Regional climate moderately influences species-mixing effect on tree growth-climate relationships and drought resistance for beech and pine across Europe

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Abstract

Increasing species diversity is considered a promising strategy to mitigate the negative impacts of global change on forests. However, the interactions between regional climate conditions and species-mixing effects on climate-growth relationships and drought resistance remain poorly documented.

In this study, we investigated the patterns of species-mixing effects over a large gradient of environmental conditions throughout Europe for European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.), two species with contrasted ecological traits. We hypothesized that across large geographical scales, the difference of climate-growth relationships between pure and mixed stands would be dependent on regional climate. We used tree ring chronologies derived from 1143 beech and 1164 pine trees sampled in 30 study sites, each composed of one mixed stand of beech and pine and of the two corresponding pure stands located in similar site conditions. For each site and stand, we used Bootstrapped Correlation Coefficients (BCCs) on standardized chronologies and growth reduction during drought years on raw chronologies to analyze the difference in climate-tree growth relationships and resistance to drought between pure and mixed stands.

We found consistent large-scale spatial patterns of climate-growth relationships. Those patterns were similar for both species. With the exception of the driest climates where pure and mixed beech stands tended to display differences in growth correlation with the main climatic drivers, the mixing effects on the BCCs were highly variable, resulting in the lack of a coherent response to mixing. No consistent species-mixing effect on drought resistance was found within and across climate zones. On average, mixing had no significant effect on drought resistance for neither species, yet it increased pine resistance in sites with higher climatic water balance in autumn. Also, beech and pine most often differed in the timing of their drought response within similar sites, irrespective of the regional climate, which might increase the temporal stability of growth in mixed compared to pure stands.

Our results showed that the impact of species mixing on tree response to climate did not strongly differ between groups of sites with distinct climate characteristics and climate-growth relationships, indicating the interacting influences of species identity, stand characteristics, drought events characteristics as well as local site conditions.

Keywords

Dendrochronology – Ecological gradient – Species mixture – *Fagus sylvatica* – *Pinus sylvestris*

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1. Introduction

The effects of global change on forest functioning are a major concern for both forest scientists and forest managers. With respect to climate, changes in local average precipitation and temperature as well as in the frequency and intensity of extreme events such as drought, are expected to impact the provision of many forest ecosystem services, including wood production (Albrich et al. 2018), in terms of both average performance and temporal stability (Boisvenue and Running, 2006; Allen et al., 2010). Indeed, numerous studies reported that the increased frequency and intensity of drought events significantly reduced growth and increased mortality risks (Allen et al., 2010; Lévesque et al., 2014; Meir et al., 2015). As a result, great research effort is devoted into finding ways to adapt forests and forest management to cope with those adverse effects of climate change (Seynave et al. 2018; Bowditch et al., 2020). In addition to selecting tree species or provenances adapted to expected future climate conditions (Bolte et al., 2009; Frischbier et al., 2019; Bert et al., 2020), increasing stand species diversity has also been proposed to cope with detrimental effects of global change on forests (Ammer 2019, Vilà-Cabrera et al., 2018). Several studies reported a significant influence of species-mixing on climate-growth relationship, including higher resistance to extreme events such as drought; yet those effects were found to be affected by environmental conditions or identity of the species involved (Lebourgeois et al., 2013; Pretzsch et al., 2013; Gazol and Camarero, 2016; Thurm et al., 2016; Bosela et al., 2018, Pretzsch et al. 2020; Steckel et al., 2020).

Specifically, the outcome of species interactions (balance between inter-specific competition and complementarity) depends on climate (Ammer 2019; Forrester 2014), leading to species-mixing effects (differences between pure and mixed stands) on tree-growth relationships to vary depending on environmental conditions (Grossiord et al. 2014; Lebourgeois et al. 2014). Climate is shaping species-mixing effects through different ways. First, individual trees of a given species might be less vulnerable to a similar drought event when growing under dry compared to humid climatic conditions due to long-term adaptation mechanisms (Martín-Benito et al. 2010; Martinez-Vilalta, 2012; Trouvé et al., 2017; Stojnić et al. 2018). Intra-specific traits variations associated with adaptation to dry environments include differences in rooting depth, root to shoot ratio, leaf/sapwood area ratio, wood anatomy (thickness of xylem walls, tracheid diameters…) or changes in leaf morphological features such as leaf area (Linton et al. 1998; Lloret et al., 1999;

Grill et al. 2004; Martinez-Vilalta et al. 2009; Pritzkow et al., 2020). Under similar drought intensities, the constraint experienced by the trees would thus differ depending on climate. On the other hand, it is also possible that the constraint resulting from a drought event in inherently water limited sites cannot be alleviated by species-mixing as suggested by de Streel et al. (2019). Climate characteristics could also affect the balance of species interactions by allowing -or not- compensatory growth (Lassoie and Salo, 1981; Lévesque et al., 2014; Seidel et al., 2019) to happen when species with distinct vegetation periods are admixed. For instance, favorable climatic conditions at the end of the growing season could allow for one species to benefit from reduced competition caused by the earlier reduction of physiological activity of another species with shorter vegetation period. As a result, the outcome of species interactions for each species will vary between climatic areas, all other things being equal. Also, average climatic characteristics could influence species-mixing effect on drought reaction by changing the relative competitivity between species. For instance the high sensitivity of beech to late frosts (Pretzsch et al., 2015; D'andrea et al., 2020) could reduce its otherwise high dominance over less competitive tree species in late frosts prone climates. Lastly, spatial and temporal variations of environmental conditions influence species-mixing effect through their impacts on both resources and modulators. According to Forrester and Bauhus (2016), the mixing effect is predicted to increase along temporal or spatial gradients of increasing environmental limitation as far as species interactions reduce the constraint.

On the other hand, the drivers of tree growth are expected to change across large geographical areas as a function of regional climate characteristics. In this respect, Babst et al. (2013) highlighted that tree growth response to climate across Europe showed consistent biogeographic patterns in relation with distinct climatic constraints, from zones where tree growth was mainly driven by precipitations to others where temperature was the main driver.

Species-mixing effects on climate-growth relationships are therefore likely to differ between such regions. Indeed, Grossiord et al. (2014) have shown that higher species diversity improved resistance to drought events in certain forest types (temperate beech and thermophilous deciduous forests) while no significant effects were found in hemi-boreal, mountainous beech and Mediterranean forests. In addition to those large-scale patterns, local site conditions can also

shape the mixing effect, resulting in the lack of any significant relationship between species diversity and drought resistance in selected regions (Grossiord et al. 2014b, Ratcliffe et al. 2017).

Species interactions are numerous and complex. Complementarity is considered as a major determinant of species-mixing effects (Ammer, 2019), and encompasses several types of interspecific interactions leading to competitive reduction and facilitation (Vandermeer, 1989). Facilitation refers to mechanisms through which one species improves the resource supply as well as biotic or abiotic conditions for another species (Forrester and Bauhus, 2016). Competitive reduction is the process by which inter-species traits variation leads to lower inter-specific competition compared to intra-specific competition (Scherer-Lorenzen et al., 2005), and result from either spatial (e.g. difference in rooting depth) or temporal (e.g. difference in growing period) niche complementarity. Because those mechanisms rely largely on inter-specific differences between associated tree species as well as on intra-specific differences resulting from interspecific interactions, trait diversity and trait plasticity are critical determinants for the outcome of mixing (Jactel and Brockerhoff, 2007; Dawud et al., 2017). Numerous traits can influence tree growth response to climate, and thus determine the species-mixing effect. For instance, by their longer vegetation period, coniferous species could have more opportunity for compensatory growth (Seidel et al., 2019) during climatically favorable periods following a drought event than broadleaves (D'Andrea et al. 2020). If conifer compensatory growth happens after the end of the admixed broadleaves vegetation period, conifer could additionally benefit from lower interspecific competition in mixed stands compared to pure stands. Traits associated with tree hydraulic and physiological characteristics are also major determinant of tree growth reaction to climatic variations. Association of species displaying variations in those traits could lead to improved drought response in mixture compared to monocultures (Schwendenmann et al. 2015, Grossiord 2020).

Species-mixing effects depend not only on the combination of traits of the species in presence but also on their interaction with environmental conditions. The environmental conditions can indeed influence the expression of the traits for the species in presence. As an example, constraints such as temporary soil waterlogging (Kozlowski, 1986) or limited depth to bedrock (Balneaves and De La Mare, 1989) could prevent any belowground niche partitioning through

their negative effect on root development, resulting in a lack of mixing effect on drought response even for species with otherwise potentially different rooting patterns.

As a result, we might expect contrasting impacts of mixing on the response to both climate-growth relationships and reaction to drought events, depending on climate as well as on local site characteristics such as microclimate or soil characteristics (maximal water availability, ...).

In this study, we investigate how growth response (measured by tree-ring width of dominant trees) to climate and drought differs between pure and mixed stands along an unprecedented gradient of environmental conditions across Europe, for European beech and Scots pine. Those two species are of high relevance in this context as they display strong differences in a series of traits potentially involved in growth response to climate variation. More specifically, they differ in the distribution of root biomass within the soil profile (heart-shape rooting pattern for beech vs. peak in most superficial soil layers for pine, higher competitivity of beech root system - Curt and Prévosto, 2003; Prévosto and Curt, 2004), in the length of the vegetation period (longer growing season of pine compared to beech) and in their hydraulic strategies (isohydric for pine vs. anisohydric for beech – Cochard, 1992; Martínez-Vilalta et al., 2004; Schäfer et al., 2017; Pflug et al., 2018). Because the ecological traits of the two species are so contrasted, complementarity effects are expected to occur. Using the same dataset from the EuMIXFOR COST action (Heym et al., 2017) as the one used in the present study, Pretzsch et al. (2015) and del Río et al. (2017) showed that both productivity and temporal stability of productivity, respectively, were on average higher in mixed pine/beech stands than expected from pure stands. They also found a high between-site variability of species-mixing effect on productivity and temporal stability. Although the authors proposed several hypotheses potentially explaining those positive species-mixing effects on productivity, they did not perform any quantitative analyses of the mechanisms at play. As a result, several studies were conducted to highlight the candidate dominant mechanisms. The considered mechanisms include light related processes (Barbeito et al. 2017; Forrester et al. 2018), water-related processes (de Streel et al. 2019) or nutrient-related processes (de Streel et al. 2021). In this paper, we extend the range of mechanisms by considering the climate-related processes. Because species-mixing effect have been found on long-term stand performances (difference in productivity between pure and mixed stands) as well as on reaction to extreme events (stability of productivity,

resilience, resistance or recovery to drought...), we explored species-mixing effects on climate-related processes using indicators of both long-term behavior and reaction to drought.

For both species, we hypothesized that the difference in climate-growth relationships including both long-term growth response to climate and short-term reaction to drought event will vary between pure and mixed stands depending on climatic characteristics, resulting in consistent regional patterns across Europe. To test this hypothesis, we conducted dendroecological analyses. First, we analyzed the climate-tree growth relationships of both species in pure and mixed stands, using Bootstrapped Correlation Coefficients. We then tested the difference in resistance to drought event between pure and mixed stands, and investigated its relationship with regional climate.

1. Materials and methods

1.1. Study area and site/stand characteristics

The tree data used in this study came from 30 sites established under the COST Action FP1206 EuMIXFOR (European Network on Mixed Forests). Each site consisted of three stands with similar ecological conditions but varied composition: pure stands of pine and beech and a mixed stand of both species. This triplet-transect approach (Pretzsch et al., 2015) allowed to cover a large environmental gradient within the overlapping natural ranges of pine and beech, while ensuring homogeneity of site conditions for all three stands related to one triplet; this way, bias due to co-variation between site conditions and stand composition was avoided. Effects of species identity and species mixing could therefore be analysed without influence of confounding factors. Elevation varied between 20 and 1475 m a.s.l; mean annual precipitation sum (P) ranged from 520 to 1175 mm and mean annual temperature (T) from 6 to 10.5 °C. In the mixtures, the percentage of basal area represented by Scots pine ranged from 25 % to 74 %; total basal area ranged from 16 to 80 m^2 ha^{-1} and stand age from 40 to 130 years. The stands were mostly even-aged and mono-layered. No silvicultural activities had been conducted in the stands during the preceding decades. A standard protocol for tree data collection (diameters, heights of trees and crown bases) and tree coring was applied. The full measurement protocol was described in details by Heym et al. (2017). Selected site and stand characteristics for each site are presented in Table A1.

206 1.2. **Climate data**

207 We used the 0.25°-gridded E-OBS dataset from the EU-FP6 ENSEMBLES project. From this dataset, we obtained series
208 of daily minimum and maximum temperatures and cumulative daily precipitation for the 1979-2013 period (i.e. the
209 length of the dendrochronological series). Climate variables were used to analyze the influence of climate on tree
210 growth. Mean monthly temperature and monthly Standardized Precipitations Evapotranspiration Index (SPEI) were
211 used. SPEI is a (monthly) multi-scalar index that can be used to determine the onset, duration and magnitude of
212 drought conditions with respect to normal conditions (Vicente-Serrano et al., 2010). Positive values indicate above-
213 normal wet conditions, whereas negative values identify dry periods. SPEI values between -0.67 and 0.67 are
214 considered normal, values between -0.67 and -1.28 indicate moderate drought, and values <-1.28 indicate severe
215 drought (Isbell et al., 2015). The potential evapotranspiration (PET) necessary to calculate SPEI was determined using
216 the modified Hargreaves equation (Choisnel et al., 1992; Droogers and Allen, 2002), which provides estimations that
217 are close to those obtained from the Penman-Monteith equation (Beguería et al., 2014). Calculations were made using
218 the SPEI-package in R software (Beguería et al., 2014; R Core Team, 2019).

219 Climatic parameters were considered from June of the previous year to October of the current year. Climate variables
220 were standardized to remove long-term variability using a smoothing spline with 50% frequency cut-off at a
221 wavelength of two-third of the length of each series (Cook and Peters, 1981). Standardized climate variables were
222 calculated by taking the difference between climatic values and the spline (Bert et al., 2020).

223

224 **1.3. Dendrochronological methods**

225 **Sampled trees and master chronologies**

226 At each site and stand, a minimum of 10 dominant or co-dominant trees per species (i.e. beech or pine in the pure
227 stands, beech and pine in the mixed stand) were cored at breast height in 2013 or 2014 (two cores per tree; northern
228 and eastern directions; last complete tree-ring in 2013). Individual tree-ring series were crossdated and series with
229 unresolvable crossdating problems were dropped (Heym et al., 2017). For each tree, measurements from the two

cores were averaged to obtain one individual series. In a limited number of cases (15% of total number of trees), however, only one core per tree could be used for the analyses. In total, 1143 beech trees (592 from pure stands; 551 from mixed stands) and 1164 pine trees (597 from pure stands; 567 from mixed stands) were used for dendrochronological analyses. To remove long- and medium-term growth trends and to focus on high-frequency growth variation, individual tree-ring series were detrended using a smoothing spline with 50% frequency cut-off at a wavelength of two-third of the length of each series (Cook and Peters, 1981). Master chronologies were calculated using biweighted robust mean (Cook and Kairiukstis, 2013) on the maximum period common to all sites (1979-2013). A master chronology was established for each stratum (Fig. 1, upper panel. A stratum is defined by a combination of site (30 in total) x species (pine or beech) x stand composition (pure or mixed – in mixed stands, a master chronology was established for each species independently); total number of strata = 120). Detrending was conducted using the DENDRO script (Mérian, 2012) within the R software (R Core Team, 2019). Expressed Population Signal (EPS) was calculated to assess the suitability of the dataset for dendroecological analyses. The high EPS values indicated that the chronologies can be used for the analyses (mean and standard deviation = 0.90 ± 0.07 and 0.90 ± 0.05 for pure and mixed beech respectively; 0.92 ± 0.07 and 0.90 ± 0.05 for pure and mixed pine respectively).

Identification of drought events

To analyze tree growth response to drought events, we selected site specific drought events that had a negative effect on tree growth. First, we identified negative pointer years for each species using the "Relative Event Year" definition of Schweingruber et al. (1990), i.e. at least 75% of the trees displayed a reduction of raw growth superior to 15% compared to the average raw growth of the previous 4-year period (Relative Growth Change (RGC) method – Becker, 1989; Schweingruber et al., 1990; Jetschke et al., 2019). Due to this 4-year window, dry years were selected within the period 1983-2013. In order to ensure that growth limitation was related to a drought event, we then only kept the negative pointer years associated with monthly SPEI values lower than -1.28 (Isbell et al., 2015) for at least one month during the growing period (March – August) of either the current year or the previous year. Taking into account the previous-year drought allowed to account for possible carry-over effects. As a result of the selection process, several

drought years could be selected for each combination of site and species, and years could vary between species within a site (see Table A2).

1.4. Statistical analyses

Climate-growth relationship

Bootstrapped Correlation Coefficients (BCC; Blasing et al., 1984; Guiot, 1991) were used to analyze the climate-growth relationship (Fig. 1, lower panel – left-hand side). Master chronologies per strata were used as dependent variable. Correlation functions were calculated using 34 climate regressors: 17 T_{mean} and 17 monthly SPEI values from June of the previous growing season to October of the current growing year. Climatic regressors were written in the form: $Variable_{Month}$; months written in full caps indicate variables from the current year while months written in lower case letters indicate climatic variables from the previous year. Sample size-related bias between strata was corrected by dividing BCC values by the square root of the Expressed Population Signal (EPS) as proposed by Mérian et al. (2013).

We first used Principal Component Analysis (PCA) on BCCs followed by hierarchical ascending clustering according to Ward D2 method to identify the different patterns in climate-growth relationships over the strata (Richman, 1986; Lebourgeois et al., 2014). Using this approach, we were able to properly account for the potentially different climate drivers affecting tree growth across such a large geographical area, and to identify groups of sites displaying similar climate-growth relationships. The optimal number of groups defined by the clustering algorithm was based on the elbow method and the Calinski-Harabasz index. Clustering allowed us to identify groups of sites displaying similar climate-growth relationships. Clustering dendrograms are presented in Figs. A1.1 to A1.4. Stand and climatic characteristics for the groups of sites resulting from the clustering are presented in Table 1 and Figure 3. Additional variables (such as mixing percentage, basal area or stand age) were also considered in the multivariate analyses but were not correlated to any PC.

Thereafter, to better highlight the difference of climate-tree growth relationship between pure and mixed stands for each species independently, we calculated the distance between the pure and the mixed stands of a given site along the principal components, using the following equation:

$$D_{ij} = \left|P_{ij}\right| - \left|M_{ij}\right|$$

Where D_{ij} corresponds to the displacement from the projection of each species in pure stand to the projection of each species in mixed stand for site *i* along PC *j*. P_{ij} is the association of the pure stand from site *i* with principal component *j*; similarly, M_{ij} is the association of the mixed stand from site *i* with principal component *j*. As a result, inward displacement (i.e. displacement in the direction of the origin of the principal component) is positive while negative values are associated with outward displacement. Inward displacement can, for instance, indicates a decrease in correlation with all variables associated with the corresponding PC. To characterize the patterns of change in climate-growth relationships between pure and mixed stands in different regions, we used the shift between pure and mixed stands positions on the compositional planes as indicator of the intensity of change in sensitivity to environment (Thimonier et al. 1994; Mérian and Lebourgeois, 2011). One-sample t-tests were then used to assess whether the average displacements within groups along a PC were significantly different from zero. In some cases, the low number of sites within a specific group prevented us to properly assess the displacement direction (inward or outward displacement) and amplitude (importance of the displacement between pure and mixed stand of a site along one PC).

Response to extreme drought

In addition to looking at the difference of correlation between growth and climate variables in pure and mixed stands, we aimed at testing the difference in trees response to punctual drought events between the two stand types (Fig. 1, lower panel – right-hand side). To assess how the growth response to punctual drought events differed between pure and mixed chronologies, we calculated the relative growth change per stand type × site × drought event for each species separately, using the corresponding species-related drought years. In a first analysis, a PCA was performed on RGC values to explore to which extent growth response to drought differed between stand types and sites. The

displacements of projection from pure to mixed stands were also calculated, and average displacements within groups were tested as described above. In a second step, we used mixed effect models for each species separately, considering year nested within site as random factor, to test for the significance of stand composition (pure *vs* mixed), average site climatic parameters (average temperature and difference between precipitation and potential evapotranspiration for the following periods: Mar-May, Jun-Aug, Sep-Nov, Dec-Feb in each site), site geographic characteristics (altitude and latitude) and stand characteristics (age and basal area) on growth reduction (RGC) during drought events, according to the original equation:

$$RGC_{sy} = \beta \times E_s + a_s(0, \sigma_s^2) + a_{y|s}(0, \sigma_y^2) + \varepsilon(0, \sigma_\varepsilon^2)$$

Where RGC_{sy} represents the stand average relative growth change for site *s*, and year *y*, β is the vector of fixed effect parameters, E is the matrix of the predictors of the fixed effects, a_s is the random factor characterized by the inter-site variance σ^2_s, $a_{y|s}$ is the random factor characterized by the interannual variance within a site σ^2_y and ε is the error term of variance σ^2_ε. A series of climatic variables ($Tmean_{spring}$, $Tmean_{summer}$, $Tmean_{fall}$, $Tmean_{winter}$, $SPEI_{spring}$, $SPEI_{summer}$, $SPEI_{fall}$, $SPEI_{winter}$), a dummy variable with two levels (pure/mixed) representing stand composition, other potential confounding factors (stand basal area and stand age) and their interactions were used as candidate variables for fixed effects. Starting from the model with the full set of parameters, the variables with the lower predictive power were then progressively removed based on the Akaike Information Criterion (AIC).

All calculations were made using the R software (R Core Team, 2019).

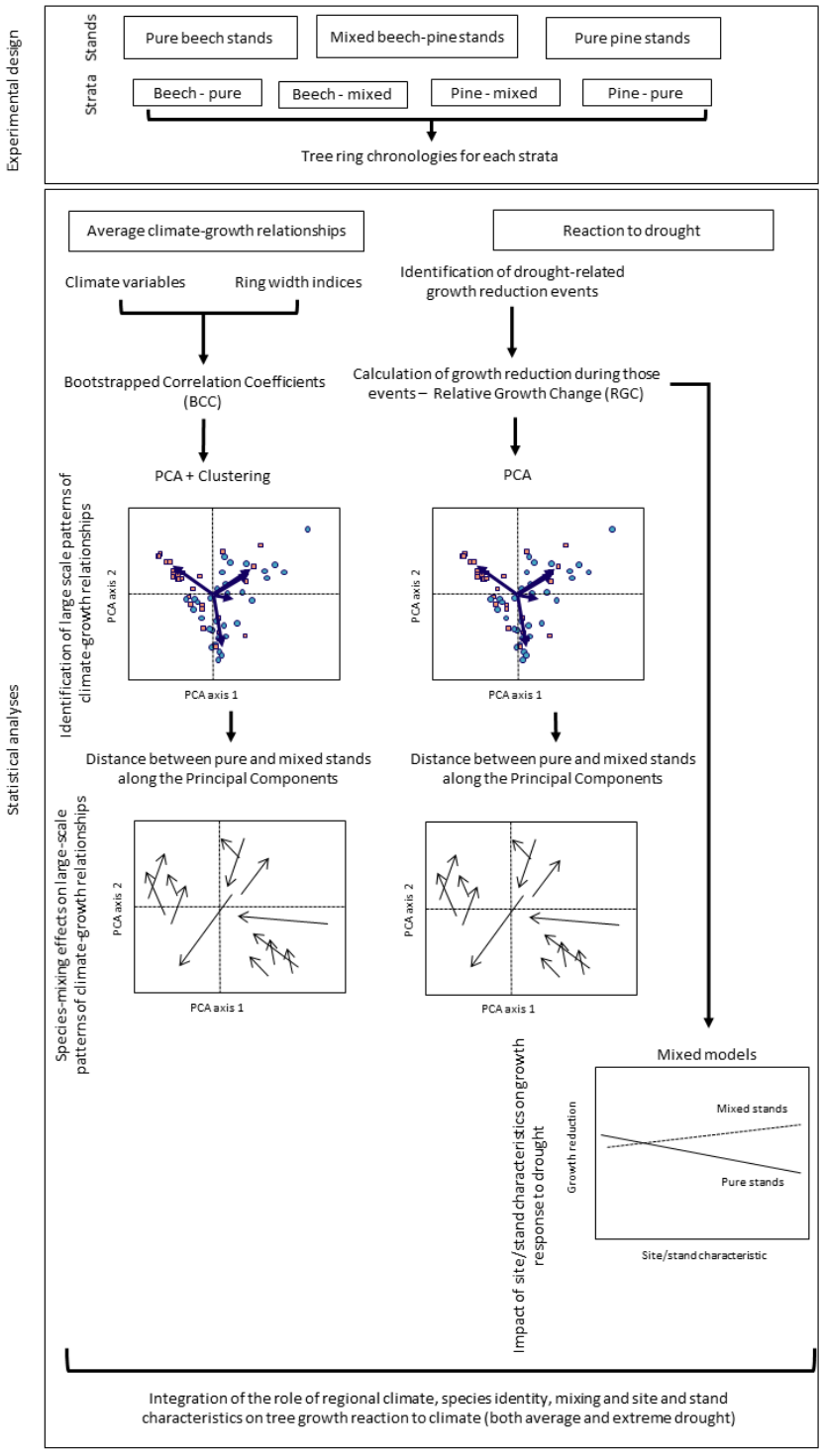


Figure 1 Flowchart showing the experimental design (upper panel) and the different steps involved in the analysis (lower panel) of the average climate-growth relationships (left-hand side) and of the response to drought (right-hand side).

Table 1 Range (minimum/maximum) of selected site and stand characteristics for groups of sites showing comparable climate-growth relationships. The groups are based on a clustering analysis performed on the first (clusters 1.1 to 1.6) and second (clusters 2.1 to 2.3) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients. Because clustering analysis performed on the second compositional planes yielded slightly different groups between the two species, characteristics are given separately for beech and pine for clusters 2.1, 2.2 and 2.3. Spring: Mar-May, Summer: Jun-Aug, Fall: Sep-Nov, Winter: Dec-Feb. T, mean air temperature (°C); WB, climatic water balance (mm): precipitation minus potential evapotranspiration; Stand type, with BE for beech, PI for pine; BA, basal area (m^2 ha^{-1}). Climate data are averages over 1979-2013. Age in mixed stands is indicated as follows: beech age range (min/max);pine age range.

Cluster	Latitude	Altitude	$Tmean_{spring}$	$Tmean_{summer}$	$Tmean_{fall}$	$Tmean_{winter}$	WB_{spring}	WB_{summer}	WB_{fall}	WB_{winter}	Stand type		BA range	Age range
1.1	48.2/56.2	27/547	6.2/10.1	15.5/18.1	7.3/11.2	-1.4/3.7	-106.5/40.9	-192.1/-10.4	1.3/165.2	58.4/244.2	Pure	BE	23/54	46/150
												PI	11/59	45/150
											Mixed	BE/PI	30/52	45/115; 45/130
1.2	48.6/55.5	20/533	6.6/9.0	16.7/17.9	7.5 /9.3	-2.6/0.6	-119.6/-54.4	-221.9/-38.9	0.4/185.7	53.3/159.3	Pure	BE	21/45	45/102
												PI	24/45	45/102
											Mixed	BE/PI	16/63	45/102; 45/102
1.3	50.0/51.0	209/383	7.6/8.6	17.1/17.9	7.8/8.7	-2.3/-1.3	-91.7/-80.5	-151.8/-136.3	11.1/23.6	59.7/82.3	Pure	BE	18/53	55/105
												PI	30/64	55/105
											Mixed	BE/PI	33/47	55/105; 55/105
1.4	44.9/46.1	1038/1475	4.7/5.2	14.2/14.7	6.9/6.9	-2.6/-1.2	-10.0/166.9	-109.9/-103.8	101.1/232.7	35.2/240.6	Pure	BE	23/41	40/55
												PI	47/52	40/55
											Mixed	BE/PI	22/41	40/55; 40/55
1.5	42.1/42.2	1099/1292	6.7/10.2	16.5/19.6	9.3/12.8	1.7/5.1	-54.4/-30.8	-387.8/-318.1	15.56/56.7	94.7/136.3	Pure	BE	33/52	40/50
												PI	40/55	40/50
											Mixed	BE/PI	32/53	40/50; 40/50
1.6	41.9/43.6	1080/1188	5.7/8.4	16.0/17.8	7.3/9.4	-2.6/-0.7	-53.4/-7.7	-275.5/-168.0	-51.6/90.4	80.0/157.0	Pure	BE	20/41	65/75
												PI	33/54	65/75
											Mixed	BE/PI	27/80	65/75; 65/70
2.1 – Beech	48.2/52.1	40/547	7.5/9.8	15.9/18.1	7.3/10.0	-1.4/2.0	-119.6/40.9	-221.9/-10.4	0.4/147.9	53.3/244.2	Pure	BE	21/54	45/150
											Mixed	BE/PI	16/52	45/100; 45/130
2.1 - Pine	48.2/50.1	40/540	7.5/9.8	16.4/18.1	7.3/10.0	-1.4/2.0	-106.5/2.4	-192.1/-10.4	0.4/100.8	53.3/177.5	Pure	PI	25/59	45/73
											Mixed	BE/PI	32/52	45/70; 45/70
2.2 – Beech	46.1/56.2	27/1038	5.2/10.1	14.7/17.6	6.9/11.1	-2.6/3.7	-96.9/-10.0	-163.6/-93.2	30.5/165.2	35.2/205.6	Pure	BE	23/52	40/115
											Mixed	BE/PI	16/46	40/115; 40/115
2.2 - Pine	40.0/56.2	27/547	6.2/10.1	15.1/17.6	7.7/11.1	-0.7/3.7	-119.6/40.9	-221.9/-56.5	7.1/165.2	90.8/244.2	Pure	PI	11/48	48/150
											Mixed	BE/PI	16/46	46/115; 46/130
2.3 - Beech	41.9/55.5	20/1475	4.7/10.2	14.2/19.6	6.9/12.8	-2.6/5.1	-91.7/166.9	-387.8/-38.9	-51.6/232.7	59.7/240.6	Pure	BE	18/53	40/105
											Mixed	BE/PI	22/80	40/105; 40/105

2.3 - Pine	41.9/55.5	20/1475	4.7/10.2	14.2/19.6	6.9/12.8	-2.6/5.1	-91.7/166.9	-387.8/-38.9	-51.6/232.7	35.2/240.6	Pure	PI	30/64	40/105
											Mixed	BE/PI	22/80	40/105; 40/105

328

2. Results

2.1. Major climatic drivers of radial growth

The first principal component accounted for 24% of the total variance for both species (Fig. 4, A and C). Both species presented similar patterns of climate-growth relationships with a major role of summer and fall temperatures. For beech, PC1 revealed an opposition between the influence of current average temperature in September ($Tmean_{SEP}$) and the influence of average temperature of previous September and July ($Tmean_{Sep}$/$Tmean_{Jul}$) on growth while for pine $Tmean_{Sep}$/$Tmean_{Jul}$ vs. $Tmean_{SEP}$/$SPEI_{Jun}$ were determinant. The second principal component accounted for 17% of the total variance. As for PC1, both species showed a rather similar response yet with a more important role of summer drought: PC2 was positively associated with $SPEI_{AUG}$ (for beech) and $SPEI_{Aug}$ (for pine) and negatively associated with $Tmean_{JUL}$ (beech) and $Tmean_{AUG}$ (beech and pine). PC3, which held 11% of total variance for both species, was determined by $SPEI_{APR}$ and $SPEI_{Sep}$. Lastly, PC4 (10% of total variance) was negatively correlated with June temperatures and April temperature of the current year.

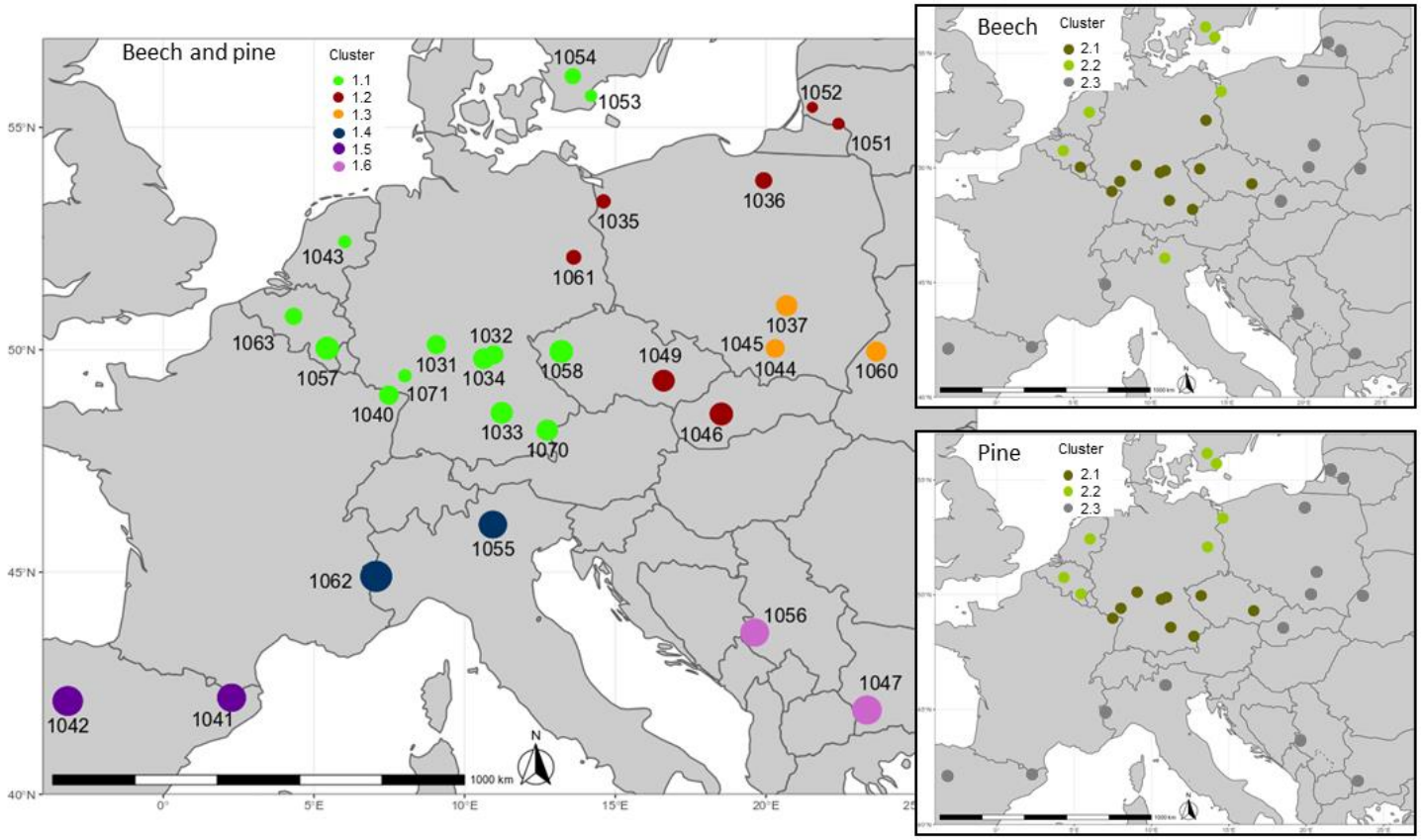


Figure 2 Distribution of the 30 study sites across Europe. Numbers are the site-ID (Table A1). The size of the points is proportional to the site altitude (20 - 1475 m). The colors refer to clusters of sites showing similar climate-growth relationships. These clusters are based on a clustering analysis performed on the first (main map common for the two species, clusters 1.1 to 1.6) and second (smaller maps, clusters 2.1 to 2.3; beech: above, pine: below) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients.

346

347 **2.2. Geographic pattern of major climatic drivers of radial growth**

348 Clustering made on PC1/2 (clusters 1.1. to 1.6.) and PC3/4 (clusters 2.1. to 2.3.) (Fig. A1.1. to A1.4.) revealed several
349 groups of sites displaying similar climate-growth relationships (Fig. 4), and those patterns were similar for both
350 species.

351 On the first compositional plane, the Spanish sites (1041, 1042; cluster 1.5) displayed distinct climate sensitivity, due
352 to a strong positive correlation with $Tmean_{SEP}$ (and $SPEI_{Jun}$ for pine) or a negative correlation with $Tmean_{Sep}$ or $Tmean_{Jul}$.
353 The sites from the southeastern part of the network (1056 and 1047; cluster 1.6) were also strongly associated with
354 PC1 but through a negative correlation. Cluster 1.4 was composed of the two Italian sites (1062 and 1055) and was
355 positively associated with PC1 and, to a lower extent, with PC2. Cluster 1.3 was equally associated with PC1 and PC2
356 as was cluster 1.2, although the correlation with climatic variables was much lower for the latter. Lastly, sites from
357 cluster 1.1 displayed low correlation with either of the first two PCs.

358 On the second compositional plane, clustering defined three groups. Two of them displayed strong and coherent
359 correlation with PC3 and PC4: clusters 2.1 and 2.2, respectively. The majority of sites associated with clusters 2.1 and
360 2.2 on the second compositional plane belonged to cluster 1.1 on the first plane. Cluster 2.1 corresponded to sites
361 from Central Europe (South of Germany, Czech Republic, Slovakia), while cluster 2.2 brought together sites from the
362 Northwestern part of Europe (Figs. 2 and 4).

363 Clusters differed both in geographic (altitude, latitude) and climatic characteristics (Table 1 and Fig. 3). Indeed, clusters
364 1.4, 1.5 and 1.6 were all low latitude/high altitude groups of sites (Fig. 2). Cluster 1.5 (and, to a lesser extent 1.6) was
365 characterized by very dry summer, while cluster1.4 showed cold and humid conditions throughout the year (Fig. 3).
366 Clusters 1.1, 1.2 and 1.3 were all mid-range latitude and low altitude groups. Cluster 1.3 displayed low P - PET values
367 during the non-growing period (fall, winter); there was a pattern of decreasing P - PET level during winter when moving
368 from cluster 1.1 to cluster 1.3. In the following, we therefore referred to the climate conditions associated with each
369 cluster as regional climates.

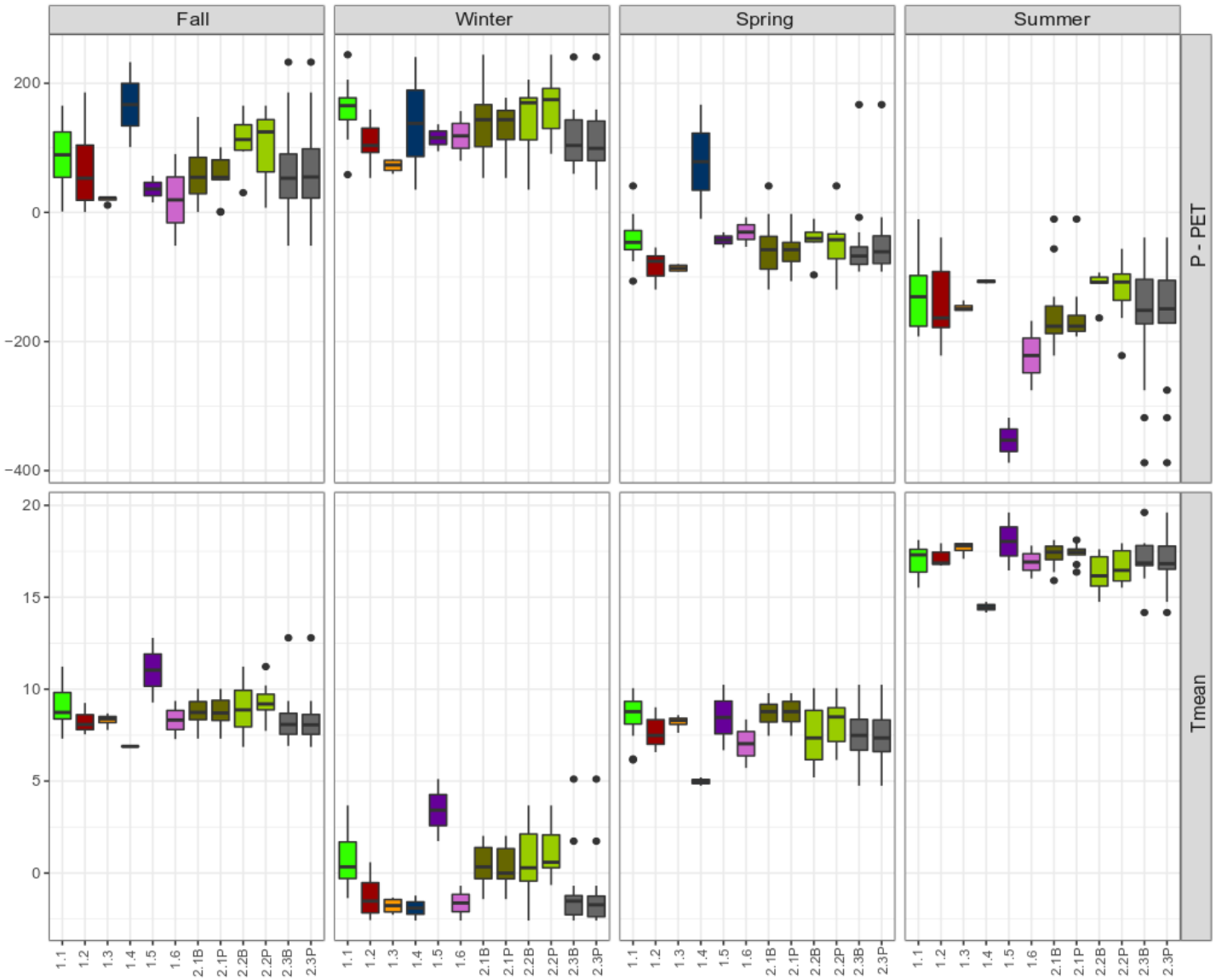


Figure 3 Climate characteristics (P-PET, an indicator of climatic water balance [mm] and Tmean [°C]) of the clusters of sites defined according to their similar climate-tree growth relationship. Lower and upper limit of the boxes represent 25 and 75% quantiles, respectively while the whiskers indicate the lowest or highest value not further than 1.5 x the inter-quartile range from the hinges. Clusters resulting from clustering performed on the second compositional plane (clusters 2.1, 2.2 and 2.3) noted "B" and "P" refer to beech and pine, respectively.

2.3. Species-mixing effect on climate-growth relationship

The amplitude and direction of change ("displacement along the PCs") of loadings values from pure to mixed chronologies on each PC were highly dependent on site identity for both species, and no global pattern could be found (Fig. 4). For pine, none of the groups displayed significant displacement in any direction. For beech, sites from clusters 1.5 and 1.6 seemed to display coherent displacement along the first and third PCs (Fig. 4) which could indicate a lowering correlation with variables associated with those PCs. However, the low number of sites in those clusters did not allow us to properly test this potential effect.

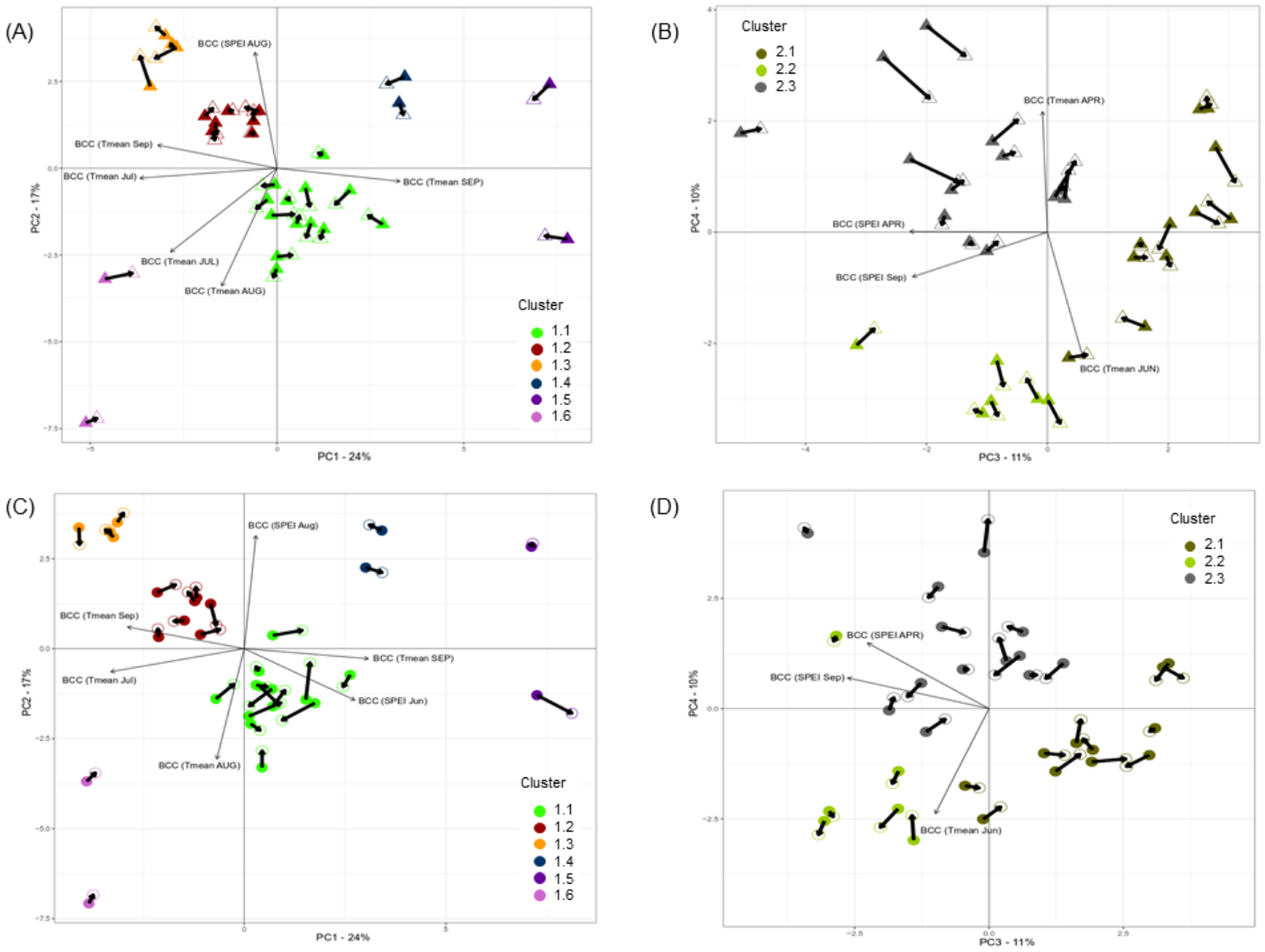


Fig. 4 Principal Component Analysis of the Bootstrapped Correlation Coefficients for beech (A and B) and pine (C and D) between standardized tree-ring width of each strata (site x species x stand) and climatic variables (monthly Tmean and SPEI values from June of the previous year to November of the current year). Strata corresponding to pure and mixed chronologies are depicted by big filled and small open symbols, respectively. Only the best represented variables are drawn. Arrows indicate the displacement from the pure to the mixed chronologies within each site. Strata and

389 climatic vectors pointing in the same direction indicates positive correlation, whereas the opposite indicates negative correlation. For climatic
390 variables, months in full caps refer to the current year (previous year otherwise). Colors indicate sites grouped together by the clustering algorithm,
391 based on the first (clusters 1.1 to 1.6) and second (clusters 2.1 to 2.3) compositional planes (Fig. A1). Clusters 2.1 and 2.2 are mostly composed of
392 sites belonging to cluster 1.1.

393

394 **2.4. Response to extreme drought**

395 The average number of drought years across the period 1983-2013 (Table A2) was similar for beech and pine (mean ±
396 standard deviation = 2.8 ± 1.3 and 2.7 ± 1.5 for beech and pine respectively). However, the number of drought years
397 strongly differed between specific combinations of site and species, ranging from 0 to 6 for beech and from 0 to 7 for
398 pine. The number of drought years that cleared the "Relative Event Year" criteria was similar between pure and mixed
399 stands of a same species (3.4 ± 1.6 vs. 3.0 ± 2.2 in pure and mixed beech, respectively; 3.5 ± 2.1 vs. 3.6 ± 2.0 in pure
400 and mixed pine, respectively).

401 In most cases (63% of cases for beech, 60% for pine), strata-level drought years corresponded to "Relative event years"
402 for both pure and mixed stands. When only one of the two plots displayed a relative event year, growth reduction
403 was found equally frequently in pure and mixed stands for beech (56% and 44% of cases, respectively); for pine, pure
404 plots responded more frequently (73% of cases). Beech and pine also tended to react to different years as, out of the
405 total of 93 drought events identified for at least one of the two species at a same site, only 15 were common to both
406 species; out of the 78 remaining events, 50 were associated with pine. Beech displayed high apparent variability in
407 species-mixing effect on growth reduction during drought years. Indeed, out of the 19 sites displaying at least one
408 drought year, 11 sites displayed situations of positive (lower growth reduction in mixed stands) and negative species
409 mixing effects, depending on the year (Table A2); the 8 remaining sites displayed systematically negative (4 sites) or
410 positive (4 sites) species-mixing effects. Species-mixing effect on drought response appeared to be more consistent
411 over the study period for pine as out of the 26 sites displaying at least one drought year, on 18 sites, all drought years
412 were associated with either systematically negative (5 sites) or systematically positive (13 sites) species mixing effects.
413 On the remaining sites, positive and negative species-mixing effects can be found. For both species, sites displaying

such consistent positive or negative species-mixing effects across years were found in all groups of sites showing comparable climate-growth relationships.

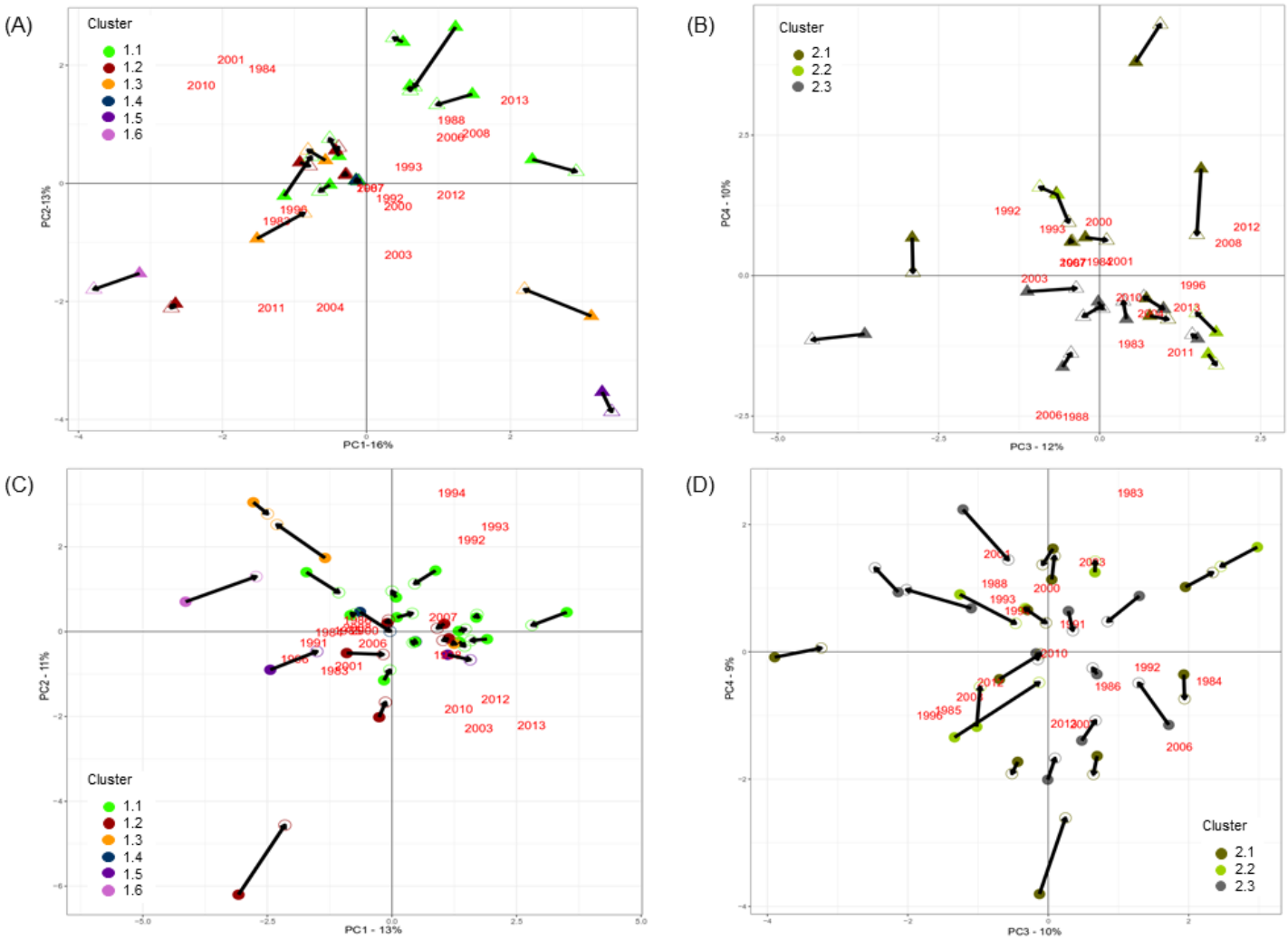


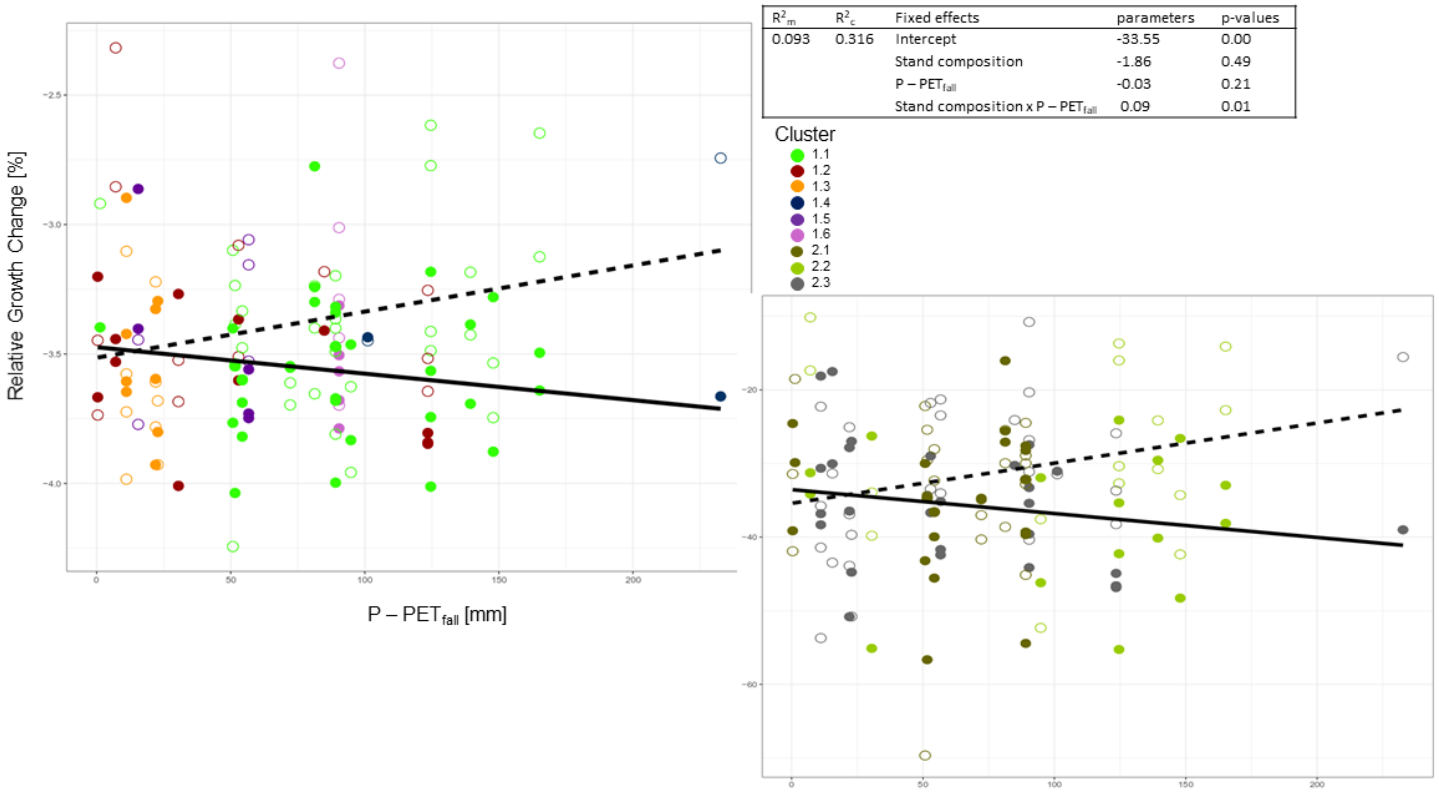
Fig. 5 Principal Component Analysis performed on the Relative Growth Variation during drought years for beech (A and B) and pine (C and D). Pure and mixed chronologies are depicted by filled and open symbols, respectively. Arrows indicate the displacement from the pure to the mixed chronologies within each site. Colors represent the clusters delimited based on the main climate-growth relationship patterns found in the PCA conducted on Boostrapped Correlation Coefficients (see Fig. 4). Red numbers indicate drought years. A total of 11 sites for beech and 4 sites for pine were found to be non responsive to drought (Table A2).

For beech, the first four axes of the PCA conducted on the drought events accounted for 16, 13, 12 and 10% of total variance respectively. For pine, they accounted for 13, 11, 10 and 9% (Fig. 5). Clusters of sites showing similar climate-

425 growth relationships and certain common climate characteristics did not show any coherent pattern of relative growth
426 variation during drought (Fig. 5). No coherent drought response could be found within the groups of BCC similar sites,
427 indicating those sites had no or only limited drought years in common. In addition, non-responsive sites (11 for beech,
428 4 for pine; Table A2) were found in all groups.

429 There was no globally coherent difference in the response to drought between pure and mixed chronologies (Fig. 5).
430 Despite large differences in the position of pure and mixed stands along the PCA planes for some sites, the
431 displacement of chronologies projections from pure to mixed stands did not show any consistent pattern for beech
432 (Fig. 5). For pine, the displacements along the first and fourth PC were significantly positive when all sites were
433 considered together (p-values of 0.03 in both cases); in addition, all sites from cluster 2.2. showed a significantly
434 positive displacement along the third PC (p-value = 0.04).

435 According to the linear mixed effect model fitted on beech RGC, pure and mixed stands did not display any significant
436 difference in growth reduction during drought years. For pine, there was no main effect of stand composition, but a
437 significant interaction between stand composition and P - PET during fall as illustrated in Fig. 6. The growth reduction
438 was less pronounced in mixed than in pure stands only for sites with high $P - PET_{fall}$.



R^2_m	R^2_c	Fixed effects	parameters	p-values
0.093	0.316	Intercept	-33.55	0.00
		Stand composition	-1.86	0.49
		$P - PET_{fall}$	-0.03	0.21
		Stand composition x $P - PET_{fall}$	0.09	0.01

Fig. 6 Predicted (lines) and observed (dots) RGC values for pine as a function of $P - PET_{fall}$ in pure and mixed stands. Parameter estimates, p values and R-squared for the linear mixed models adjusted on pine RGC values are presented in the enclosed table. Marginal R-squared (R^2_m) represents the variance explained by fixed factors; conditional R-squared (R^2_c) represents the variance explained by both fixed and random factors (full model). Reference level for stand composition is "pure". Open symbols and dashed line represent mixed stands; filled symbols and continuous line represent pure stands. The colors refer to groups of sites showing similar climate-growth relationships; those groups are based on a clustering analysis performed on the first (main figure, clusters 1.1 to 1.6) and second (smaller figure, clusters 2.1 to 2.3) compositional planes of a PCA performed on Bootstrapped Correlation Coefficients.

3. Discussion

3.1. Geographical pattern of climate-growth relationship

The response of tree growth to climate at the European scale is primarily driven by the regional climate conditions, for both tree species (pine/beech) and all stand composition (pure/mixed). Summer/fall temperatures (July/September – Figs. 4 and A2) of current and previous years are the main climatic drivers of tree growth which is consistent with previous studies also led at the European scale (Briffa et al., 2002; Wettstein et al., 2011). Our clusters (Fig. 4) also agree with biogeographical patterns of climate-tree growth highlighted by Babst et al. (2013) over Europe. On the other hand, in contrast to previous studies conducted at local

scales (e.g. González de Andrés et al., 2018), both species showed similar climate-growth relationships suggesting that at European scale, the site geographical and climatic characteristics appeared to be stronger determinants of response to climate than species identity.

3.2. Species-mixing effect on climate-growth relationships

An apparent coherent displacement from pure to mixed stands was observed for beech only under warm (low latitude) and dry (low summer P-PET) conditions, while no such effect was detected for pine whatever the ecological conditions.

The low number of sites corresponding to those specific conditions did not allow us to accurately test the significance of those displacements for beech. However, we can point out that these displacement from pure to mixed stands correspond to strong ecological constraint suggesting a positive interaction between species on stand functioning (complementarity). Under the less restrictive ecological conditions (Fig. 3), the strong heterogeneity in term of displacement according to mixing confirms that there is a need to have some overwhelming common constraint to express the complementary between species in mixed stands. This pattern clearly fits within the general framework proposed by previous authors (Bertness and Callaway, 1994; Forrester and Bauhus, 2016) stating that complementarity increases when environmental conditions become harsher, provided that species-mixing has an impact on the limiting factor. Similar patterns have been highlighted by Lebourgeois et al. (2013) who found that the shift in the response of silver fir (*Abies alba* Mill) to climate induced by mixing was restricted to the driest sites. In our study, complementarity could lead to a reduction of the summer constraint and therefore to a lower dependency to previous summer and current September climatic conditions. Nevertheless, future research effort should be dedicated to high constrained conditions to assess the significance of species-mixing effects and the mechanisms at play. In the absence of any major climatic constraint, the effects of species interactions on climate-growth relationships would be mainly driven by local site conditions, whose diversity within a region would explain the lack of any coherent response (see next section).

While admixing pine in beech stands was shown to reduce the constraint on beech trees in water-limited conditions (González de Andrés et al., 2017), other climatic variables might also impose limitations which could be more difficult to alleviate through mixing such as low temperatures throughout the year. Change in microclimate conditions resulting from difference in canopy structure, phenology or modifications in the length of the growing period, have been reported for some mixtures with respect to their monocultures (e.g. Lebourgeois et al. 2013; Ehbrecht et al. 2017), yet the extent to which this affects growth still remains to be documented.

3.3. **Response to a drought event**

We found limited evidence that species-mixing effects on drought resistance were shaped by the climate variables controlling tree growth. The fact that drought reaction was different between sites from groups showing similar climate-growth relationships and common climatic characteristics suggests a strong influence of local characteristics such as soil condition. Only the low-elevation and non water-limited sites from the Northwestern part of Europe (Fig. 2), showed a coherent species-mixing effect on drought resistance, yet limited to pine (Fig. 5D). As shown in Figs. 3 and 6, for pine many sites displaying high $P - PET_{fall}$ values showed lower growth reduction during drought events in mixed stands than in pure ones. Such favorable climatic conditions at the end of the vegetation period would allow pine to take advantage of its longer vegetation period to compensate for any drought limitation experienced during spring and/or summer; during this late growing period, pine growth could be further favored by the earlier reduction of beech photosynthetic activity.

Such effect may however be offset by factors varying at the site level, such as difference in the characteristics of triggering years (e.g. differences in droughts timing – D'Orangeville et al. 2018) or in local conditions of soil water availability (Carrière et al., 2020). Although we were not able to consistently assess the impact of potential available soil water on drought response due to a lack of soil data in many sites, the information available at some sites shows it ranged between 28 and 715 mm (de Streel et al., 2019); such a large range is expected to greatly impact tree response to drought (Lévesque et al., 2013).

Last, the interannual variation of drought response and of its modulation by mixing within a given site suggests that the timing, duration and intensity of the drought events is important. For instance, Bhuyan et al. (2017) showed that beech was sensitive to both short- and long-term drought although this sensitivity to drought length was dependent on site climate. Several studies have also shown that drought timing and intensity were major determinants of tree growth response. Tree growth proved to be more severely affected by more intense drought (D'Orangeville et al. 2018) and, depending on its timing, droughts have specific effects on different species depending on their characteristics such as phenology (Vanhellemont et al., 2019).

Our results also showed contrasting patterns between beech and pine, in terms of both response to drought and mixing effects. Regarding the reaction to drought, the number of non-responsive sites was much higher for beech compared to pine. In addition, pine and beech most often differed in the timing of their drought response within similar sites, reflecting contrasting sensitivity to drought and suggesting a large decoupling in possible mixing effects between those two species. As previously stated, while no main effect of mixing could be detected for neither species, pine showed a positive mixing effect in sites with high (P – PET) in the late growing period.

Those differences in drought response and mixing effects between the two species remain difficult to clearly explain and could be linked to their respective stomatal adjustment capacity to avoid water stress (isohydric vs. anisohydric behavior) (Bello et al. 2019) or to their carbon storage and carbon mobilization strategies during drought (Michelot et al. 2012; Lassoie and Salo, 1981; Lévesque et al., 2014; Seidel et al., 2019).

Because beech and pine were found to respond to distinct drought events, we might expect temporal stability to be higher in mixed compared to pure stands. This is coherent with the results from del Río et al. (2017) using the same triplet network who found an increased in temporal stability of productivity at the community level in mixed stands.

Conclusion

We explored the large-scale spatial patterns of species-mixing influence on climate-growth relationships and resistance to drought events for European beech and Scots pine across Europe. We found limited support to our initial hypothesis that the impact of mixing on the response to climate and drought event would be mostly driven by the regional climate, resulting in a coherent response of both climate-tree growth relationships and drought resistance to mixing within climatic groups.

Our results show that there seldom is a coherent species mixing effect, even when considering sites that display similar climate-growth relationships and that share similar climatic characteristics. In absence of strong limiting climate conditions, forest managers should therefore not expect species-mixing to have a coherent effect on climate-growth relationships. Species-mixing could have beneficial or detrimental effects on growth sensitivity to climate depending on local conditions. If there is no major climatic constraint or if species-mixing does not alleviate it, the relative sensitivity of tree climate-growth relationship to climatic and edaphic conditions will lead to positive, neutral or negative species-mixing effects, depending on local factors.

Regarding the resistance to drought, we were unable to detect any significant mixing effect for neither of the species, and no clear geographical pattern emerged. Interestingly however, regional climate was found to potentially impact pine resistance, through a positive effect of higher climatic water balance in autumn, suggesting compensatory growth.

Our results showed that the regional climate only partly determined the impact of mixing on the tree-growth relationships, and highlight the interacting influences of species identity, stand characteristics, drought events characteristics as well as local site conditions. Integrating all those factors into mechanistic models of tree growth such as HETEROFOR (Jonard et al. 2020) is the next step to quantify the relative contribution of each, and to be able to make reliable context-dependent predictions.

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Table A1 Selected site and stand characteristics of the 30 sites. P: *Mean annual precipitation sum [mm], T: Mean annual temperature [°C].* Age and basal area data in mixed stands are provided first for beech, then for pine.

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Bel1	1057	545	1175	7.5	Beech	150	27
					Pine	150	11
					Beech/Pine	100/130	20/10
Bel2	1063	160	852	10.5	Beech	115	28
					Pine	115	40
					Beech/Pine	115/115	17/29
Bul1	1047	1187	750	6	Beech	65	41
					Pine	65	54
					Beech/Pine	65/65	37/42
Cze1	1049	440	620	7.5	Beech	45	36
					Pine	45	43
					Beech/Pine	45/45	13/26
Cze2	1058	545	656	7.1	Beech	55	38
					Pine	55	40
					Beech/Pine	55/55	13/22
Fra1	1040	275	948	9.7	Beech	60	26
					Pine	60	41
					Beech/Pine	60/60	15/17
Ger1	1033	430	700	8.5	Beech	53	23
					Pine	65	25
					Beech/Pine	50/50	16/17
Ger2	1031	250	720	9	Beech	55	44
					Pine	55	53
					Beech/Pine	55/55	53/27
Ger3	1032	250	650	8	Beech	50	34
					Pine	45	43
					Beech/Pine	45/45	13/31
Ger4	1071	40	675	9	Beech	60	54
					Pine	70	59
					Beech/Pine	70/70	28/24
Ger5	1034	370	675	10	Beech	58	40
					Pine	51	55
					Beech/Pine	64/64	17/22
Ger6	1070	400	560	8	Beech	64	23
					Pine	73	34
					Beech/Pine	60/60	11/28
Ger7	1061	74	520	8.6	Beech	80	21
					Pine	80	24
					Beech/Pine	80/80	12/4
Ita1	1055	1037	1050	7.8	Beech	40	23
					Pine	40	52
					Beech/Pine	40/40	10/12
Ita2	1062	1475	938	7.9	Beech	55	41
					Pine	55	47
					Beech/Pine	55/55	20/21

Table A1 (continued) Selected site and stand characteristics of the 30 sites. P: *Mean annual precipitation sum [mm], T: Mean annual temperature [°C].* Age and basal area data in mixed stands are provided first for beech, then for pine.

Site name	Site number	Altitude [m]	P [mm]	T [°C]	Stand composition	Age [Years]	Basal area [$m^2.ha^{-1}$]
Lit1	1051	25	750	6.5	Beech	90	26
					Pine	90	35
					Beech/Pine	90/90	20/43
Lit2	1052	20	800	6.5	Beech	102	43
					Pine	102	41
					Beech/Pine	102/102	18/41
Net1	1043	34	825	9.7	Beech	46	38
					Pine	48	39
					Beech/Pine	46/46	19/27
Pol2	1036	136	666	7.9	Beech	84	37
					Pine	74	36
					Beech/Pine	84/84	18/21
Pol1	1035	60	556	9.2	Beech	54	38
					Pine	54	42
					Beech/Pine	54/54	12/26
Pol3	1037	383	662	7.8	Beech	80	31
					Pine	81	41
					Beech/Pine	83/83	24/20
Pol4	1044	209	650	8.2	Beech	57	18
					Pine	57	30
					Beech/Pine	57/57	23/13
Pol5	1045	215	650	8.2	Beech	55	25
					Pine	55	34
					Beech/Pine	55/55	16/16
Ser1	1056	1080	1020	7.7	Beech	75	20
					Pine	75	33
					Beech/Pine	75/75	10/17
Sk1	1046	530	730	6.9	Beech	55	45
					Pine	55	45
					Beech/Pine	55/55	13/27
Sp1	1042	1293	860	8.9	Beech	40	33
					Pine	40	55
					Beech/Pine	40/40	14/39
Sp2	1041	1106	1100	8	Beech	50	52
					Pine	50	40
					Beech/Pine	50/50	21/11
Swe1	1054	118	700	8	Beech	84	29
					Pine	56	32
					Beech/Pine	106/106	20/20
Swe2	1053	26	800	7	Beech	65	29
					Pine	65	32
					Beech/Pine	65/65	20/20
Ukr1	1060	315	673	7.6	Beech	105	53
					Pine	105	64
					Beech/Pine	105/105	22/25

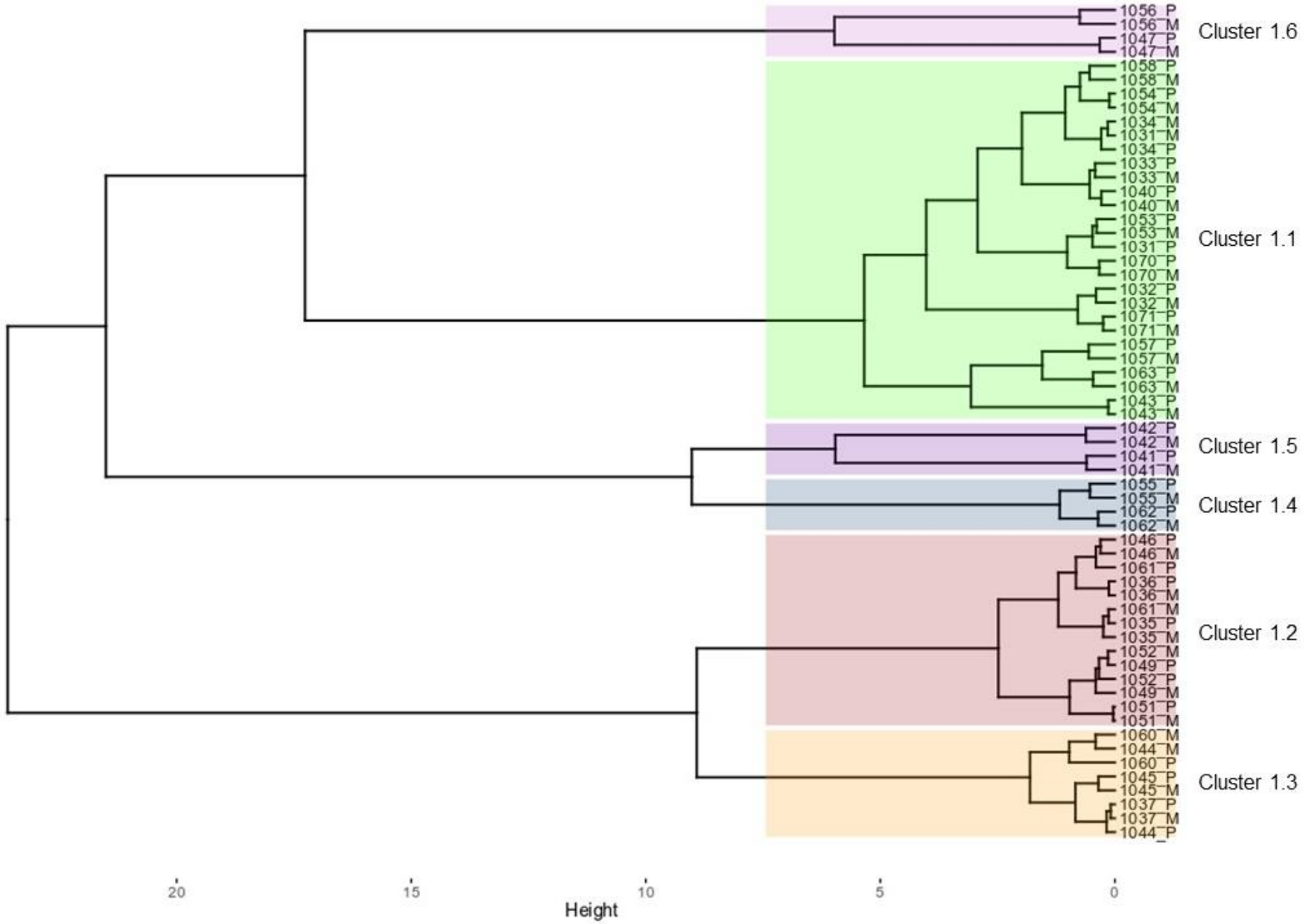

Fig. A1.1. Dendrograms of the ward D2 clustering performed on the first two principal components of the *PCA of the Bootstrapped Correlation Coefficients for beech between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table S1); P and M, refers to pure and mixed stands, respectively*

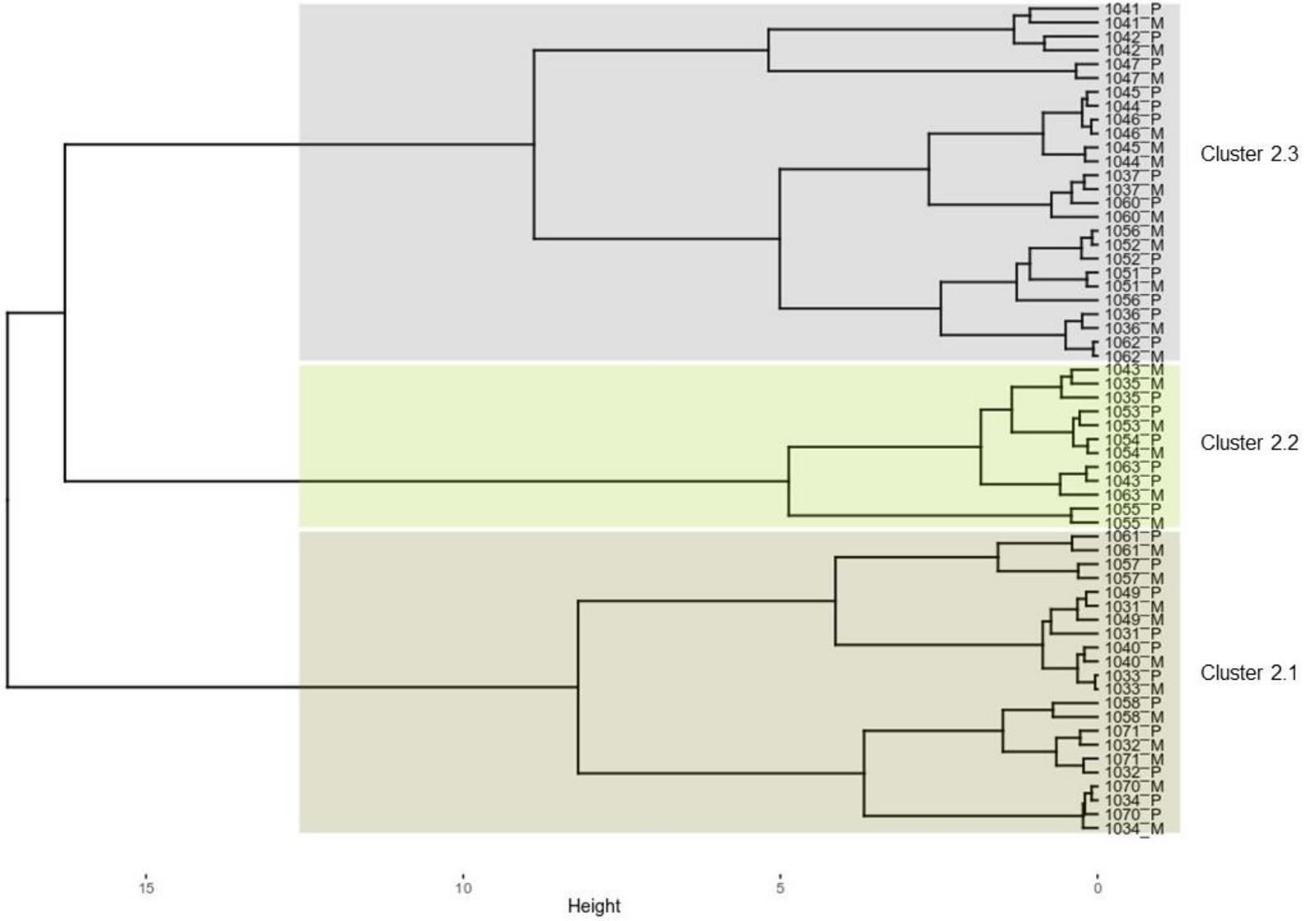

Figure A1.2. Dendrograms of the ward D2 clustering performed on the third and four principal components of the *PCA of the Bootstrapped Correlation Coefficients for beech between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table S1); P and M, refers to pure and mixed stands, respectively*

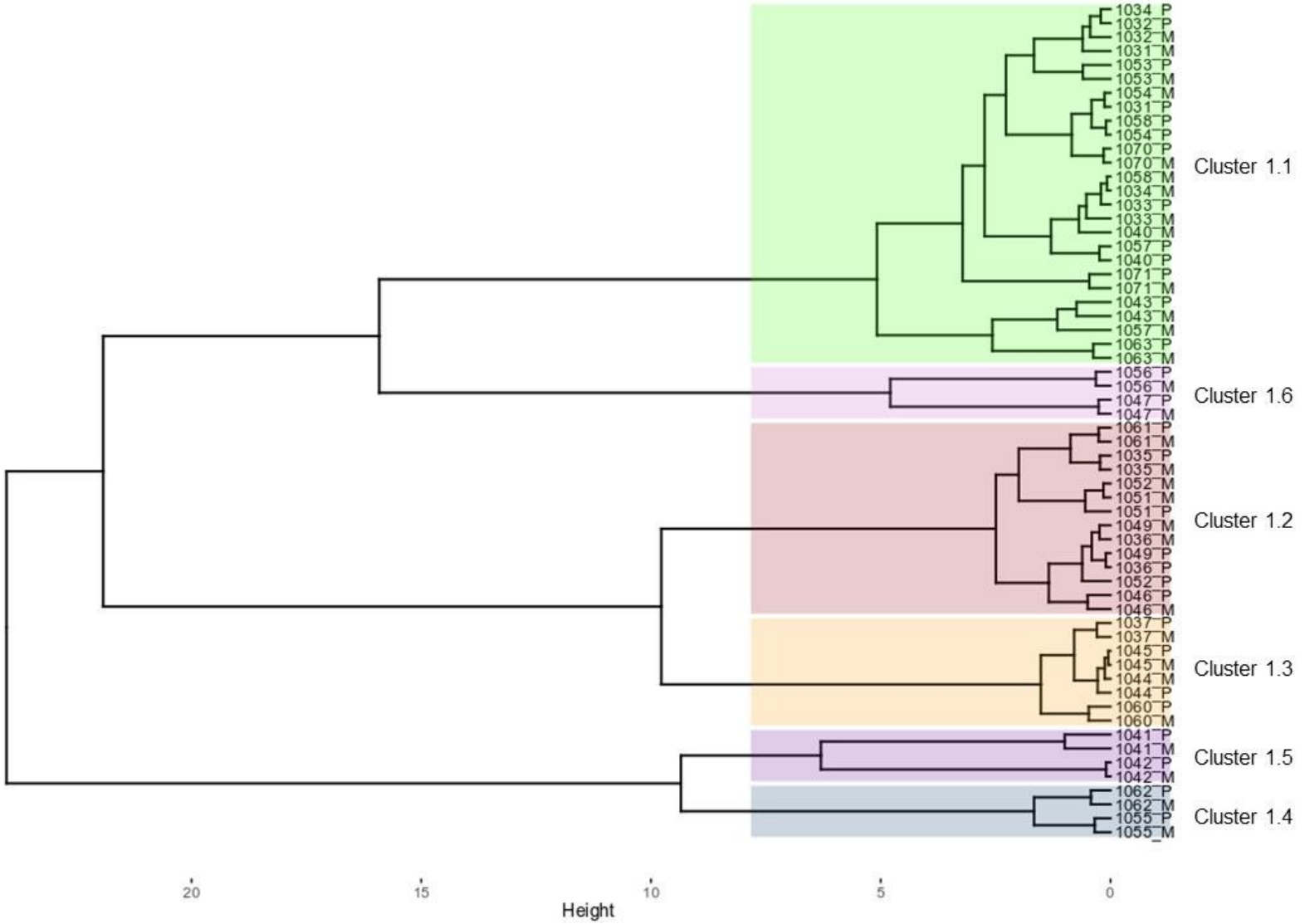

Figure A1.3. Dendrograms of the ward D2 clustering performed on the first two principal components of the *PCA of the Bootstrapped Correlation Coefficients for pine between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table S1); P and M, refers to pure and mixed stands, respectively*

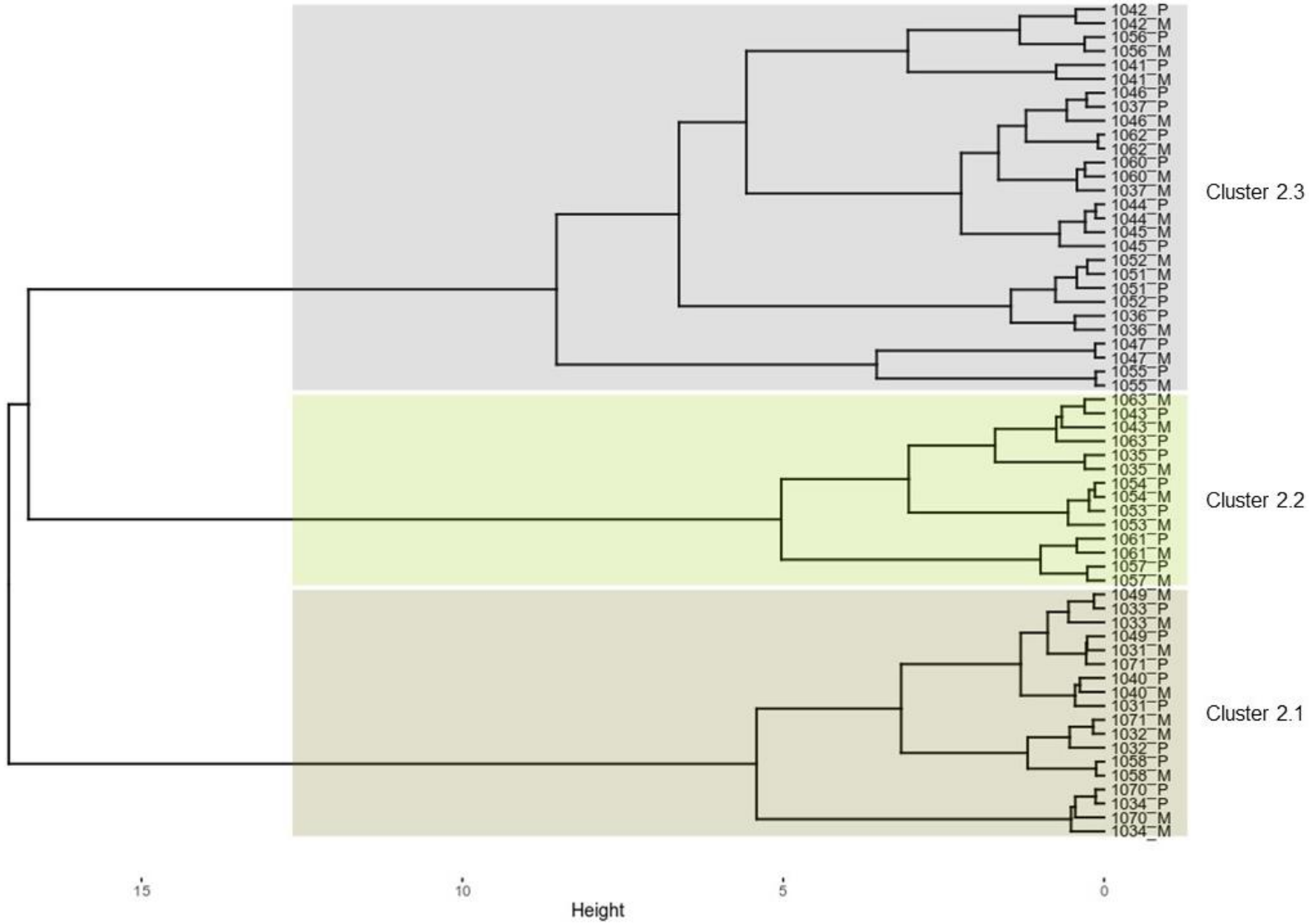

Figure A1.4. Dendrograms of the ward D2 clustering performed on the third and four principal components of the *PCA of the Bootstrapped Correlation Coefficients for pine between standardized tree-ring width of each strata (site x species x stand) and climatic variables. Numbers are the site id (Table S1); P and M, refers to pure and mixed stands, respectively.*

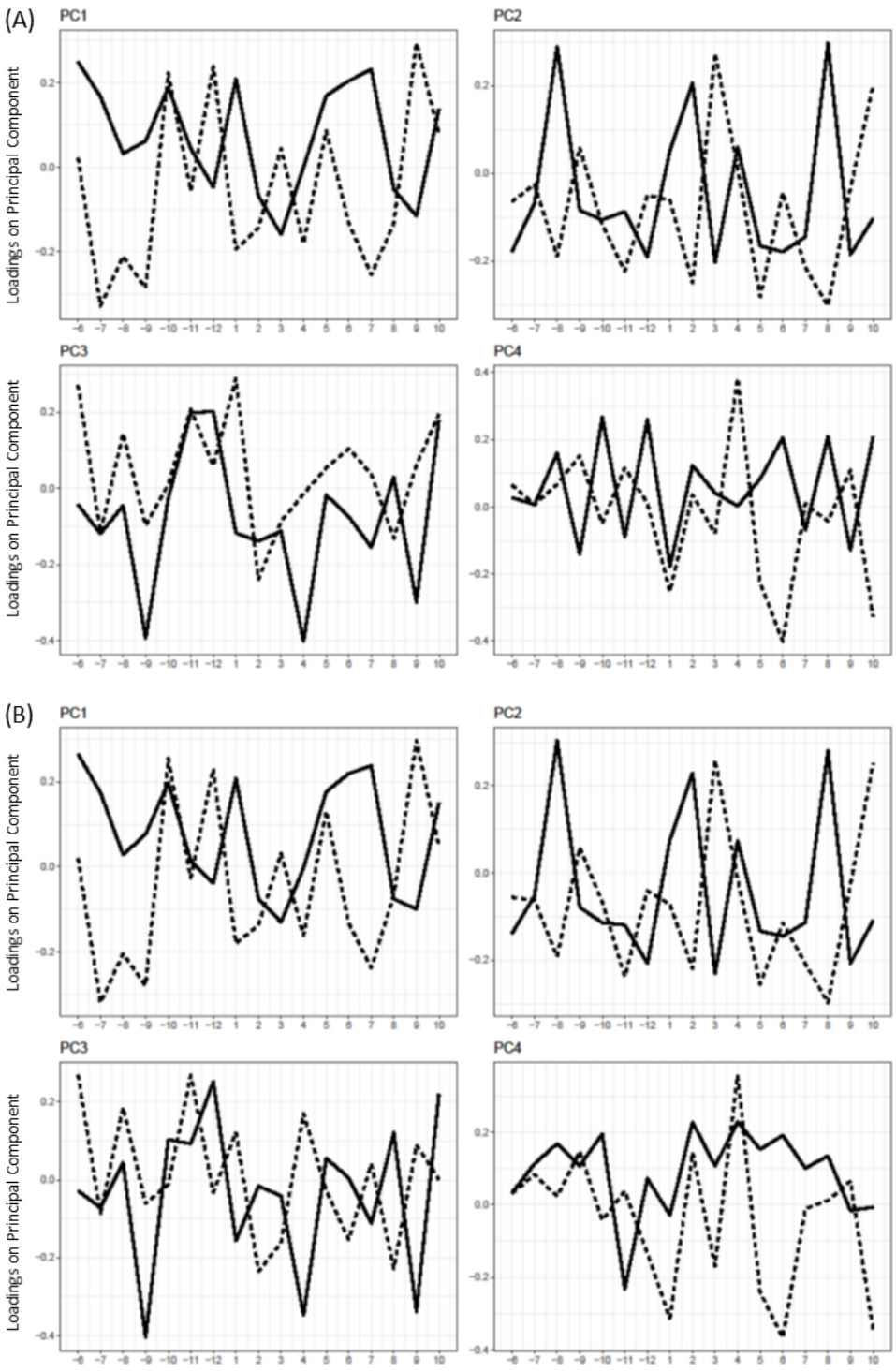

Fig. A2 SPEI (plain lines) and Tmean (dashed lines) loadings values on each of the 4 first principal components of the Principal Component Analysis performed on the Bootstrapped Correlation Coefficients between standardized tree-ring width of each stratum for beech (A) and pine (B). Months -6 to -12 correspond to June – December of the previous year.

Table A2.1. Radial Growth Variation during dry negative pointer years of cluster 1.1. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1031	mixed	beech														-38	-51					-33		
1031	pure	beech														-22	-61					-31		
1031	mixed	pine											-30					-39						-25
1031	pure	pine											-16					-27						-26
1032	mixed	beech	-11																			-62		
1032	pure	beech	-31																			-59		
1032	mixed	pine	-37													-40								
1032	pure	pine	-35													-35								
1033	mixed	beech																						
1033	pure	beech																						
1033	mixed	pine											-22							-70				
1033	pure	pine											-30							-43				
1034	mixed	beech												-28		-36								
1034	pure	beech												-25		-18								
1034	mixed	pine	-25												-30	-35								
1034	pure	pine	-57												-34	-35								
1040	mixed	beech																						
1040	pure	beech																						
1040	mixed	pine																						
1040	pure	pine																						
1043	mixed	beech	-28																		-50	-53		
1043	pure	beech	-34																		-31	-37		
1043	mixed	pine	-16	-14					-30				-33											
1043	pure	pine	-55	-35					-24				-42											
1053	mixed	beech																						
1053	pure	beech																						
1053	mixed	pine			-24								-31											
1053	pure	pine			-30								-40											

Table A2.1. (continued). Radial Growth Variation during dry negative pointer years of cluster 1.1. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1054	mixed	beech								-35	-31													
1054	pure	beech								-40	-19													
1054	mixed	pine								-23								-14						
1054	pure	pine								-33								-38						
1057	mixed	beech											-34				-15					-49	-41	
1057	pure	beech											-36				-54					-55	-25	
1057	mixed	pine											-42		-34									
1057	pure	pine											-48		-27									
1058	mixed	beech																	-36					
1058	pure	beech																	-17					
1058	mixed	pine																-19						
1058	pure	pine																-30						
1063	mixed	beech																						
1063	pure	beech																						
1063	mixed	pine											-52					-38						
1063	pure	pine											-46					-32						
1070	mixed	beech														-44		-14						
1070	pure	beech														-25		-31						
1070	mixed	pine	-30	-24						-32						-29		-45						-33
1070	pure	pine	-32	-28						-40						-39		-54						-28
1071	mixed	beech															-32					-43		
1071	pure	beech															-38					-39		
1071	mixed	pine																-37					-32	-28
1071	pure	pine																-37					-46	-40

Table A2.2. Radial Growth Variation during dry negative pointer years for sites of cluster 1.2. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1035	mixed	beech								-24						-32								
1035	pure	beech								-44						-26								
1035	mixed	pine	-40															-34						
1035	pure	pine	-55															-26						
1036	mixed	beech								-46														
1036	pure	beech								-51														
1036	mixed	pine										-24												
1036	pure	pine										-30												
1046	mixed	beech												-40									-27	
1046	pure	beech												-50									-31	
1046	mixed	pine	-22											-33										
1046	pure	pine	-29											-37										
1049	mixed	beech						-40										-29						-34
1049	pure	beech						-36										-22						-45
1049	mixed	pine	-31					-42																
1049	pure	pine	-25					-39																
1051	mixed	beech																						
1051	pure	beech																						
1051	mixed	pine								-26	-38	-34												
1051	pure	pine								-45	-47	-47												
1052	mixed	beech																						
1052	pure	beech																						
1052	mixed	pine																						
1052	pure	pine																						
1061	mixed	beech																						
1061	pure	beech																						
1061	mixed	pine								-17						-10								
1061	pure	pine								-34						-31								

Table A2.3 Radial Growth Variation during dry negative pointer years for sites of cluster 1.3. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1037	mixed	beech																						
1037	pure	beech																						
1037	mixed	pine		-40														-51						
1037	pure	pine		-45														-27						
1044	mixed	beech									-16													-26
1044	pure	beech									-34													-44
1044	mixed	pine														-37					-25			-44
1044	pure	pine														-36					-28			-51
1045	mixed	beech														-29							-35	
1045	pure	beech														-20							-23	
1045	mixed	pine											-22			-41							-38	-54
1045	pure	pine											-31			-18							-37	-38
1060	mixed	beech											-12		-31						-33			
1060	pure	beech											-32		-48						-32			
1060	mixed	pine																						
1060	pure	pine																						

Table A2.4. Radial Growth Variation during dry negative pointer years for sites of cluster 1.4. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1055	mixed	beech																						
1055	pure	beech																						
1055	mixed	pine																-31						
1055	pure	pine																-31						
1062	mixed	beech					-19																	
1062	pure	beech					-45																	
1062	mixed	pine																						-16
1062	pure	pine																						-39

Table A2.5. Radial Growth Variation during dry negative pointer years for sites of cluster 1.5. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1041	mixed	beech																						
1041	pure	beech																						
1041	mixed	pine								-21									-23					-34
1041	pure	pine								-35									-42					-42
1042	mixed	beech		-43											-30						-35			
1042	pure	beech		-30											-33						-42			
1042	mixed	pine		-31		-43																		
1042	pure	pine		-18		-30																		

Table A2.6. Radial Growth Variation during dry negative pointer years for sites of cluster 1.6. Values in red indicate negative pointer years for which the drought happened the previous year. For brevity, only years with at least one dry pointer year are listed. Cells highlighted in yellow indicates year that are characteristic at the plot level.

Triplet	plot	species	1983	1984	1985	1986	1987	1988	1991	1992	1993	1994	1996	2000	2001	2003	2004	2006	2007	2008	2010	2011	2012	2013
1047	mixed	beech																						
1047	pure	beech																						
1047	mixed	pine																						
1047	pure	pine																						
1056	mixed	beech																		-32			-51	-73
1056	pure	beech																		-31			-37	-55
1056	mixed	pine						-27			-11					-20							-40	-31
1056	pure	pine						-33			-35					-27							-44	-40