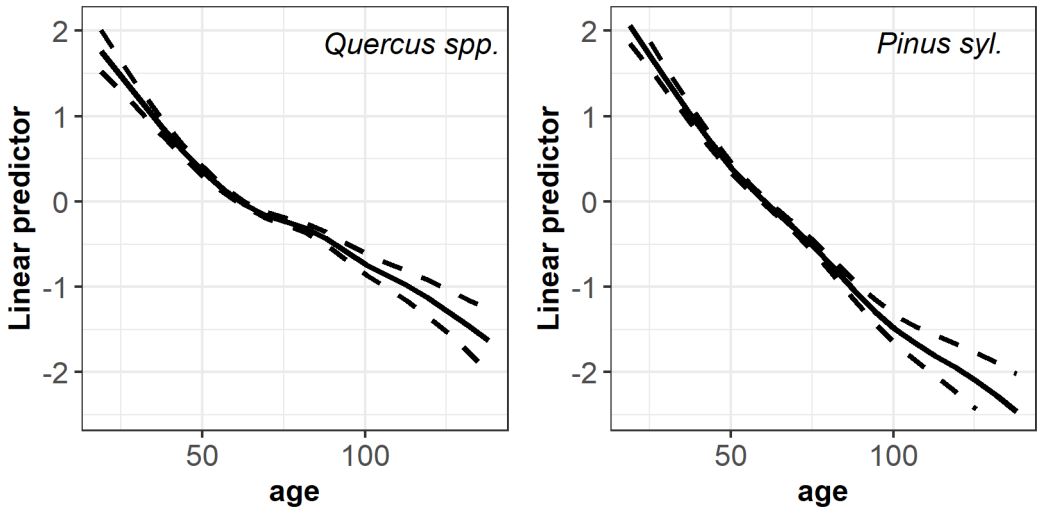
	Quercus spp.		***Pinus syl.***	
Variable	**Estimate**	**p.value**	**Estimate**	**p.value**
Intercept	-1.66	0.000	-2.03	0.000
Mixture	*0.05*	*0.574*	0.24	0.030
Variable	**edf**	**p.value**	**edf**	**p.value**
s(age)	7.53	0.000	6.80	0.000
s(local SDI)	6.08	0.000	7.83	0.000
s(rel. dbh)	6.28	0.000	6.95	0.000
s(Gini coefficient)	4.32	0.010	6.12	0.004
s(LTM temp)	*2.44*	*0.057*	1.00	0.020
s(PET Sept. prev)	1.79	0.000	4.45	0.003
s(PET April)	-	-	1.00	0.001
s(PET May)	2.37	0.000	*1.00*	*0.100*
s(PET June)	1.67	0.000	1.28	0.001
s(PET July)	2.04	0.000	3.66	0.000
s(PET April, rel. dbh)	-	-	6.01	0.010
s(PET July, rel. dbh)	7.23	0.000	-	-
s(PET Sept, prev. rel.dbh)	5.06	0.000	-	-
s(**Tree ID)**	641.94	0.000	700.33	0.000
s(**Tree ID**, age)	653.24	0.000	706.16	0.000
s(**Triplet, Year**)	645.99	0.000	641.47	0.000
R^2	0.874		0.870	
AIC	-52605.71		-47896.73	
n	16696		17284	
Tweedie (p)	1.651		1.347	

Table 3: Variance components (as standard deviation) and their upper and lower confidence limits for the models of *Quercus spp.* and *Pinus sylvestris.* Note the two variance components for the tensor product smooth indicated by ti. The first is the variance component of the tensor product smooth for the marginal basis of the first variable, the second is the variance component of the tensor product smooth for the marginal basis of the second variable. Variables modelled as random effects are indicated in bold letters.

	Quercus spp.			***Pinus sylvestris***		
Variable	**std.dev**	**lower**	**upper**	**std.dev**	**lower**	**upper**
s(age)	0.0031	0.0016	0.0064	0.0026	0.0014	0.0049
s(local SDI)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0001
s(rel. dbh)	0.8516	0.1435	5.0527	0.9739	0.9736	0.9742
s(Gini coefficient)	1.9878	1.1261	3.5090	4.4684	2.3557	8.4760
s(LTM temp)	0.1728	0.0115	2.6057	0.0003	0.0000	1069e+107
s(PET Sep. prev)	0.0004	0.0001	0.0012	0.0024	0.0000	0.0101
s(PET April)	-	-	-	0.0000	0.0000	1055e+263
s(PET May)	0.0006	0.0000	0.0133	0.0000	0.0000	0.0033
s(PET June)	0.0003	0.0000	0.0021	0.0002	0.0001	0.0005
s(PET July)	0.0003	0.0001	0.0012	0.0010	0.0003	0.0033
ti(PET Sep. prev, rel. dbh)1	0.0201	0.0054	0.0749	-	-	-
ti(PET Sep. prev, rel. dbh)2	0.0014	0.0013	0.0015	-	-	-
ti(PET April, rel. dbh)1	-	-	-	0.0083	0.0028	0.0248
ti(PET April, rel. dbh)2	-	-	-	0.0248	0.0043	0.0049
ti(PET July, rel.dbh)1	0.0087	0.0032	0.0235	-	-	-
ti(PET July, rel.dbh)1	0.0093	0.0009	0.0934	-	-	-
s(**Tree ID**)	1.0398	0.9760	1.1077	1.3867	1.3078	1.4704
s(**Tree ID**, age)	0.0161	0.0152	0.0171	0.0220	0.0208	0.0234
s(**Triplet, Year**)	0.1580	0.0895	0.2789	0.1761	0.0928	0.3340
Residual	0.1517	0.1494	0.1540	0.1350	0.1330	0.1370

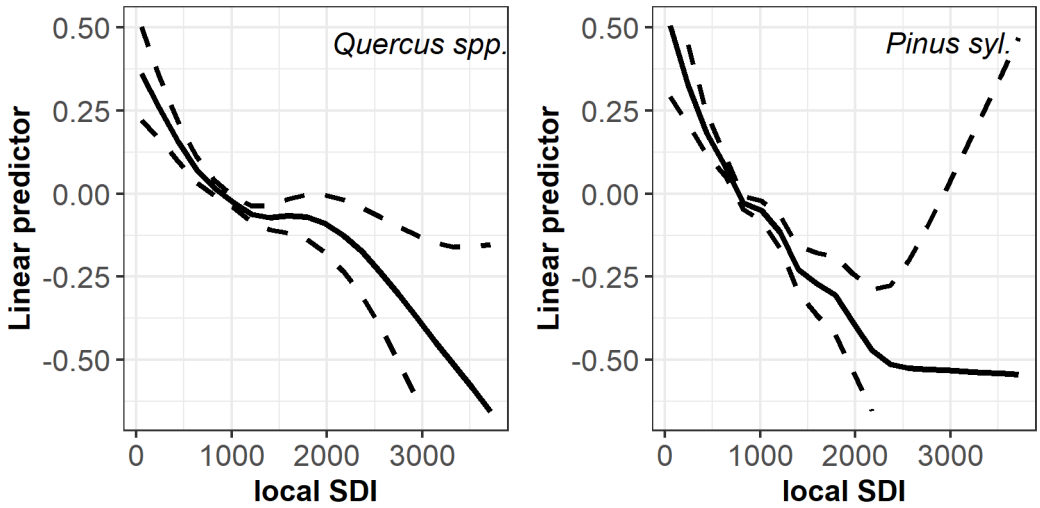
3.2 Fixed effects – parametric and smooth terms

The species mixture increased diameter increment for both *Q. spp.* and *P. sylvestris* (Table 2), but the effect was significant for *P. sylvestris* only. Both tree species showed a decrease in diameter increment with age (Fig. 2) and local SDI (Fig. 3). the decrease being sharper for *P. sylvestris* than for *Q. spp.* (Fig. 2,3). Confidence intervals were narrow for age for the total range of values, but became very large for high SDI values.



422

423 **Figure 2**: Effect of age on diameter increment for *Quercus robur* and *Quercus petraea* (left) and *Pinus sylvestris*
424 (right). Solid line: prediction, dashed lines: confidence interval. Note that the linear predictor (*ln*(diameter
425 increment)) is zero at the mean of the covariate age.
426
427



428

429 **Figure 3**: Effect of local SDI on diameter increment for *Quercus robur* and *Quercus petraea* (left) and *Pinus*
430 *sylvestris* (right). Solid line: prediction, dashed lines: confidence interval. Note that the linear predictor
431 (*ln*(diameter increment)) is zero at the mean of the covariate local SDI.
432

433 Both species showed an almost linear increase in diameter increment with relative

434 dbh; Thus trees in the stand upper layer had higher increment rates (Fig. 4).

435
436
437

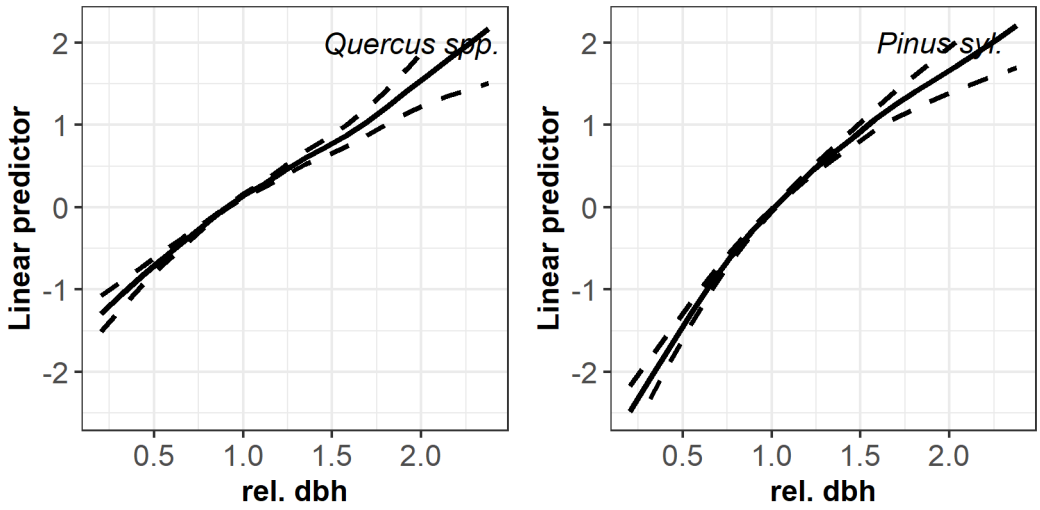


Figure 4: Effect of relative dbh (dbh divided by quadratic mean diameter) on diameter increment for *Quercus robur* and *Quercus petraea* (left) and *Pinus sylvestris* (right). Solid line: prediction, dashed lines confidence interval. Note that the linear predictor (*ln*(diameter increment)) is zero at the mean of the covariate relative dbh.

Non-linear patterns were observed for the relationship between Gini coefficient and diameter increment and the patterns for the two tree species differed (Figure 5). It might point to the fact, that this variable captures different tree structures in the observed data, but that this pattern might not be generalizable.

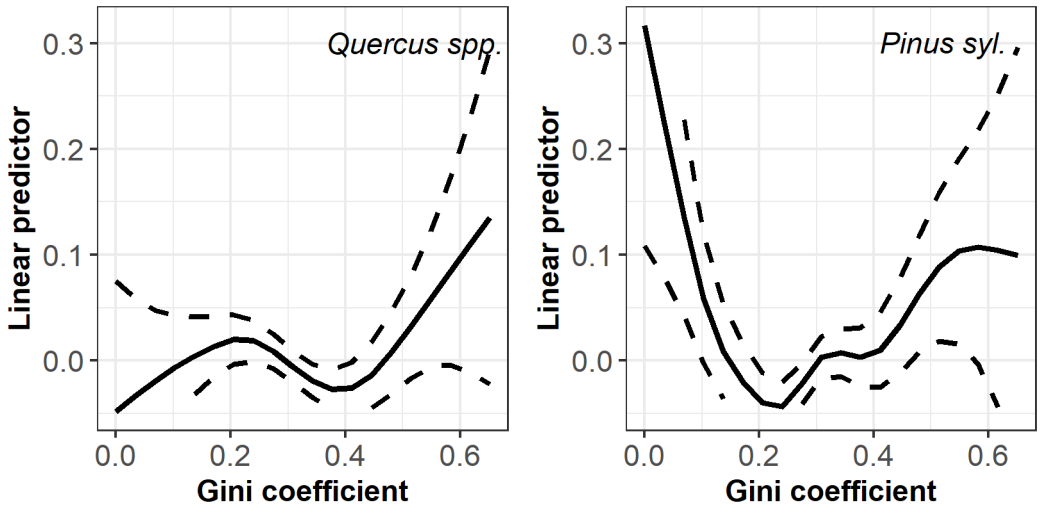
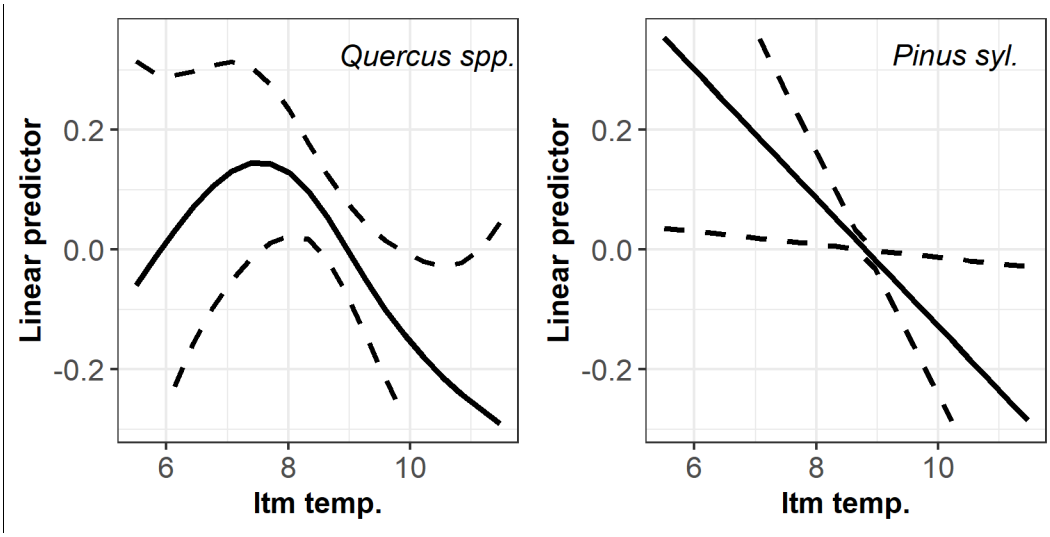


Figure 5: Effect of Gini coefficient on diameter increment for *Quercus robur* and *Quercus petraea* (left) and *Pinus sylvestris* (right). Solid line: prediction, dashed lines confidence interval. Note that the linear predictor (*ln*(diameter increment)) is zero at the mean of the covariate Gini coefficient.

The effect of long-term mean temperature for both tree species is illustrated in Fig. 6, but the effect was significant for *P. sylvestris* only. Effects differed for the two tree species:

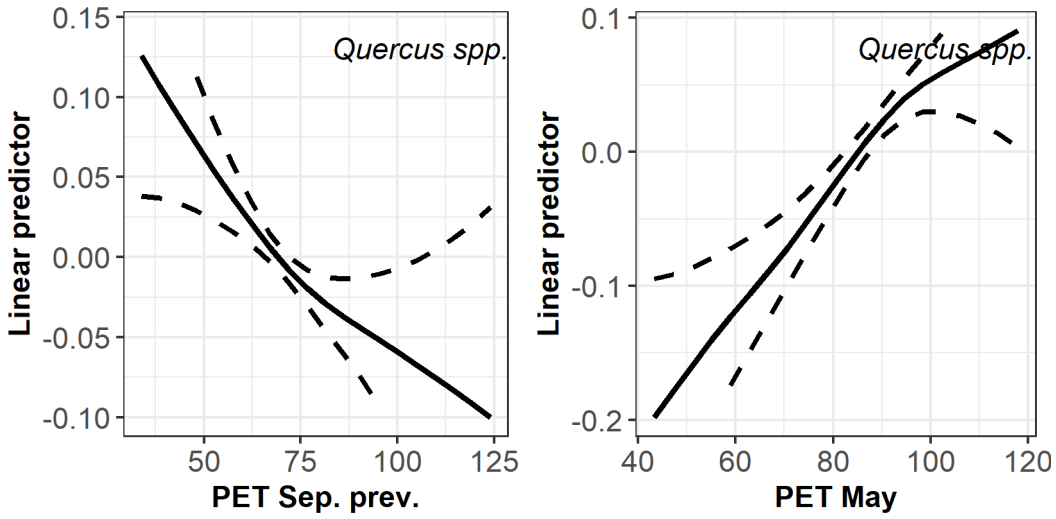
455 the growth of *Q. spp.* indicated an optimum temperature at 7° C, but the *P. sylvestris* growth
456 showed a linear decrease with temperature (Fig. 6). Both relationships have very large
457 confidence intervals.



458

459 **Figure 6**: Effect of long-term mean temperature (ltm temp.) from the years 1976-2015 on diameter increment
460 for *Quercus robur* and *Quercus petraea* (left) and *Pinus sylvestris* (right). Solid line: prediction, dashed lines
461 confidence interval. Note that the p-value for *Q. spp.* is 0.1. Note also that the linear predictor (*ln*(diameter
462 increment)) is zero at the mean of the covariate ltm temp. The relationship between the linear predictor and
463 ltm temp. is linear and could also be represented by a parametric linear term.
464
465 In addition to long-term mean temperature, both species responded to
466 evapotranspiration in different months. In general, autumn of the previous year and spring and
467 summer of the current year influenced tree growth. Influential months differed between
468 species. For both species, the influential months were September of the previous year and
469 June and July of the current year (Fig. 7, Fig. 8); An additional month of the current year had
470 also a significant influence: May for *Q. spp.* and April for *P. sylvestris.* Patterns significantly
471 differed between months and often showed opposite trends. The diameter increment showed a
472 decrease with increasing PET of September of the previous for *Q. spp*. and was highly non-
473 linear for *P. sylvestris*. In spring, at the onset of growth, tree growth increased with increasing
474 PET for both species, which switched to a sharp decrease in June. Note the very different
475 scales of observed PET values on the x-axis for various months and the different scale for the
476 linear predictor. A larger effect of climate on diameter increment was observed in spring

compared to autumn, but effects for both tree species had a similar magnitude for the same month. June is the most influential month for both tree species. Interactions of PET with relative dbh were significant for September of the previous year and July of the current year for *Q. spp.* (Fig. 9) and with PET in April of the current year for *P. sylvestris* (Fig. 10). The climate-growth relationship shown in the figures (Fig. 9, Fig. 10) differs for trees of different social position (the most dominant and suppressed trees) in particular at the beginning and the end of the growing season. These are the only significant interactions at the logarithmic scale of diameter increment. Such interactions are, however, significant for all months, when modelling diameter increments on a linear scale; As the fit of a concurrent linear model showed, different social classes behave differently to the climate in a specific month.



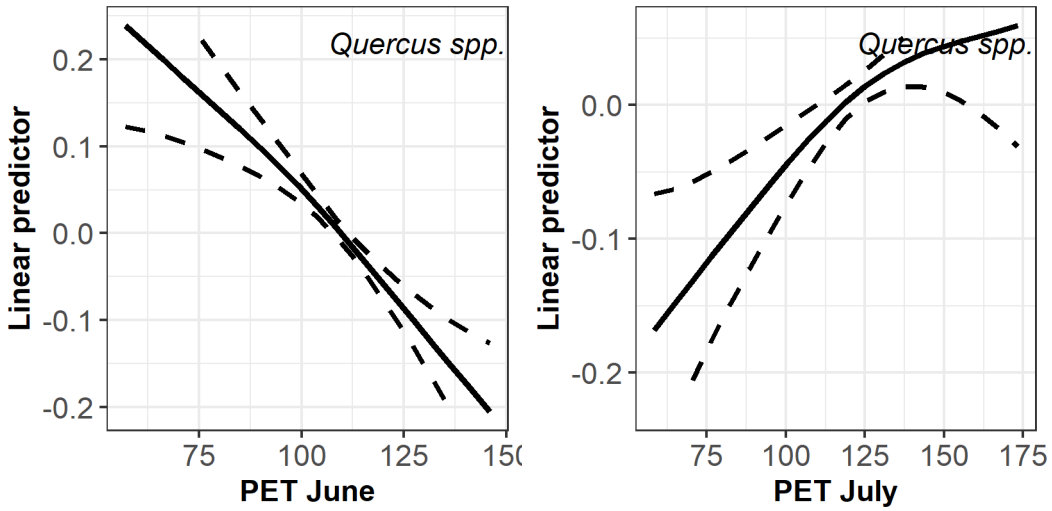
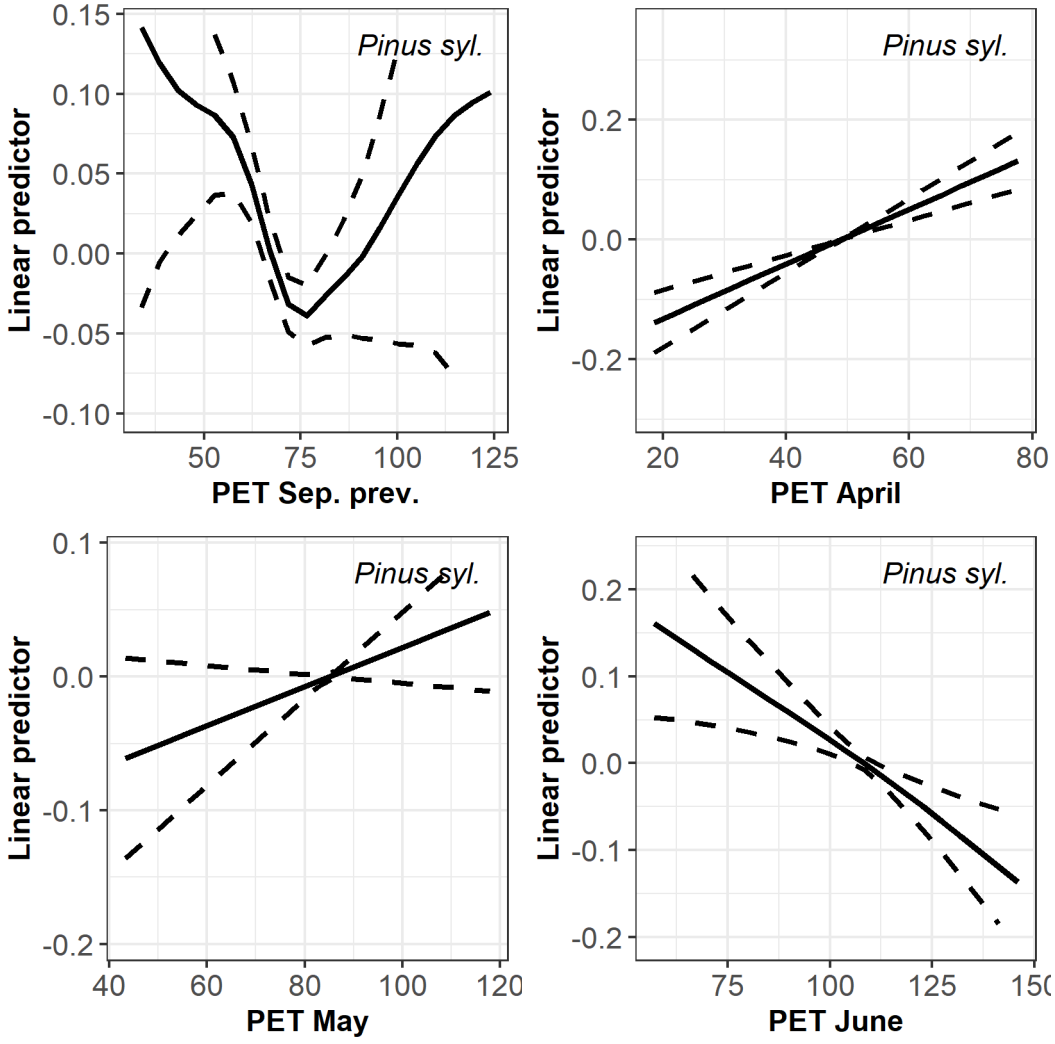


Figure 7: Effect of potential evapotranspiration (PET) in the month of September of the previous year and April—July of the current year on diameter increment for *Quercus robur* and *Quercus petraea*. Solid line: prediction, dashed lines confidence interval. Note that the linear predictor ((*ln*(diameter increment)) is zero at the mean of the covariate PET in the respective month.



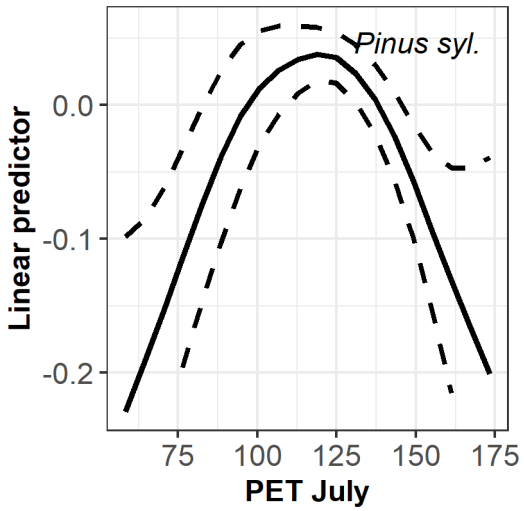


Figure 8: Effect of potential evapotranspiration (PET) in the month of September of the previous year and April—July of the current year on diameter increment for *Pinus sylvestris*. Solid line: prediction, dashed lines confidence interval. Note that the linear predictor (*ln*(diameter increment)) is zero at the mean of the covariate PET in the respective month.

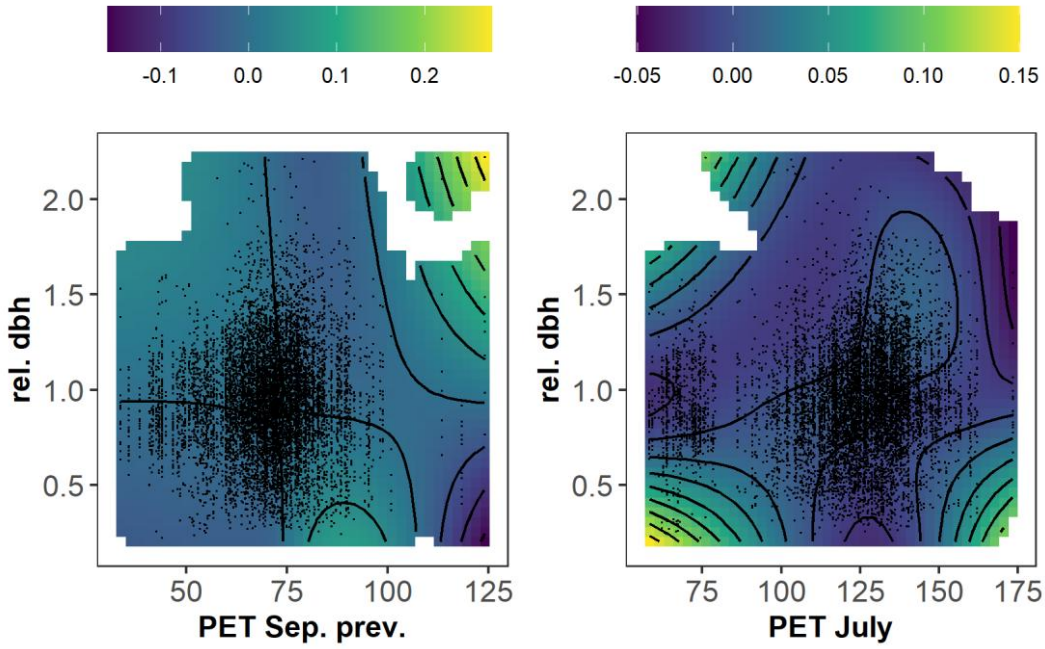


Figure 9: Interaction between potential evapotranspiration in the month September of previous year (left) and July from current year (right) for *Quercus robur and Quercus petraea* with relative dbh (dbh divided by quadratic mean diameter). Z-values (top of graph) represent the linear predictor (*ln*(diameter increment)). Dots indicate observed data points. White parts indicate regions with no data points.

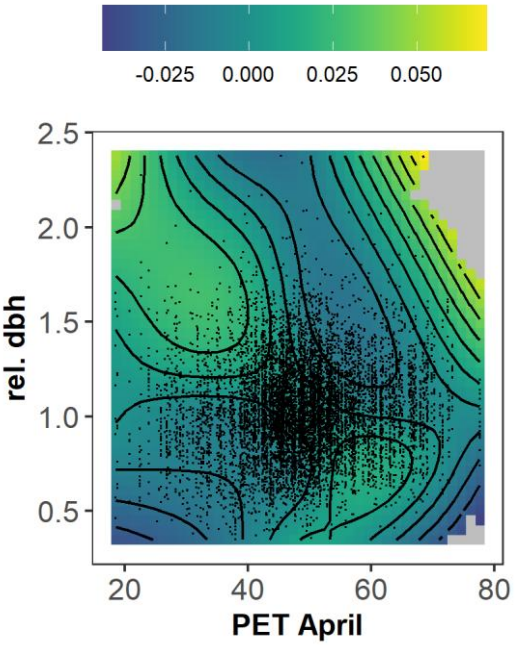
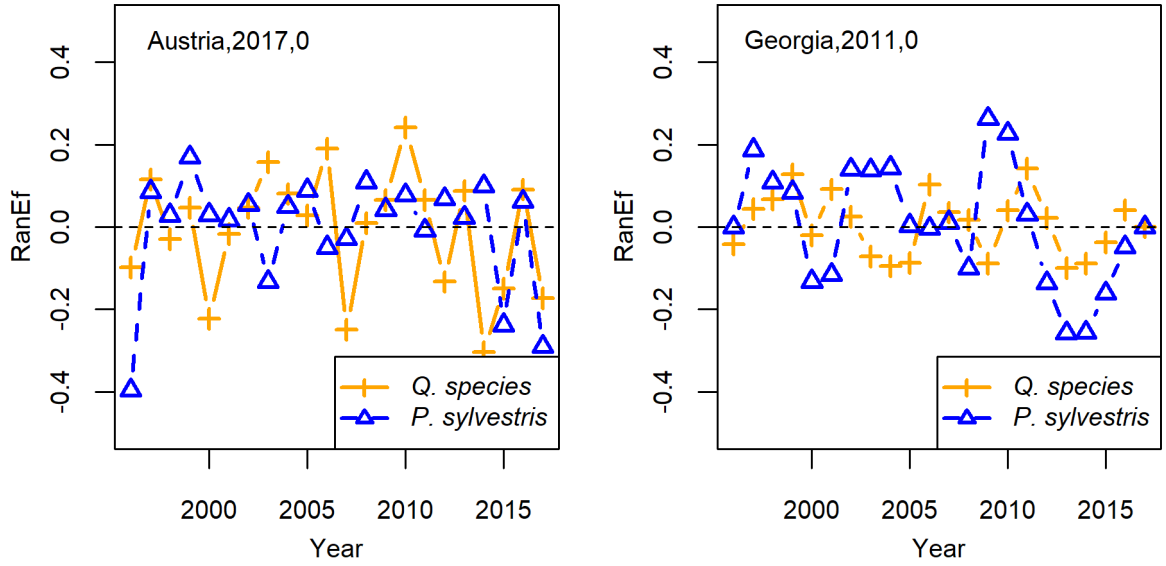


Figure 10: Interaction between potential evapotranspiration in the month from April of the current year for *Pinus sylvestris* with relative dbh (dbh divided by quadratic mean diameter). Z-values (top of graph) represent the linear predictor (*ln*(diameter increment)). Dots indicate observed data points. White parts indicate regions with no data points.

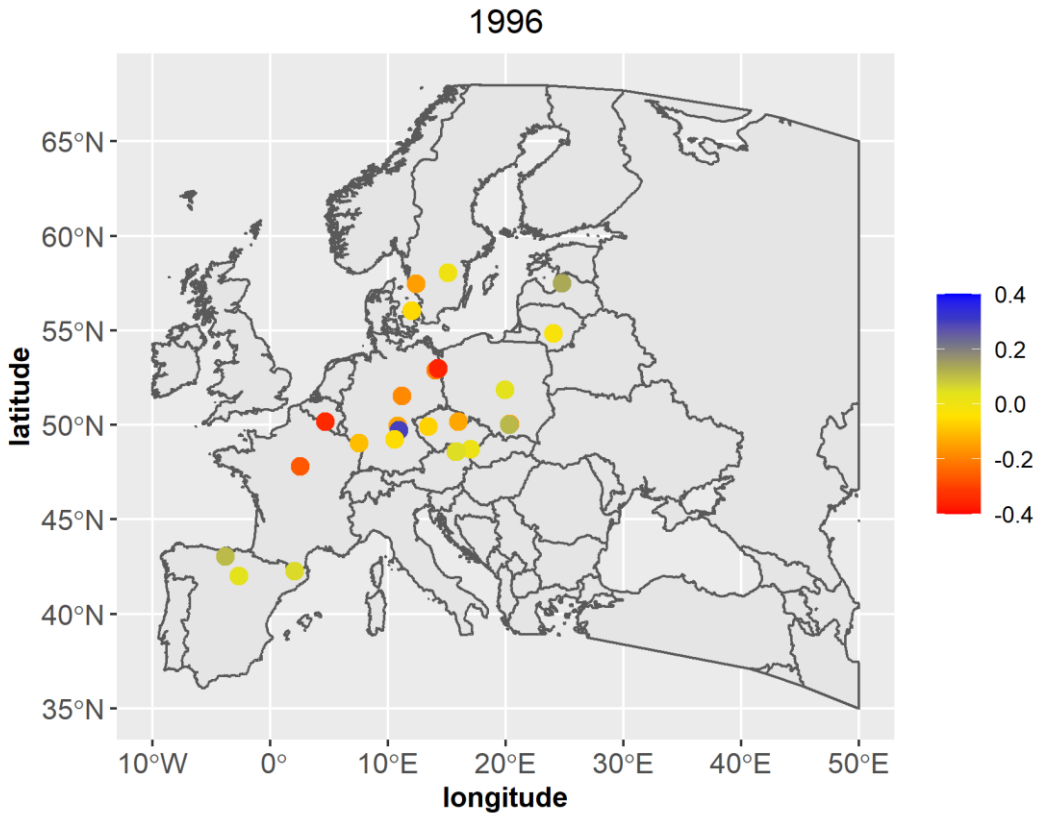
3.3 Random effects

The temporal trends for both tree species at the same site (Figure 11: two selected plots. Supplementary material 1: all plots) clearly indicate the same growth reaction for both tree genera in some years, but in the years investigated, contrasting patterns prevail at all sites. Similarly, random effects vary between triplets and the triplet effect is year specific (Figure 12: two selected years for *Q. spp.*. Supplementary material 2 and 3: all years for both species). The regional site- specific effect is not correlated with the classification in the three broad



climatic classes: Mediterranean climate, temperate climate and boreal climate. Residual diagnostics (Supplementary material 4) indicate an adequate model fit.

Figure 11: Random temporal trend for two selected plots. Left: Austria, Plot 2017, 0. Right: Georgia, Plot 2011 0. RanEf=Random effects (*ln*(diameter increment))



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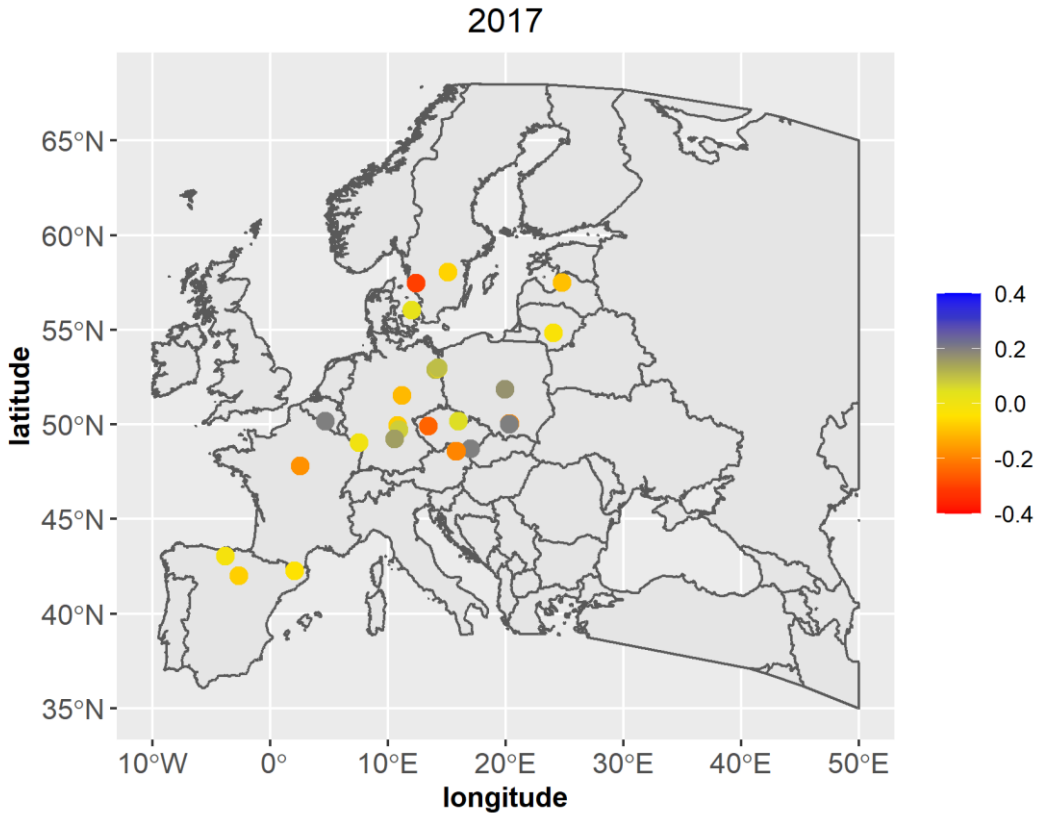

533

534 **Figure 12:** Random triplet effects for *Quercus robur* and *Quercus petraea* for 1996 and 2017. Z-Values represent
535 the linear predictor (*ln*(diameter increment))

4. Discussion

4.1 Long-term climate and site effects on tree growth

Large-scale spatial patterns drive the occurrence of tree species and the occurrence of specific mixtures or ecotones (Thurm et al. 2018). With climate warming, many tree species will shift their centroids of occurrence and migrate northward (Thurm et al. 2018). Also, tree growth depends on long-term climate (Vospernik 2021), which was also confirmed in this study. However, only long-term mean temperature was included to represent climatic effects in the best model since the data does not cover all combinations of temperature and precipitation, though covering a large gradient of the single variables. Since not all combinations were covered, long term precipitation was shrunk to the null-space because of concurvity with long-term temperature.

Other site factors, such as soil type, soil water holding capacity, solar radiation or aspect were represented by the random triplet and plot effects accounting for site-specific growth response. Local soil conditions and local climate between plots within a year are very diverse. The site can be highly contrasting even at small spatial scales (Oberhuber et al. 1998).

The overall variation explained by the models is 87 %, which is considerably more than 30-70 % reviewed for tree ring studies in an opinion paper by Wilmking et al. (2020). This result indicates that it is important to account for the site and the hierarchical structure of the data by including random effects. Influential factors at the tree level, considered by the random effects, could be tree genetics, management history, or defoliation elicited by insects, which explain a larger proportion of the variation than the site-level random effects.

4.2 Climate during the growing season

Climate during the growing season and tree growth are well correlated, as confirmed by many tree ring studies (Linderholm 2001, Bose et al. 2021, Gillner et al. 2013). The tricky

561 part might be to define the growing season correctly in data sets that span large environmental
562 gradients. Frequently, the period from August of the previous year to September of the current
563 year is considered (Sánchez-Salguero et al. 2013). Surprisingly, significant months found in
564 this study were rather consistent across sites with the influential month being the same on all
565 plots. Tree growth in our study was related to PET in September of the previous year and PET
566 in April-July, whereas PET in late summer and autumn of the current year were not
567 significant. Variables related to ring-width in other tree ring studies were temperature and
568 precipitation (Linderholm and Linderholm 2004, Nothdurft and Engel 2020, Vospernik
569 2021a, Jacobs et al. 2022), PET (Toïgo et al. 2018), vapour pressure deficit (Timofeeva et al.
570 2017, Lindner et al. 2010) or climatic water balance (Árvai et al. 2018) and drought indices
571 (Gomes Marques et al. 2018, Marqués et al. 2021). In our study, PET resulted in the highest
572 R^2 and lowest AIC, but model fit with other climatic variables resulted in a similar model
573 performance except for models including drought indices, with the choice between climate
574 variables being almost arbitrary. Thus, in our study the climate variables themselves are better
575 suited to explain tree growth, then the tested drought indices (De Martonne-index (Martonne
576 1926), SPI (McKee et al. 1993), SPEI (Vicente-Serrano et al. 2010). Models including climate
577 variables have a slightly higher R^2 and lower AIC than models including drought indices. The
578 better overall performance of climate variables may be due to the fact that climate-growth
579 patterns in spring are mainly temperature limited, which in turn might not be well captured by
580 drought indices. The better performance of climate variables is in line with results from
581 temperate sites (Linderholm and Linderholm 2004, Nothdurft and Engel 2020, Vospernik
582 2021a, Toïgo et al. 2018, Timofeeva et al. 2017, Lindner et al. 2010); whereas on
583 Mediterranean sites, drought indices are used in tree ring studies (Gomes Marques et al. 2018,
584 Marqués et al. 2021). We did, however, not detect a dependence of random site effects on the
585 bio-climatic region, and thus think that PET accurately describes tree growth even on
586 Mediterranean sites.

Quercus-Pinus sites are mostly xeric sites, where water availability is a more important limiting factor for tree growth than temperature (Bose et al. 2021), but the importance of different climatic factors varies throughout the year and is tightly linked to tree ring formation. Tree growth was positively related with higher PET in the spring and early summer month. With sufficient soil moisture from winter rainfall, warm conditions are favourable for tree growth, whereas this pattern switches to a sharp decrease of growth in June with increasing PET. Surprisingly, the climatic influence is again opposite already in July, possibly because of a switch to late-wood production in this month (Rathgeber et al. 2016).

Quercus, as ring-porous species, re-establish their vessels from stored carbohydrates early in spring before leaf-unfolding (Morecroft and Roberts 1999). *P. sylvestris* is anatomically very different and, as conifer species can do photosynthesis during warm periods in winter (Pakharkova et al. 2016). Nevertheless, the beginning of cell formation and tree growth for *P. sylvestris* are also linked to increasing temperatures in spring (e.g. Strieder and Vospernik 2021), with the beginning of tree growth of *P. sylvestris* being sometimes earlier at the same site than for *Q. spp.* (Michelot et al. 2012a), which is confirmed by the significant influence of PET in April for the *P. sylvestris* model and no significant effect of April climate on ring width for *Q. spp.*. With increasing spring temperatures, cell formation and growth rates increase, and maximum growth rates are often observed around the summer solstice (e.g. Strieder and Vospernik 2021). Cell formation takes several weeks (Rathgeber et al. 2016), and for *Q. spp.* there can be a 50-day delay from leaf-unfolding till the trees reach maximum photosynthetic capacity (Morecroft and Roberts 1999). As a consequence, June PET has the most considerable influence on tree growth in our model across all sites. This behaviour is also supported by the fact that spring and early summer droughts are usually crucial for tree growth and better correlated with ring width (Bose et al. 2021, Gillner et al. 2013) than summer or autumn droughts. Subsequently, in July, trees switch from early-wood formation

to late-wood formation, and the production of new cells ceases in time before winter to protect the sensitive cambium from frost (Rathgeber et al. 2016). Photosynthetic products from autumn are stored and affect next years' tree ring formation in *Quercus*, but less so for *P. sylvestris* (Michelot et al. 2012b). In line with this physiological behaviour, tree ring width for both tree genera (*Quercus, Pinus*) is influenced by September PET, but patterns are more evident for *Q. spp.*. Such correlations with last years' temperature are likewise reported in other studies (*Quercus* (e.g. Gillner et al. 2013); *Pinus* (e.g. Sánchez-Salguero et al. 2013)). Similarly, to the lagged influence of autumn climate, growth reductions due to drought are also observed in the following years (Bose et al. 2021, Gillner et al. 2013), but the long-term impact of drought must be considered marginal for *Quercus spp.* (Gillner et al. 2013) since post-drought effects for *Quercus spp.* are observed for 1-2 years (Gillner et al. 2013, Vitasse et al. 2019). In contrast, growth of conifers is enduringly reduced by spring drought (Vitasse et al. 2019) and recovery from drought spells for *P. sylvestris* is reported to be slower (more > 5 years) (Galiano et al. 2011) than for *Quercus*. Moreover, results by Bose et al. 2020 indicate that *P. sylvestris* trees that experienced more frequent droughts (e.g. series of drought years like 2015, 2018, 2019 in Europe) over the long-term are less resistant to extreme droughts. Thus, more frequent and longer predicted drought periods in the future may overstrain *P. sylvestris* potential for acclimation. This, however, could be buffered to some extent by favoring *Quercus-Pinus* mixed forest stands over monocultures of both tree species on mesotrophic xeric and mesic sites (Steckel et al. 2020a).

4.3 Age, competition and social position

Tree growth declined with age; this age trend was modelled for the whole population and tree ring series specific. Modelling or removing the age trend is key in studying the climate-growth relationship and is the standard in tree ring research (e.g. Linderholm 2001, Bose et al. 2021, Gillner et al. 2013, Schmitt et al. 2020). In this study, we opted for modelling the age trend, since we were interested in the trend itself. The age trend was

consistent, showing a steady decline with age. This is because the stands investigated are all at an age past the maximum of individual tree diameter increment. Similarly, we included other factors such as competition and social position, which are treated as noise in tree ring studies and a smooth from tree ring series using splines. From the various competition indices tested, local SDI was included in the final model. This index resulted in the highest R^2 and lowest AIC, although differences were almost identical (<0.01 difference in R^2) compared to potential models including different competition indices. The major advantage of local SDI is that it showed consistent patterns in many model formulations, indicating little concurvity with other variables. In particular, its independence of age facilitates the development of multivariate models (e.g. Burkhart and Tomé 2012). The relationship found for studied tree species is quite similar in both magnitude and form, with a stronger decrease for *P. sylvestris* at higher densities. We refrained from including dbh in the model since tree size increases with both age and social position making it difficult to separate the respective effects. Social position is known to significantly affect growth duration, with suppressed trees having a shorter period of growth than dominant ones (e.g. Rathgeber et al. 2011, Strieder and Vospernik 2021). Interactions between social position and climate found in this study might reflect this different behavior observed in studies on intra-annual growth.

4.4 Mixture and stand structure

Positive mixture effects on productivity at the stand level were reported for the *Quercus-Pinus* triplet gradient (Pretzsch et al. 2020, Steckel et al. 2020a, del Rio et al. 2022). At the individual tree level, positive mixture effects are also observed, but are only significant for *P. sylvestris*, once the overall model accounts for stand density and structure. Beneficial mixture effects at the individual tree level result from higher nutrient availability (Thelin et al. 2002, Aubert et al. 2006, Nickmans et al. 2015), hydraulic lift (Muñoz-Gálvez et al. 2021) and complementary light use efficiency because of different crown structure and leave phenology (Kelty et al. 1992, Pretzsch and Schütze 2016, Ammer 2019) all of which seem to affect *Pinus*

mainly positively. This behavior is in line with the ecophysiology of the two genera since *Q. spp.* has the more nutrient-rich leaves (Yuste et al. 2005) and a deeper rooting system. Differences in stand density between species and differences in stand structure may be important reasons why the effects of mixture on productivity differ between stand and individual tree levels (Pretzsch and Schütze 2016). For the species investigated here, *P. sylvestris* has a considerably higher maximum density than *Q. spp.* (Vospernik and Sterba 2015) and this higher potential density of *P. sylvestris* may be an important reason for differing results at the stand level and the individual tree levels, because it indicates different use of space of the two species. The temporal patterns of the random effects show that trees´ species-specific effects can strongly vary between tree species at the same site and for particular years. Other studies also reported varying between-year effects (Strieder and Vospernik 2021). Given the 20-years analyzed in this study, the population results reported characterize tree species behavior, but also show that caution needs to be exercised when analyzing shorter periods since effects strongly fluctuate. There was no consistent interaction effect between climate and mixture. Thus, the mitigating effect of mixture on growth for the species investigated could not be shown.

5. Conclusions

The relationship between tree growth and climate change is an important contemporary question at large spatial scales. Inference from single case studies is complex. and pooling Europe-wide data or data from different sources is needed to enhance understanding of the climate growth relationship and facilitate growth prognosis at larger scales. This study shows that tree ring data can be modelled over large environmental gradients by accounting for random tree and site effects, explaining 87 % of the total variation. This correct statistical specification results in climate – growth relationships that are well in line with our current physiological understanding from more detailed dendrometer

studies. Climate reactions across Europe have a standard population signal, and the most significant influence of climate on tree growth is in June, at the maximum day length, but the direction and magnitude of climatic effects vary throughout the growing seasons. This varying strength and direction of seasonal climatic effects are rarely accounted for in modelling tree growth response, where the average climate for the whole growing season is often included. In future studies, accounting for a monthly or daily climate in forest growth models should receive more emphasis.

An interesting finding is the high temporal dynamic at the same site, emphasizing the importance of considering several years in tree growth analysis. Tree species mixture has a positive effect on productivity. However, this effect is small compared to the climatic impacts. Thus, the mixture may only partly mitigate growth reductions due to drought. Rather large effects on diameter increment are observed due to stand structure but cannot be systematically explained in this study or related to silvicultural management.

Growth factors are manifold and interrelated, and tree ring models are thus prone to concurvity. Nevertheless, we advocate an overall model approach, which in contrast to dendrochronological studies, allows testing other growth factors and interactions thereof with climate. Concurvity can be well avoided by including variables that are considered free of the influence of other growth factors.

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References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* Second international symposium on information theory Akademiai. *Edited by* B.N. Petrov and F. Csaksi. Kiado Budapest. pp. 267–281.

Ammer, C. 2019. Diversity and forest productivity in a changing climate. New Phytol **221**: 50–66. doi:10.1111/nph.15263

Arend, M., Kuster, T., Günthardt-Goerg, M.S., and 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 Physiol. 31(3)287-297. doi:10.1093/tr **31**(3): 287–297. doi:10.1093/treephys/tpr004.

Árvai, M., Morgós, A., and Kern, Z. 2018. Growth-climate relations and the enhancement of drought signals in pedunculate oak (*Quercus robur* L.) tree-ring chronology in Eastern Hungary. IForest **11**(2): 267–274. doi:10.3832/ifor2348-011.

Aubert, M., Margerie, P., Ernoult, A., Decaëns, T., and Bureau, F. 2006. Variability and heterogeneity of humus forms at stand level: Comparison between pure beech and mixed beech-hornbeam forest. Ann. For. Sci. **63**: 177–188. doi: 10.1051/forest:2005110

Barsoum, N., Eaton, E.L., Levanič, T., Pargade, J., Bonnart, X., and Morison, J.I.L. 2015. Climatic drivers of oak growth over the past one hundred years in mixed and monoculture stands in southern England and northern France. doi:10.1007/s10342-014-0831-5.

Bhuyan, U., Zang, C., and Menzel, A., 2017. Different Responses of Multispecies Tree Ring Growth to Various Drought Indices Across Europe. Dendrochronologia **44** (6): 1–8. doi: 10.1016/j.dendro.2017.02.002.

Biging, G., and Dobbertin, M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. **38**(3): 695–720.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **41**(2): 360–377.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., and Rigling, A. 2006. Drought as an inciting mortality factor in scots pine stands of the Valais. Switzerland. Ecosystems **9**(3): 330–343. doi:10.1007/s10021-005-0126-2.

Binkley, D., Kashian, D.M., Boyden, S., Kaye, M.W., Bradford, J.B., Arthur, M.A., Fornwalt, P.A., Ryan, M.G. 2006. Patterns of growth dominance in forests of the Rocky

Mountains. USA For. Ecol. Manage. **236**: 193-201

Bose, A.K., Scherrer, D., Camarero, J.J., Ziche, D., Babst, F., Bigler, C., Bolte, A., Dorado-Liñán, I., Etzold, S., Fonti, P., Forrester, D.I., Gavinet, J., Gazol, A., de Andrés, E.G., Karger, D.N., Lebourgeois, F., Lévesque, M., Martínez-Sancho, E., Menzel, A., Neuwirth, B., Nicolas, M., Sanders, T.G.M., Scharnweber, T., Schröder, J., Zweifel, R., Gessler, A., and Rigling, A. 2021. Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. Sci. Total Environ. **784**: 147222. doi:10.1016/j.scitotenv.2021.147222.

Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarer, J.J., Haeni, M., Hereş, A.M., Hevia, A., Lévesque, M., Linares, J.C., Martinez-Vilalta, J., Matías, L., Menzel, A., Sánchez-Salguero, R., Saurer, M., Vennetier, M., Ziche, D., Rigling, A., 2020. Growth and resilience responses of Scots pine to extreme droughts across Europe depend on predrought growth conditions. Glob. Chang. Biol. **26**: 4521–4537. https://doi.org/10.1111/gcb.15153

Burkhart, H.E., and Tomé, M, 2012. Modeling Forest Trees and Stands. Springer Netherlands. Dordrecht. doi:10.1007/978-90-481-3170-9.

Collet, C., Manso, R., and Barbeito, I. 2017. Coexistence. association and competitive ability of *Quercus petraea* and *Quercus robur* seedlings in naturally regenerated mixed stands. For. Ecol. Manage. **390**: 36–46. doi:10.1016/j.foreco.2017.01.021.

Del Río, M., Pretzsch, H., Ruiz- Peinado, R, Jactel, H., Coll, L., Löf, M., Aldea, J., Ammer, C., Avdagić, A., Barbeito, I., Bielak, K., Bravo, F., Brazaitis, G., Cerný, J., Collet, C., Condés, S., Drössler, L., Fabrika, M., Heym, M., Holm, S.-O., Hylen, G., Janson, A., Kurylak, V., Lombardi, F., Matović, B., Metslaid, M., Motta, R., Nord-Larsen, T., Nothdurft, A., den Ouden, J., Pach, M., Pardos, M., Poeydebat, C., Ponette, Q., Pérot, T., Reventlow, D., Sitko, R., Sramek, V., Steckel, M., Svoboda, M., Verheyen, K., Vospernik, S., Wolff, B., Zlatanov, T., Bravo-Oviedo, A., 2022. Emerging Stability of Forest Productivity by Mixing Two Species Buffers Temperature Destabilizing Effect. Journal of Applied Ecology. 59(11): 2730-2741. doi: 10.1111/1365-2664.14267.

Dirnberger, G., Sterba, H., Condés, S., Ammer, C., Annighöfer, P., Avdagić, A., Bielak, K., Brazaitis, G., Coll, L., Heym, M., Hurt, V., Kurylyak, V., Motta, R., Pach, M., Ponette, Q., Ruiz-Peinado, R., Skrzyszewski, J., Šrámek, V., de Streel, G., Svoboda, M., Zlatanov, T., and Pretzsch, H. 2017. Species proportions by area in mixtures of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.). Eur. J. For. Res. **136**(1): 171–183. doi:10.1007/s10342-016-1017-0.

Durrant, T.H., de Rigo. D., and Caudullo, G. 2016. *Pinus sylvestris* in Europe: distribution. habitat usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.). European Atlas of Forest Tree Species. Publ. Off. EU. Luxembourg. pp. e016b94++

Eaton, E., Caudullo, G., Oliveira, S., and de Rigo, D. 2016. *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threads. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.). European Atlas of Forest Tree Species. Publ. Off. EU. Luxembourg. pp. e01c6df+

Eilmann, B., Weber, P., Rigling, A., and Eckstein, D. 2006. Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia **23**(3): 121–132. doi:10.1016/j.dendro.2005.10.002.

798 Epron D., and Dreyer, E. 1993. Long- term effects of drought on photosynthesis of adult oak
799 trees [*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.] in a natural stand. New
800 Phytol. **125**(2): 381–389. doi:10.1111/j.1469-8137.1993.tb03890.x.

801 Feichtinger, L.M., Eilmann, B., Buchmann, N., and Rigling, A. 2014. Growth adjustments of
802 conifers to drought and to century-long irrigation. For. Ecol. Manage. **334**: 96–105.
803 doi:10.1016/j.foreco.2014.08.008.

804 Forrester, D.I. 2014. The Spatial and Temporal Dynamics of Species Interactions in Mixed-
805 Species Forests: From Pattern to Process. For. Ecol. Manage. **312**: 282-292 doi:
806 10.1016/j.foreco.2013.10.003.

807 Galiano, L., Martínez-Vilalta, J., and Lloret, F. 2011. Carbon reserves and canopy defoliation
808 determine the recovery of Scots pine 4yr after a drought episode. New Phytol. **190**(3):
809 750–759. doi:10.1111/j.1469-8137.2010.03628.x.

810 Gillner, S., Vogt, J., and Roloff, A. 2013. Climatic response and impacts of drought on oaks
811 at urban and forest sites. Urban For. Urban Green. **12**(4): 597–605.
812 doi:10.1016/j.ufug.2013.05.003.

813 Gomes Marques, I., Campelo, F., Rivaes, R., Albuquerque, A., Ferreira, M.T., and Rodríguez-
814 González, P.M. 2018. Tree rings reveal long-term changes in growth resilience in
815 Southern European riparian forests. Dendrochronologia **52**: 167–176.
816 doi:10.1016/j.dendro.2018.10.009.

817 Harris, I., Osborn, T.J., Jones, P., and Lister, D. 2020. Version 4 of the CRU TS monthly
818 high-resolution gridded multivariate climate dataset. Sci. Data **7**(1): 1–18.
819 doi:10.1038/s41597-020-0453-3.

820 Hastie, T.J., and Tabshirani, R.J. 1990. Generalized Additive Models. New York.

821 Hegyi, F. 1974. A simulation model for managing jack-pine stands. *In:* Growth models for
822 tree and stand simulation. *Edited by* J. Fries: 74–90.

823 Höwler, K., Vor, T., Seidel, D., Annighöfer, P., Ammer, Ch. 2019. Analyzing Effects of
824 Intra- and Interspecific Competition on Timber Quality Attributes of *Fagus Sylvatica*
825 L.—from Quality Assessments on Standing Trees to Sawn Boards. Eur. J. For. Res. ***138*:**
826 327-343. doi:10.1007/s10342-019-01173-7

827 Jacobs, K., Jonard, M., Muys, B., Ponette, Q. 2022. Shifts in dominance and complementarity
828 between sessile oak and beech along ecological gradients. Journal of Ecology. 110:
829 2404-2417. doi: 10.1111/1365-2745.13958

830 Kelty, M.J., Larson, B.C., Oliver, C.D. 1992. The ecology and silviculture of mixed-species
831 forests: a festschrift for David M. Smith. Springer Netherlands. Dordrecht. doi:
832 10.1007/978- 94-015-8052-6

833 Leuzinger, S., Zotz, G., Asshoff, R., and Körner, C. 2005. Responses of deciduous forest trees
834 to severe drought in Central Europe. Tree Physiol. **25**(6): 641–650.
835 doi:10.1093/treephys/25.6.641.

836 Linderholm, H.W., 2001. Climatic influence on scots pine growth on dry and wet soils in the
837 central Scandinavian mountains. interpreted from tree-ring widths. Silva Fenn. **35**(4):
838 415–424. doi:10.14214/sf.574.

839 Linderholm, H.W., and Linderholm, K. 2004. Age-dependent climate sensitivity of *Pinus*
840 *sylvestris* L. in the central Scandinavian Mountains. Boreal Environ. Res. **9**(4): 307–317.

841 Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl,
842 R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., and Marchetti, M. 2010. Climate
843 change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For.
844 Ecol. Manage. **259**(4): 698–709. doi:10.1016/j.foreco.2009.09.023.

845 Marqués, L., Camarero, J.J., Zavala, M.A., Stoffel, M., Ballesteros-Cánovas, J.A., Sancho-
846 García, C., and Madrigal-González, J. 2021. Evaluating tree-to-tree competition during
847 stand development in a relict Scots pine forest: how much does climate matter? Trees -
848 Struct. Funct. **35**(4): 1207–1219. doi:10.1007/s00468-021-02109-8.

849 Marra, G., Wood, S.N. 2011. Practical Variable Selection for Generalized Additive Models
850 Computational Statistics & Data Analysis **55** (7): 2372–87. doi:
851 10.1016/j.csda.2011.02.004.

852 Martín-Gómez, P., Aguilera, M., Pemán, J., Gil-Pelegrín, E., and Ferrio, J.P. 2017.
853 Contrasting ecophysiological strategies related to drought: the case of a mixed stand of
854 Scots pine (*Pinus sylvestris*) and a submediterranean oak (*Quercus subpyrenaica*). Tree
855 Physiol. **37**(11): 1478–1492. doi:10.1093/treephys/tpx101.

856 Martonne, D. 1926. Une novelle fonction climatologique: L'indice d'aridité. La Météorologie
857 **21**: 449–458.

858 McKee, T.B., Doesken, N.J., and Kleist, J. 1993. The relationship of drought frequency and
859 duration to time scales. *In* Proceedings of the Eighth Conference on Applied
860 Climatology. 17–22 January 1993 Boston. American Meteorological Society. Anaheim.
861 California. Pp. 179-184.

862 Mellert, K.H., Göttlein, A., 2012. Comparison of new foliar nutrient threshold derived from
863 van den Burg's literature compilation with established central European references. Eur.
864 J. For. Res. **131**: 1461-1472. doi: 10.1007/s10342-012-0615-8

865 Mérian, P., Pierrat, J.C., and Lebourgeois, F. 2013. Effect of sampling effort on the regional
866 chronology statistics and climate-growth relationships estimation. Dendrochronologia
867 **31**(1): 58–67. doi:10.1016/j.dendro.2012.07.001.

868 Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand
869 composition and tree size on resistance and resilience to drought in sessile oak and Scots
870 pine. For. Ecol. Manage. **339** 22-33. doi: 10.1016/j.foreco.2014.11.032

871 Michelot, A., Bréda, N., Damesin, C., and Dufrêne, E. 2012a. Differing growth responses to
872 climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus*
873 *sylvestris* in a temperate forest. For. Ecol. Manage. **265**: 161–171.
874 doi:10.1016/j.foreco.2011.10.024.

875 Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E., and Damesin, C. 2012b. Comparing the
876 intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus*
877 *petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural
878 carbohydrate dynamics. Tree Physiol. **32**(8): 1033–1045. doi:10.1093/treephys/tps052.

879 Morecroft, M.D., and Roberts, J.M. 1999. Photosynthesis and stomatal conductance of mature
880 canopy Oak (*Quercus robur*) and Sycamore (*Acer pseudoplatanus*) trees throughout the
881 growing season. Funct. Ecol. **13**(3): 332–342. doi:10.1046/j.1365-2435.1999.00327.x.

Muller, S. 1992. Natural acidophilous *Quercus* and *Pinus* forests in the northern Vosges, France, from a geographical perspective. J. Veg. Sci. **3**(5): 631–636. doi:10.2307/3235830.

Muñoz-Gálvez, F.J., Herrero, A., Esther Pérez-Corona, M., and Andivia, E. 2021. Are pine-oak mixed stands in Mediterranean mountains more resilient to drought than their monospecific counterparts? For. Ecol. Manage. **484:** 118955 doi:10.1016/j.foreco.2021.118955.

Nickmans, H., Verheyen, K., Guiz, J., Jonard, M., Ponette, Q. 2015. Effects of neighbourhood identity and diversity on the foliar nutrition of sessile oak and beech. For. Ecol. Manage. **335**: 108-117. doi: 10.1016/j.foreco.2014.09.025

Nothdurft, A., and Engel, M. 2020. Climate sensitivity and resistance under pure- and mixed-stand scenarios in Lower Austria evaluated with distributed lag models and penalized regression splines for tree-ring time series. Eur. J. For. Res. **139**(2): 189–211. doi:10.1007/s10342-019-01234-x.

Oberhuber, W., Stumböck, M., Kofler, W. 1998. Climate-tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. Trees **13**: 19–27 doi: 10.1007/PL00009734.

Pakharkova, N. V., Heilmeier, H., Gette, I.G., Andreeva, E.B., Grachev, A.M., Gaevskiy, N.A., and Grigoriev, Y.S. 2016. Quantitative characteristics of the phases of winter dormancy of conifer species at a site in Central Siberia. Rev. Bras. Bot. **39**(4): 1005–1014. doi:10.1007/s40415-016-0298-3.

Pommerening, A., and Stoyan, D. 2006. Edge-correction needs in estimating indices of spatial forest structure. Can. J. For. Res. **36**(7): 1723–1739. doi:10.1139/X06-060.

Pretzsch, H. 2009. Forest Dynamics. Growth and Yield. Springer Verlag.

Pretzsch, H., and Biber, P. 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Can. J. For. Res. **40**(2): 370–384. doi:10.1139/X09-195.

Pretzsch, H., and Biber, P. 2016. Tree species mixing can increase maximum stand density. Can. J. For. Res. **46**(10): 1179–1193. doi:10.1139/cjfr-2015-0413.

Pretzsch, H., Forrester, D.I., and Bauhus, J. 2017. Mixed-species forests: ecology and management. Springer. Heidelberg.

Pretzsch, H., and Del Río, M. 2020. Density regulation of mixed and mono-specific forest stands as a continuum: A new concept based on species-specific coefficients for density equivalence and density modification. Forestry **93**(1): 1–15. doi:10.1093/forestry/cpz069.

Pretzsch, H., and Schütze, G. 2016. Effect of tree species mixing on the size structure. density. and yield of forest stands. Eur. J. For. Res. **135**(1): 1–22. doi:10.1007/s10342-015-0913-z.

Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K., Jansons, A., de-Dios-García, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika,

M., Svoboda, M., Černý, J., Wolff, B., Ruíz-Peinado, R., and del Río, M. 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. Eur. J. For. Res. **139**(3): 349–367. doi:10.1007/s10342-019-01233-y.

Prodan, M. 1968a. Einzelbaum. Stichprobe und Versuchsfläche. Allg. Forst- und Jagdzeitung **139**(10): 239–248.

Prodan, M. 1968b. Zur Gesetzmäßigkeit der Flächenverteilung von Bäumen. Allg. Forst- und Jagdzeitung **139**.

Radtke, P.J., and Burkhart, H.E. 1998. A comparison of methods for edge-bias compensation. Can. J. For. Res. **28**(6): 942–945. doi:10.1139/x98-062.

Ramírez-Valiente, J.A., López, R., Hipp, A.L., and Aranda, I. 2020. Correlated evolution of morphology, gas exchange, growth rates and hydraulics as a response to precipitation and temperature regimes in oaks (*Quercus*). New Phytol. **227**(3): 794–809. doi:10.1111/nph.16320.

Rathgeber, C.B.K., Rossi, S., Bontemps J.-D. 2011. Cambial activity related to tree size in a mature silver-fir plantation. Ann Bot-London **108**: 429–438. https://doi.org/10.1093/aob/mcr168

Rathgeber, C.B.K., Cuny, H.E., and Fonti, P. 2016. Biological basis of tree-ring formation: A crash course. Front. Plant Sci. 7: 1–7. doi:10.3389/fpls.2016.00734.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. **46**: 627–638.

Rigling, A., Waldner, P.O., Forster, T., and Bräker, O.U. 2001. Ecological interpretation of tree-ring width and intraannual density fluctuations in *Pinus sylvestris* on dry sites in the central Alps and Siberia. **31**: 18–31.

Rogers, B.M., Solvik, K., Hogg, E.H., Ju, J., Masek, J.G., Michaelian, M., Berner, L.T., and Goetz, S.J. 2018. Detecting early warning signals of tree mortality in boreal North America using multiscale satellite data. Glob. Chang. Biol. **24**(6): 2284–2304. doi:10.1111/gcb.14107.

Roloff, A., Bärtels, A. 2006. Flora der Gehölze.Stuttgart: Ulmer

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G., Stegehuis, A. I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B. JW., Lindner, M., Martinez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx G., Bär, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiller, D., Blaženec, M., Čada, V., Carraro, V., Cecchini, S., Chan, T., Conedera, M., Delpierre, N., Delzon, S., Ditmarová, L., Dolezal, J., Dufrêne, E., Edvardsson J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Güney, A., Heinrich, I., Hentschel, R., Janda, P., Ježík, M., Kahle, H.-P., Knüsel, S., Krejza, J, Ł., Kuberski, Ł., Kučera, J., Lebourgeois, F., Mikoláš, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbel, I., Rathgeber, C.B.K, Salmon, Y., Saunders, M., Scharnweber, T., Sitková, Z., Stangler, D. F., Stereńczak, K., Stojanović, M., Střelcová, K., Světlík, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavrčík, H., Vejpustková, M., Walthert L., Wilmking, M., Zin, E., Zou, J.

967 & Steppe, K. (2022). The 2018 European heatwave led to stem dehydration but not to
968 consistent growth reductions in forests. Nature communications. **13**(1): 1-11.

969 Sánchez-Salguero, R., Camarero, J.J., Dobbertin, M., Fernández-Cancio, Á., Vilà-Cabrera, A.,
970 Manzanedo, R.D., Zavala, M.A., and Navarro-Cerrillo. R.M. 2013. Contrasting
971 vulnerability and resilience to drought-induced decline of densely planted vs. natural
972 rear-edge *Pinus nigra* forests. For. Ecol. Manage. **310**: 956–967.
973 doi:10.1016/j.foreco.2013.09.050.

974 Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., and Bräker, O.U. 1990. Identification.
975 presentation and interpretation of event years and pointer years in dendrochonology.
976 Dendrochronologia **9**: 9–38.

977 Speer, J.H. 2010. Fundamentals of tree-ring research. University of Arizona Press.

978 Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J., Pretzsch, H. 2019. Transgressive
979 overyielding in mixed compared with monospecific Scots pine (*Pinus sylvestris* L.) and
980 oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) stands – Productivity gains
981 increase with annual water supply. For. Ecol. Manage. **439**: 81-96. doi:
982 10.1016/j.foreco.2019.02.038.

983 Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L.,
984 Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q.
985 Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., and Pretzsch H. 2020a.
986 Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak
987 (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility
988 modify the mixing effect. For. Ecol. Manage. **461**: 117908.
989 doi:10.1016/j.foreco.2020.117908.

990 Steckel, M., Moser, W.K., del Río, M., Pretzsch, H. 2020b. Implications of Reduced Stand
991 Density on Tree Growth and Drought Susceptibility: A Study of Three Species under
992 Varying Climate. Forests. **11(6)**: 627. doi:10.3390/f11060627.

993 Strieder, E., and Vospernik, S. 2021. Intra-annual diameter growth variation of six common
994 European tree species in pure and mixed stands. Silva Fenn. **55**(4): 10449.
995 doi:10.14214/sf.10449.

996 Suzuki, M., Yoda K., Suzuki, H. 1996. Phenological comparison of the onset of vessel
997 formation between ring-porous and diffuse porous deciduous trees in a Japanese
998 temperate forest. IAWA J **17**: 431–44. https://doi.org/10.1163/22941932-90000641

999 Team R.C. 2018. R: a language and environment for statistical computing. Available from
1000 https://www.r-project.org.

1001 Thelin, G., Rosengren, U., Callesen, I., and Ingerslev, M. 2002. The nutrient status of Norway
1002 spruce in pure and in mixed-species stands. For. Ecol. Manage. **160**(1–3): 115–125.
1003 doi:10.1016/S0378-1127(01)00464-9.

1004 Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. Geogr.
1005 Rev. **38**(1): 55–94. doi: 10.2307/210739.

1006 Thurm, E.A., Hernandez, L., Baltensweiler, A., Ayan, S., Rasztovits, E., Bielak, K., Zlatanov,
1007 T.M., Hladnik, D., Balic, B., Freudenschuss, A., Büchsenmeister, R., and Falk, W. 2018.
1008 Alternative tree species under climate warming in managed European forests. For. Ecol.
1009 Manage. **430**: 485–497. doi:10.1016/j.foreco.2018.08.028.

Timofeeva, G., Treydte, K., Bugmann, H., Rigling, A., Schaub M., Siegwolf, R., and Saurer, M. 2017. Long-term effects of drought on tree-ring growth and carbon isotope variability in Scots pine in a dry environment. Tree Physiol. **37**(8): 1028–1041. doi:10.1093/treephys/tpx041.

Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.C., Longuetaud, F., Jactel, H., and Vallet, P. 2018. Difference in shade tolerance drives the mixture effect on oak productivity. J. Ecol. **106**(3): 1073–1082. doi:10.1111/1365-2745.12811.

Trouvé, R., Bontemps, J.D., Collet, C., Seynave, I., and Lebourgeois, F. 2017. Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. Trees **31**: 517-529 doi:10.1007/s00468-016-1479-1.

Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I. 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. J. Clim. **23**(7): 1696–1718. doi:10.1175/2009JCLI2909.1.

Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., and Wohlgemuth, T. 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob. Chang. Biol. **25**(11): 3781–3792. doi:10.1111/gcb.14803.

Vospernik, S. 2021. Basal area increment models accounting for climate and mixture for Austrian tree species. For. Ecol. Manage. **480**. 118725 doi:10.1016/j.foreco.2020.118725.

Vospernik, S. and Sterba, H. 2015. Do competition-density rule and self-thinning rule agree? Ann. For. Sci. **72**(3): 379–390. doi:10.1007/s13595-014-0433-x.

Vospernik, S. and Nothdurft, A. 2018. Can trees at high elevations compensate for growth reductions at low elevations due to climate warming? Can. J. For. Res. **48**(6): 650–662. doi:10.1139/cjfr-2017-0326.

Wigley, T.M.L., Briffa K.R., Jones P.D. 1984. On the average value of correlated time series. with applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol **23**:201–213

Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., and Trouillier. M. 2020. Global assessment of relationships between climate and tree growth. Glob. Chang. Biol. **26**(6): 3212–3220. doi:10.1111/gcb.15057.

Wood, S.N. 2006. Generalized Additive Models: An Introduction with r. CRS Press.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. **73**(1): 3–36. doi: 10.1111/j.1467-9868.2010.00749.x.

Wood, S.N. 2017. Generalized Additive Models: An Introduction with R.

Yuste, J.C., Konôpka, B., Janssens, I.A., Coenen, K., Xiao, C.W., and Ceulemans, R. 2005. Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. Tree Physiol. **25**(6): 701–712. doi:10.1093/treephys/25.6.701.

1051 Zweifel, R., Rigling, A., and Dobbertin, M. 2009. Species-Specific Stomatal Response of
1052 Trees to Drought - a Link to Vegetation Dynamics? J. Veg. Sci. **20**(3): 442–54. doi:
1053 10.1111/j.1654-1103.2009.05701.x.

1054