1 **Title:** Contrasting pattern of tree species-mixture effects on wood $\delta^{13}C$ along a gradient of

2 environmental conditions

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Abstract

Context Over the last decades, there has been an increasing interest in mixed species forests because of their expected positive impacts on ecosystem services (including productivity), ecosystem stability and risk management. However, the mechanisms at play in species interaction and their dependency on spatial and temporal variations of environmental conditions are still insufficiently understood.

Methods To assess the impact of species mixture on tree response to water availability, we constructed 22-year time series of wood carbon isotope compositions from a network of 17 sites covering a large gradient of environmental conditions throughout Europe. Each site included a mixed *Fagus sylvatica* L. / *Pinus sylvestris* L. stand and one monospecific stand of each species, with all the stands at a given site in similar environmental conditions.

Results A positive species-mixture effect for both species was found on dry sites. On moderately wet sites, the results were contrasted, with pine showing a negative effect and beech a positive one. The contrasted results can be explained by the differences in how each species manages the trade-off between carbon acquisition and water loss, which are highlighted in pure plots. No species-mixture effect was found on extremely dry or extremely wet sites. There were no differences in reactions to drought between pure and mixed stands.

Conclusion Mixing species did not improve trees response to a drought event but influenced their average isotopic composition according to the species-specific functional traits and average site conditions. The pattern of mixing effect along the gradient of water availability was not linear but showed threshold points.

1. Introduction

Over the last few decades, forest research has given increasing attention to mixed-species forests. This increased interest in mixed-species stands and their effect on ecosystem functions and services arose from several observations. First, mixed-species forests can be more productive than monospecific ones in certain conditions (Forrester 2014; Forrester and Bauhus 2016; Zhang et al 2012). Second, mixing species could lead to increased stability of aboveground biomass production (Ammer 2018). Third, there are increasing concerns about the effects of biodiversity losses on ecosystem functions (Loreau 2001; Cardinale et al. 2012). Finally, mixed-species forests are thought to be one of the most important tools to help manage the risks caused by global changes (Reif et al. 2010).

In a context of ongoing climate change, both the frequency and intensity of droughts are expected to increase in the Northern hemisphere in the upcoming decades (IPCC 2013). The negative impacts on tree functioning due to water shortages are an important concern to foresters. Such impacts include hydraulic failure leading to mortality (McDowell et al. 2008), carbon starvation due to stomatal closure (Hartmann 2011) or fine root death (Jany 2003). Favouring mixed-species stands has become an important management strategy to help forests adapt to the increasing risk of low water availability.

However, there have been many contrasting results concerning the effects of mixing tree species on ecosystem functioning (drought resistance for instance) and services, thus indicating that those effects are influenced by a large number of variables (Forrester 2014). For instance, Lebourgeois et al. (2013) and Pretzsch et al. (2013) found an improved drought response in more diverse plots while Bosela et al. (2018), Merlin et al. (2015), Toïgo et al. (2015) and Vanhellemont et al. (2019) found the opposite effect. Environmental conditions are a major determinant of species-mixture effect and their variations can partially explain the contrasted species-mixture effects observed on ecosystem performance. Bertness and Calloway (1994), who established the Stress Gradient Hypothesis (SGH), first theorized this effect. According to the SGH, positive effects of species mixture are expected to be higher in harsh conditions. This hypothesis has been discussed, and refined, over time. For instance, Tielbörger and Kadmon (2000), Pennings et al. (2003), Maestre and Cortina (2004), and Holmgrem and Scheffer (2010) introduced the idea that facilitation would be higher in mild situations than in harsh ones. Such spatial and temporal variations in the species-mixture effect are due to mechanisms that depend on factors limiting productivity (complementarity and competition). For instance, for a given set of environmental conditions, species mixture can improve the availability of a resource (light aboveground and water or nutrients belowground), its uptake or its use efficiency, which can lead to greater productivity and, ultimately, to higher stand density. It is worth noting that belowground and aboveground resources are not independent in terms of improved availability, uptake or use efficiency (Ammer 2018). For instance, a positive species-mixture effect on belowground resources (competitive reduction or facilitation) can lead to increased biomass allocation in aboveground biomass (balanced-growth hypothesis, Shipley et al. 2002) that can translate into higher aboveground biomass plasticity and increased canopy packing. Spatial variations in species-mixture effect along a gradient of decreasing resource availability can then occur if species mixture improves the availability, uptake or use efficiency of the limiting resource, and complementarity can be expected to increase with decreasing resource availability. Temporal variations in species-mixture effect can also occur due to temporary changes in environmental conditions (del Rio et al. 2014; Forrester 2014). These temporal variations can express themselves at difference time scales. For instance, in a given set of conditions, a positive species-mixture effect could lead to increased stand density through complementarity. However, the increased competition associated with higher stand density could then

106 hamper the positive species-mixture effect or even result in a negative effect. In addition to such long-
107 term variations in species-mixture effect, short-term temporal variations can occur (over a course of one
108 to several years), for example as in the case of an annual drought (Grossiord 2014; Lebourgeois et al. 2013;
109 Pretzsch et al. 2013). On sites with high average water availability, complementarity with regard to this
110 resource could be absent, and might express itself only when water becomes limiting due to a drought. It
111 is also important to note that, although complementarity in water-related processes would probably be
112 absent on such sites in average conditions, it could be at play for other resources (e.g. light) and could
113 switch from non-water-related mechanisms to water-related ones during drought events. This means that
114 there could be trade-offs among different types of complementarity processes depending on both long-
115 term environmental conditions and temporal fluctuations in those conditions.

116 The general pattern of tree response to low water availability is well known. One of its effects is a
117 modification in the ratio between carbon assimilation and water loss. Indeed, as a reaction to low water
118 availability, trees reduce their stomatal conductance in order to limit transpiration. The carbon
119 assimilation rate is also reduced, though to a lesser extent, leading to a reduction in the ratio between
120 intracellular (C_i) and ambient (C_a) CO_2 concentrations (Farquhar et al. 1989). Stable carbon isotopes in tree
121 rings give a good indication of the water availability level to which trees have been subjected. Indeed,
122 during photosynthetic assimilation of atmospheric CO_2, trees tend to discriminate against $^{13}CO_2$ and in
123 favor of $^{12}CO_2$. This preferential use of the lighter isotope is related to the fact that $^{12}CO_2$ diffuses more
124 easily and interacts more readily with the primary carboxylating enzyme (Farquhar et al. 1982). Because
125 the relative amount of the two carbon isotopes assimilated during photosynthesis is dependent on the
126 C_i/C_a ratio (Farquhar et al. 1982), carbon isotope composition in plant tissues is influenced by water
127 shortages (O'Leary, 1995).

128 We studied two tree species with very different functional traits (*Fagus sylvatica* L. and *Pinus sylvestris* L.).
129 The traits that differ between the two species, and which are relevant to water-related processes, include:
130 root-system shape (heart-shaped for beech and tap root for pine), shade tolerance (high vs. low), stomatal
131 density (around 200/mm^{-2} for beech vs. 84/mm^{-2} for pine), and strategies in regard to drought resistance
132 (anisohydric tendency for beech vs. isohydric for pine) (Cochard 1992, Martinez-Vilalta et al. 2004, Pflug
133 et al. 2018, Schäfer et al. 2017, Yang et al. 2016). We investigated beech and pine occurring along a large
134 gradient of environmental conditions across Europe. We hoped to answer the following questions:

135 i) How does the wood carbon isotope composition of the two species compare in pure stands?
136   Here, we investigated the functional diversity of the two species. This type of information is
137   useful when interpreting species-mixture effect, as one would not expect functionally
138   redundant species to display much difference in their physiological processes in pure and
139   mixed stands. We addressed this point through two sub-questions: How does the pattern of
140   *(i)* spatial and *(ii)* temporal variations in isotope composition for the two species compare?

141 ii) Is there a species-mixture effect on wood isotope composition (an indicator of water use
142   efficiency) and, if so, are there spatial and/or temporal variations in this effect? Are the
143   potential spatial/temporal variations in isotope composition linked to climatic variables and
144   site and stand characteristics? We further investigated temporal variations in the species-
145   mixture effect on wood isotope composition through an additional question: Is there a
146   difference between pure and mixed stands in tree wood isotopic composition after a severe
147   drought?

148   iii)   Because mixing species can improve the temporal stability of ecosystem properties by
149   reducing competition, or because the species respond differently to environmental variations
150   or react at different speeds to environmental variations (Morin et al, 2014), we asked the
151   following questions: *(i)* Is there a species-mixture effect on the temporal stability of the wood
152   isotopic composition of each species; *(ii)* Is there a difference between the temporal stability
153   of wood isotopic composition in beech and in pine; and *(iii)* Do beech and pine react
154   synchronously to climatic variations?

155

2. Materials and methods

157

2.1.   Study area and site/stand characteristics

159   The trees used in this study come from pine-beech triplets established under the umbrella of the COST
160   Action FP1206 EuMIXFOR (European Network on Mixed Forests). This network is composed of 32 sites and
161   covers a large gradient of environmental conditions within the overlapping natural ranges of Scots pine
162   and European beech (Figure 1). Each triplet consists of three distinct stands located in similar site
163   conditions: a pure stand of Scots pine, a pure stand of European beech and a mixed stand of both species.
164   The stands are mostly even-aged and mono-layered. Within a triplet, tree age is similar in the pure and
165   mixed stands for a given tree species, but may differ between species. A standard protocol for data
166   collection was applied in each triplet. Briefly, the following variables were recorded on each tree with a
167   diameter at breast height above 7 cm: species identity, status (alive, dead or damaged), diameter at breast
168   height (dbh), tree height (h) and crown base height (cbh). Stand-level data per plot and species were then
169   derived from this information. In addition, a subsample of 10-20 dominant trees per plot and species were
170   cored to the pith at 1.30 m in height in two perpendicular directions (north and east) (Pretzsch et al. 2015;
171   del Rio et al. 2017; Dirnberger et al. 2017; Heym et al. 2017).

172   No silvicultural activities had been conducted in the stands during the preceding decade.

173   We discarded the triplets where pre-treatment of the core samples might have affected the wood isotopic
174   signal; this resulted in a final subset of 17 study sites.

175   Site characteristics are presented in Table S1.

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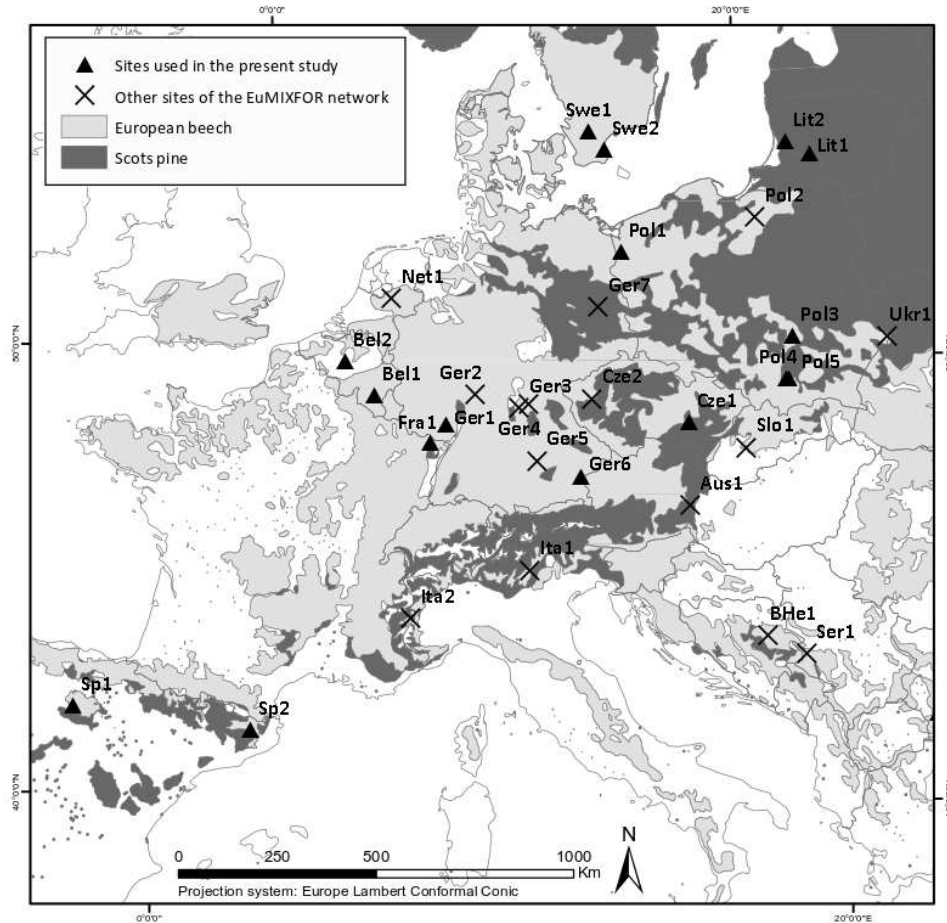
Fig. 1 *Distribution of the triplets in the EuMIXFOR network across Europe and distribution of European beech and Scots pine according to EUFORGEN (www.euforgen.org). Triangles represent triplet locations used in the present study. Crosses indicate other sites in the EuMIXFOR network, which were not included in the present study*

The selected triplets are distributed throughout the network (Figure 1), and cover a wide range of environmental conditions and stand productivity classes (Table 1 and Figure 2). Elevations range from 20 to 1339 m; mean annual precipitation (P) from 556 to 1175 mm; mean annual temperature (T) from 6 to 10.5 °C; and the de Martonne index (M = annual precipitation (mm)/mean annual temperature (°C + 10); de Martonne, 1926) from 29 to 67. The Site Index (height of the 100 largest-diameter trees of that species per hectare in monospecific stands at age 50 years; Forrester et al., 2017) ranges from 11.7 to 27.6 m for *F. sylvatica*, and from 9.5 to 26.9 m for *P. sylvestris*.

Table 1 *Selected characteristics of the 17 sites sorted by average water balance calculated over the vegetation period (March-September - WB$_{VP}$). For characteristics that vary between stands at a given site, the range of variation over all the stands at the site is indicated. Explanation of variables: elevation (m); slope (degrees); mean temperature calculated over the vegetation period (March-September) and averaged over the period 1950 - 2014, T$_{VP}$ [°C]; mean precipitation calculated over the vegetation period (March-September) and averaged over the period 1950 - 2014, P$_{VP}$ [mm]; de Martonne Index (1926), M (M = annual precipitation (mm)/(mean annual temperature °C + 10)); maximum Soil Water Availability, SWA (mm); and water balance calculated over the vegetation period and averaged over the period 1950- 2014, WB$_{VP}$ (WB$_{VP}$ = total precipitation over the vegetation period + potential available soil water – total potential evapotranspiration over the vegetation period). Site index is the height (m) of the 100 largest-diameter trees per ha at age 50 years in pure plots and is an indicator of site productivity for each species (Forrester et al. 2017); it is provided first for pine, then for beech*

Country	Triplet name - ID	Longitude	Latitude	Elevation	Slope	Mean temperature - T$_{VP}$	Mean precipitation - P$_{VP}$	De Martonne Index - M	SWA	WB$_{vP}$	Site Index
Spain	Sp1 - 1042	03°10'19.00"	42°05'57.00"	1252 - 1339	43 - 53	13.9	351	46	30 – 108	-415 - -337	20.9 – 24.8
Bulgaria	Bul1 – 1047	23°21'03"	41°53'43"	1180 - 1190	15 - 20	12.3	331	47	90	-262	25.1 – 25.9
Spain	Sp2 – 1041	02°15'44.23"	42°10'18.09"	1065 - 1209	24.4 – 39.8	16.9	371	61	84	-249	9.5 – 24.3
Czech Republic	Cze1 – 1049	16°36'08.78"	49°18'14.40"	435 - 445	0 - 15	13.1	384	35	146	-136	23 – 23.8
France	Fra1 – 1040	07°29'13.60"	48°58'41.80"	275	28 - 38	14.6	474	48	61 – 95	-124 - -94	22.2 - 23
Germany	Ger1 – 1033	11°14'12.49"	48°34'57.95"	430	1	14.5	382	38	158 – 273	-108 – 7	22.7 – 27.6
Belgium	Bel1 – 1057	5°27'00"	50°01'48.00"	535 - 550	0 - 8	13.1	439	57	151 - 172	-45	13.2 – 17.3
Poland	Pol1 – 1035	14°36'17.51"	53°20'07.40"	60	0	13.7	347	37	280	5	26.9 – 27.3
Poland	Pol4 – 1044	20°13'45.84"	50°01'27.60"	205 - 210	0 - 4	13.2	471	36	215 – 286	-3 – 68	21.3 - 15.8
Poland	Pol5- 1045	20°19'37.26"	50°01'36.00"	210 - 220	0	13.4	463	36	229 – 286	-11 – 46	25.8 - 24.5
Sweden	Swe1 – 1054	13°35'35.00"	56°09'12.00"	110 - 130	10 - 17	12.1	421	39	135 – 194	7 – 66	21 - 13.3
Poland	Pol3 – 1037	20°41'08.90"	50°59'27.96"	383	2	12.7	419	37	280	32	20.5 – 22.6
Belgium	Bel2 – 1063	04°19'29.60"	50°45'06.10"	157 - 165	0	15.0	540	49	122	139 - 160	10.9 - 12
Sweden	Swe2 – 1053	14°11'46.00"	55°42'33.00"	20 - 30	4 - 15	12.9	359	47	272	149	22.0
Germany	Ger6 – 1070	12°44'08.30"	48°11'12.47"	400	0	13.6	675	31	184	201	12.8 – 15.8
Lithuania	Lit1 – 1051	22°24'24.01"	55°04'47.30"	25	0	12.5	415	45	715	568	19.5 – 22.3
Lithuania	Lit2 - 1052	21°32'23.44"	55°27'02.80"	20	0	12.8	431	48	715	632	13.6 – 22.9

1
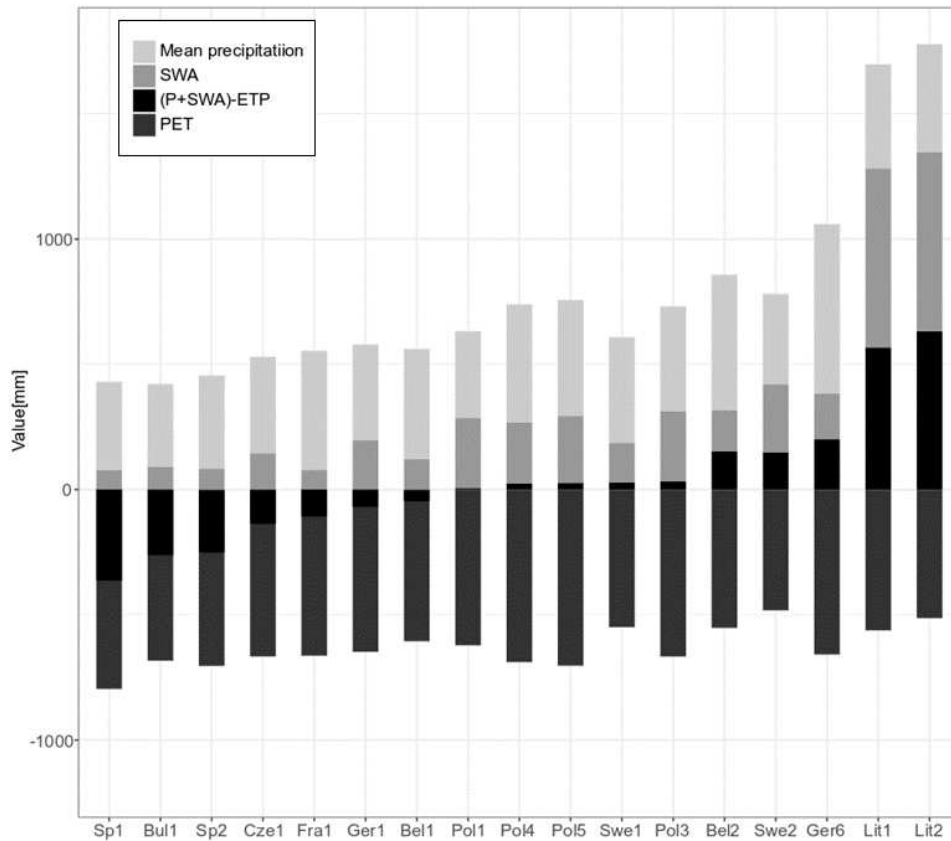
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3 **Fig. 2** *Components of the water balance (Precipitation + maximum Soil Water Available (SWA) – Evapotranspiration (PET)) for*
4 *each site. Climatic components of the water balance are calculated over the vegetation period (March – September) and*
5 *averaged over the 1950-2014 period*

6

7 A summary of stand characteristics is provided in Table S2. In the mixtures, the percentage of basal area
8 represented by *P. sylvestris* ranged from 33% to 74%; total basal area ranged from 30 to 79m^2 ha^{-1}, the
9 total number of trees per hectare from 248 to 2,421 and stand age from 40 to 130 years.

10

11 **2.2.   Isotopic data**

12 For each site, five trees per species and stand type (pure or mixed stands) were randomly selected from
13 the 10-20 trees that had been cored in each stand. For each of those cores, we used a scalpel and a
14 stereomicroscope to sample the last third of each ring, corresponding to the period 1993-2014. We only
15 took the last third of the ring in order to avoid carry-over effects on wood isotope composition (Michelot
16 et al. 2012). The five samples were then pooled per species in each stand resulting in four samples per
17 triplet and year (total number of samples: 4 × 17 [number of triplets] × 22 [years] = 1,496).

18 At the INRA Silvatech platform (Nancy, France), the pooled samples were ground to a fine powder in a ball
19 mill (MM400, Retsch). The $^{13}C/^{12}C$ ratio was measured with a mass spectrometer (Isoprime 100 (Isoprime
20 Ltd., Cheadle Hulme, UK) coupled with an elemental analyser (Elementar vario, ISOTOPE cube, Elementar
21 Analysen Systeme GmbH, Hanau, Germany)). The standard deviation for the analysis of standard
22 saccharose was 0.12‰.

23 The isotopic composition ($\delta^{13}C$) relative to the standard Vienna Pee Dee Belemnite scale was calculated as
24 follows (Equation 1):

25 $$\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000 \qquad (1)$$

26 with $R_{standard}$ being the isotopic ratio of a belemnite fossil from the Pee Dee Formation, corresponding to
27 the international standard (IAEA 1995).

28 Isotopic composition was corrected to take into account the change in the isotopic composition of
29 atmospheric CO_2 due to industrialization, Equation 2 (McCarroll and Loader 2004):

30 $$\delta^{13}C_{cor} = \delta^{13}C_{plant} - (\delta^{13}C_{atm} + 6.4) \qquad (2)$$

31 with $\delta^{13}C_{plant}$ being the isotope ratio of the plant, $\delta^{13}C_{atm}$ being the isotope ratio of the atmosphere and -
32 6.4‰ corresponding to a preindustrial standard value.

33 Isotopic composition was also corrected to reflect rising atmospheric CO_2 concentrations since 1850
34 (reference period) following the method suggested by McCarrol et al (2009). This non-linear method aims
35 to extract low frequency variations in $\delta^{13}C$ series based on a theoretical plant's reaction to rising
36 atmospheric CO_2 (Lévesque et al. 2013). Corrected $\delta^{13}C$ series are hereafter referred to as $\delta^{13}C_{cor}$.

37

2.3.   Climate data

39 We used the 0.25°-gridded E-OBS dataset from EU-FP6 ENSEMBLES project. From this dataset, we
40 obtained series of daily minimum, maximum and mean temperatures along with cumulative daily
41 precipitation and daily average sea level pressure for the period 1950-2014. Monthly potential
42 evapotranspiration (PET) was derived from these data following the modified Hargreaves equation
43 (Droogers and Allen 2002). We chose the Hargreaves equation over the Thornthwaite method because is
44 it the best thermic formula (Choisnel et al. 1992) and its results are closer to those obtained from the
45 Penman-Monteith equation (considered as the reference) (Beguería et al. 2014).

46 Because our sites were located in contrasting climatic conditions (Table 1, Figure 2), we used both long-
47 term (averaged over the 1950-2014 period) and short-term water-balance indices. As a long-term index of
48 water availability, we used a simplified water balance calculated over the vegetation period (March -
49 September), WB$_{VP}$, defined as: total Precipitation over the vegetation period (P) – total Potential
50 Evapotranspiration over the vegetation period (PET) + Maximum Soil Water Available (SWA). Maximum
51 Soil Water Available (Forrester et al. 2017) is calculated from soil depth, soil water holding capacity
52 estimated from soil texture, and the amount of stones in the soil. To take into account short-term (inter-
53 annual) variations in water availability during the 1993-2014 period, we used the Standardized
54 Precipitation Evapotranspiration Index (SPEI). SPEI (Vicente-Serrano et al. 2010) is a (monthly) multi-scalar
55 index that can be calculated (integrated) over different time scales, and which can be used to determine

56   the onset, duration and magnitude of drought conditions with respect to normal conditions. The average
57   SPEI value over 1993-2014 was zero for each site. Positive values indicate above-normal wet conditions,
58   whereas negative values identify dry situations. SPEI values between -0.67 and 0.67 are considered
59   normal, values between -0.67 and -1.28 indicate moderate drought, and values <-1.28 indicate severe
60   drought (Isbell et al. 2015). SPEI was calculated over the second half of the vegetation period (June-
61   September) with the SPEI-package in R (R Core Team, 2014).

62

63   2.4.   Statistical analysis
64   2.4.1.   Explanatory analyses

65   First, linear regression models between SPEI and $\delta^{13}C_{cor}$ were performed on each site and each tree species
66   separately for the monospecific stands only. For five sites (Sp1 (1042), Sp2 (1041), Swe1 (1054), Lit1 (1051)
67   and Lit2 (1052)), the inter-annual variability of wood isotope composition could not be successfully
68   explained by SPEI, even when additional starting time and aggregation periods were considered (Figure
69   S1). No extreme average climatic conditions (e.g. extremely wet sites on which annual variations in climatic
70   conditions would have less impact) could explain this lack of response.

71   2.4.2.   Spatial and temporal variations in $\delta^{13}C$ in pure stands

72   Comparison of each species time-series pattern of reaction to environmental variations

73   First, we studied the stand characteristics and climate effects on $\delta^{13}C_{cor}$ series (1993-2014) and compared
74   the two species.

75   t-tests were used to test the significance of the difference between average $\delta^{13}C_{cor}$ values of both species
76   within each site. We then used a linear model to test the effect of characterization variables (see Table S4)
77   on those differences. An ln-transformation was used to reduce the heteroscedasticity of the residuals.

78   Next, we fitted linear mixed models for each species separately on corrected $\delta^{13}C_{cor}$ time series from the
79   pure stands, considering the site as a random factor:

80    $$\delta^{13}C_{cor} = \beta \times E + S(0, \sigma^2_{site}) + \varepsilon(0, \sigma^2_{\varepsilon})$$

81   where β is the vector of the fixed effects parameters, E is the matrix of the predictors of the fixed effects,
82   S the random factor characterized by the inter-site variance σ^2_{site} and ε is the error term. A series of
83   climatic variables, site and stand attributes (see full list in Table S4) and their interactions were used as
84   candidate variables for fixed effects. We used various selection procedures (Lasso, Elastic Net and stepwise
85   forward selection with Akaike Information Criterion (AIC) and Bayasien Information Criterion (BIC)) and
86   retained the variables selected by at least one method. Starting from the model with all selected variables,
87   the variables with the lower predictive power were progressively removed based on the likelihood ratio
88   test (Gonzalez de Andres et al. 2018; Zuur et al. 2009). Variance Inflation Factors (VIF) were calculated in
89   order to measure the degree of multi-collinearity of the variables. The low VIF values (<4) indicate that
90   multi-collinearity was not a problem (O'brien 2007).

91   In order to investigate whether the two species had a similar temporal response to environmental
92   fluctuations (synchronism), we also calculated correlation coefficients between the beech and pine time-

93   series of raw $\delta^{13}C_{cor}$ in pure plots, following del Rio et al. (2017). Values can range from -1 (complete
94   asynchrony of species response to environmental fluctuations) to +1 (complete synchrony).

95   **Comparison of species reaction to drought**

96   For each site, we selected one year that we called "characteristic year" because of its specific water
97   conditions (year with limited climatic water availability). We selected characteristic years in the following
98   manner. First, we selected the year with the lowest SPEI (June – September) values during the 1994-2013
99   period. Then, we checked that the SPEI value for the previous year had been normal or moderately wet/dry
100   (i.e. within the interval [-1.28 – 1.28]). If this specification was not met, we shifted to the year with the
101   second lowest SPEI value and started over. Selected characteristic years and their associated SPEI and P –
102   PET values are presented in Table S7.

103   Resilience component indices (resistance and resilience) were calculated to analyze tree reaction to
104   drought (Lloret 2011); we used differences in $\delta^{13}C_{cor}$ values between years of interest, as in Bonal et al.
105   (2017) and Weigt et al. (2015) instead of ratios. The resistance index is defined as the $\delta^{13}C_{cor}$ difference
106   between the wettest year preceding the drought and the drought year. The resilience index was calculated
107   as the $\delta^{13}C_{cor}$ difference between the wettest year preceding the drought and the wettest year after the
108   drought.

109   The resistance index should be negative since $\delta^{13}C_{cor}$ values are expected to rise during drought events.
110   The more negative the resistance index (low resistance), the higher the drought effect (stress). A resilience
111   value not significantly different from zero indicates that trees have a high capacity to return to pre-drought
112   $\delta^{13}C_{cor}$ levels after being subject to a drought event (high resilience). A negative value indicates low tree
113   resilience.

114   For each of these indices, we analyzed species-identity effects according to the following mixed model:
115   $$R_{ij} = (a_0 + a_{oj}) + a_1 \times Species\ identity + \epsilon_{ij}$$

116   where R_{ij} is the resilience component index (resistance or resilience) of species i at site j; a_0 and a_1 are the
117   fixed parameters of the model; a_{oj} is the random parameter associated to site j; and ε is the error term.
118   Species identity is a dummy variable with two levels (pine and beech). Site and stand characterization
119   variables (e.g. BA, altitude, WB_{VP}…) that could potentially influence R were also included as additional
120   variables in the model (Table S4).

121

2.4.3. Species-mixture effect on $\delta^{13}C$

123   The main questions we examine in this section are: *(i)* Is there a species-mixture effect on wood isotope
124   composition, and *(ii)* What is the influence of site and climate conditions on this potential species-mixture
125   effect?

126   For this analysis, we used raw (non-corrected) $\delta^{13}C$ series. We defined $\Delta\ \delta^{13}C$ as the difference in $\delta^{13}C$
127   between pure and mixed stands at a given site and for a given species. Using the difference in $\delta^{13}C$ values
128   from a same site cleaned the signal of long-term trends without any risk of removing information, as is
129   often the case when time-series correction procedures are used. t-tests were conducted on $\Delta\ \delta^{13}C$ time-
130   series for each site and both species in order to assess whether the average site $\Delta\ \delta^{13}C$ of each species was

131   significantly different from zero. t-tests were also conducted on Δ δ^{13}C data across all sites to test for a
132   global species-mixture effect for each species.

133   Linear mixed models were then fitted on the Δ δ^{13}C series of each species, following the same procedure
134   as previously explained for the $\delta^{13}C_{cor}$ time-series from the pure stands.

135   We also investigated the effect of species mixture on species asynchrony by analyzing the relationship
136   between correlation coefficients of beech and pine time series in pure and mixed stands.

137   In order to investigate the impact of mixing on tree resilience component indices for both species,
138   resistance and resilience indices were calculated in the mixed stands in the same way as in the pure stands.
139   Linear mixed models including a stand composition effect were then used to compare drought reaction in
140   pure and mixed stands for each species separately.

141
142    $$R_{ij} = \left(a_0 + a_{oj}\right) + a_1 \times Stand\ composition + \epsilon_{ij}$$

143   where R_{ij} is the resilience component index (resistance or resilience) of species i at site j; a_0 and a_1 are the
144   fixed parameters of the model; a_{oj} is the random parameter associated to site; and ϵ is the error term.
145   Stand composition is a dummy variable with two levels (pure and mixed).

146

2.4.4. Temporal constancy

148   Two types of indices were used to analyze the temporal constancy of carbon isotope series: *(i)* the
149   Temporal Stability index (TS – Equation 3), and *(ii)* sensitivity (Equation 4). TS is an indicator of the
150   dispersion of corrected δ^{13}C values with regard to the mean isotopic composition of the site, while
151   sensitivity is an indicator of the year-to-year variability of the time series.

152    $$TS = |\mu|/\sigma \quad (3)$$

153    $$Sensitivity = \frac{\overline{\sum_{i=1}^{n-1}|S_{i+1}|}}{n-1} \quad (4)$$

154   where μ is the mean of the corrected δ^{13}C series; σ is its standard deviation; n is the year; and $S_{i+1} = (\delta_{i+1} -$
155    $\delta_i)$ and δ_i are the corrected isotope values (Saurer et al. 1997).

156   We used mixed effects models with site as a random intercept to test the species-mixture effect on these
157   two indices, as follows:

158    $$TC_{ij} = \left(a_0 + a_{oj}\right) + a_1 \times S + \epsilon_{ij}$$

159   where TC_{ij} is the temporal constancy index (temporal stability or sensitivity) of species i at site j; a_0 and a_1
160   are the fixed parameters of the model; a_{oj} is the random parameter associated to site; S is a dummy
161   variable with two levels (pure/mixed); and ϵ is the error term. Site characterization variables (e.g. BA,
162   altitude, WB_{VP} …) that could potentially influence R were also included as additional variables in the model
163   (Table S4).

164   All statistical analyses were conducted with the R software, version 3.4.1 (R Core Team, 2014). Mixed
165   models were fitted with the package "nlme".

166

3. Results

3.1. Spatial and temporal variations in δ¹³C in pure stands

3.1.1. Comparison of time-series patterns of each species and impact of environmental conditions

In general, Scots pine reached higher (less negative) mean isotope ratio values than did beech (Figure 3). Average beech and pine $\delta^{13}C_{cor}$ values across all sites were -25.3‰ and -23.7‰ respectively. The range of site average values were [-27.9‰ to -22.2‰] for beech and [-26.0‰ to -21.1‰] for pine. With the exception of Pol1, average $\delta^{13}C_{cor}$ values were always significantly lower for beech than for pine (Table S6), but the magnitude of the difference between species was site-dependent with values ranging from 0.25‰ (Pol1) to 3.23‰ (Lit2). None of the variables tested in the linear model (Table S4) had a significant effect on this difference (data not shown).
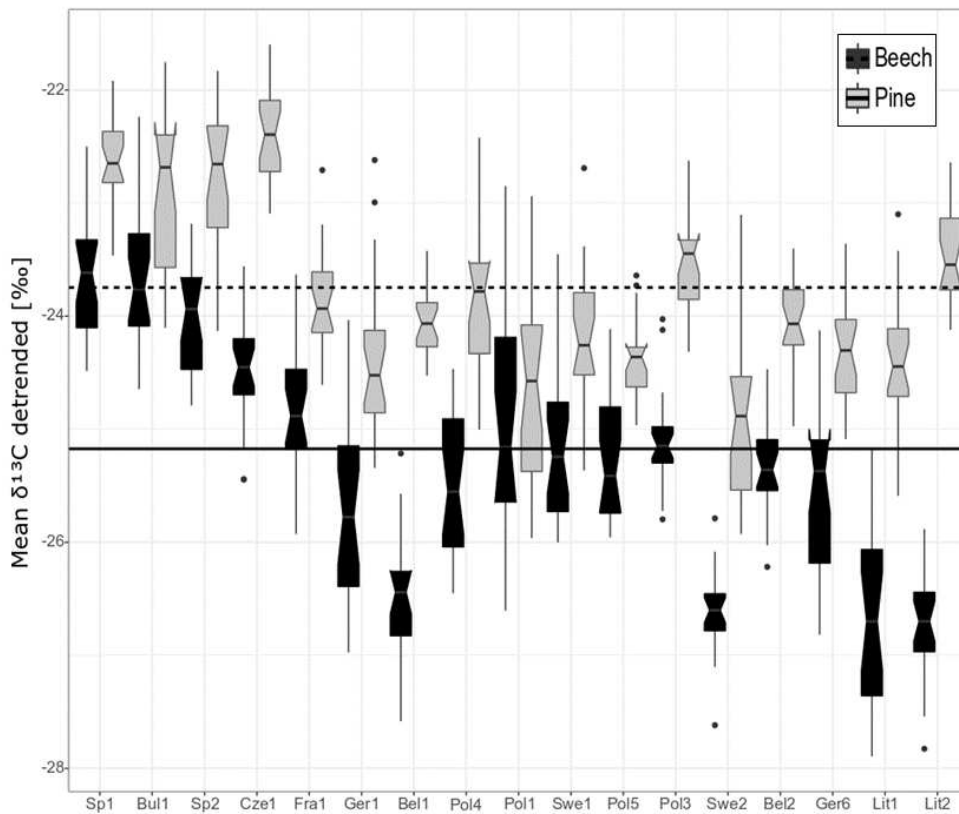

Fig. 3 *Mean $\delta^{13}C_{cor}$ values for each site and each species in the pure stands. Horizontal bars represent the median; notches in the boxes indicate the confidence interval for comparing medians. Upper and lower hinges on the boxes indicate the 25th and 75th percentiles; whiskers extend from the hinges to the largest value no further than 1.5 x the interquartile range. The horizontal bars (dashed: Pine, plain: Beech) represents average values for all sites considered. Sites are shown by increasing value of mean water resources (WBVP calculated on the approximate vegetation period (March-September) and averaged over the 1950-2014 period and over the two types of stands (pure beech and pure pine))*
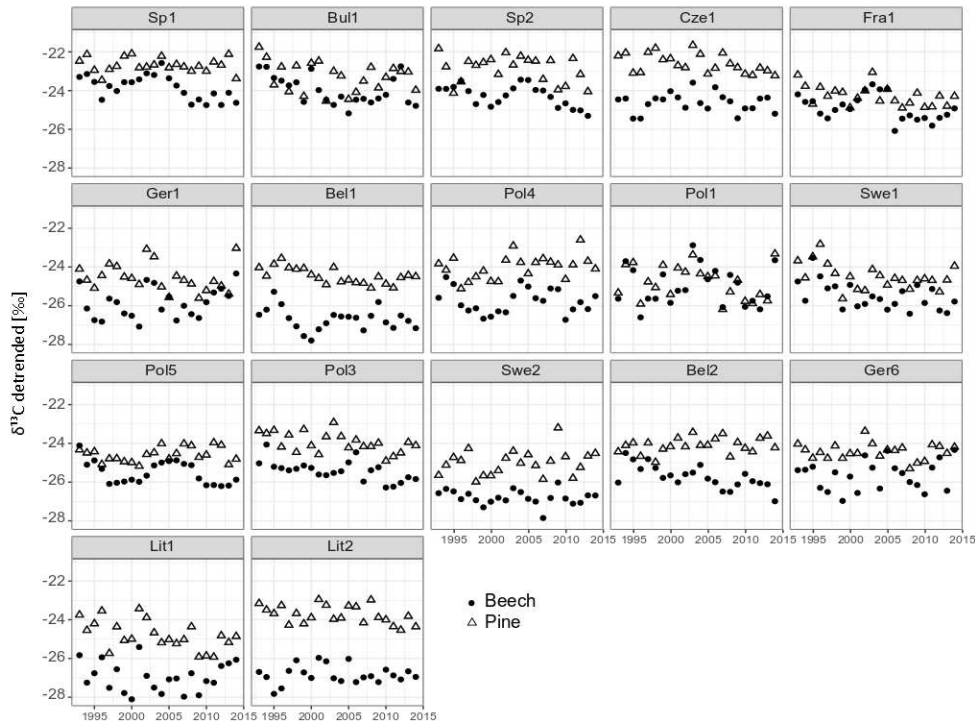
Fig. 4 Time series of carbon isotopic ratios for both species and every study site in the pure stands. Study sites are ordered by increasing value of mean water resources (WB$_{VP}$ calculated on the approximate vegetation period (March-September) and averaged over the 1950-2014 period and over the two types of stands (pure beech and pure pine))

On most sites, there was visual coherence between the time-series of both species (Figure 4). The most notable exception was Bel1 where a significant drop in δ^{13}C$_{cor}$ occurred for beech around 1995-2003 but not for pine. This global coherence between the beech and pine time-series was confirmed by the correlation coefficients, even though there was a large range of variation in the correlation values (Table S5, Figure 6). Sites with a lower level of correlation between the two species' time-series are well distributed along the gradient of average water availability (sites with WB$_{VP}$ ranging from -249 to 632 mm while water availability across the whole gradient ranged from -366 to 632 mm).

Linear mixed models adjusted on each species δ^{13}C$_{cor}$ time-series highlighted a significant, negative effect of SPEI $_{June-September}$ on δ^{13}C$_{cor}$ for both beech and pine (Table 2). In pine stands, this effect was dependent on basal area only, while in beech stands, it was dependent on basal area, WB$_{VP}$ and slope (Table 2). In pine stands, higher basal area was associated with a more negative slope of the δ^{13}C$_{cor}$/SPEI relationship. In beech stands, higher basal area, lower WB$_{VP}$ and less steeper stand slopes were associated with a more negative slope of the δ^{13}C$_{cor}$/SPEI relationship.

Only beech showed a significant influence of WB$_{VP}$ on isotopic composition. This influence followed the expected pattern; i.e. higher values of average water resources were related to lower δ^{13}C$_{cor}$ values.

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Species	R^2m	R^2c	Fixed effects	parameters	p-values
Scots pine	0.2634	0.7043	Intercept	-23.812	<.001
			SPEI June-September	-.220	<.001
			Basal area	.023	.15
			WB_{VP}	-.001	.10
			SPEI June-September x Basal area	-.005	.042
European beech	0.5300	0.7603	Intercept	-25.336	<.001
			SPEI June-September	-.371	<.001
			Basal area	-.002	.91
			Slope	.017	.30
			WB_{VP}	-.003	.005
			SPEI June-September x WB_{VP}	.001	<.001
			SPEI June-September x Basal area	-.009	.024
			SPEI June-September x Slope	.016	<.001

214

215

3.1.2. Comparison of species response to drought

217 Pine displayed a negative index for resistance to drought, indicating that drought significantly affected the
218 physiological functioning of the pine trees in pure stands. This effect was not significant for beech (p-value
219 = .07). The resilience index was not significantly different from 0 for pine but was significantly positive for
220 beech (Table 3 and Figure 7). No effects of site or of stand characterization variables were found except
221 for the beech resilience index, which was significantly influenced by stand age (estimate = -0.022; p-value
222 = .00) and site WB_{VP} (estimate = 0.002; p-value = .01).

223

224

| Resilience components	Species	Estimate	Std. err.	P value
Resistance index	Beech	-.441	.226	.07
	Pine - Beech	-.096	.163	.56
	Pine	-0.537	.226	.03
Resilience	Beech	.397	.164	.03
	Pine - Beech	-.208	.214	.34
	Pine	.189	.164	.27

228

229 3.2. Species-mixture effects on $\delta^{13}C$

230 For beech, seven sites showed no significant species-mixture effect on $\delta^{13}C$, while two showed a negative
231 effect and eight showed a significant positive effect (lower $\delta^{13}C_{raw}$ values in mixed stands compared to
232 pure ones) (Figure 5). The mean $\Delta \delta^{13}C$ across all sites was significantly positive (value = 0.3183, p-value =
233 <.001).

234 For pine, eight sites showed a significant negative effect of species mixture, five showed a significant
235 positive effect and four showed no significant effect (Figure 5). The mean $\Delta \delta^{13}C$ across all sites was
236 significantly negative (value = -0.1080, p-value = .01).

237 Four sites showed positive species-mixture effects for both species and two showed negative effects for
238 both species. When species-mixture effect was positive for pine, it was either also positive for beech (four
239 sites) or neutral (no significant species-mixture effect; one site), but never negative. On the other hand,
240 when species-mixture effect was positive for beech, it was positive (four sites), negative (three sites) or
241 neutral (one site) for pine. Three sites also displayed a negative species-mixture effect for pine but no
242 significant effect for beech, and three sites displayed no significant species-mixture effect for either
243 species (Figure S2).

244
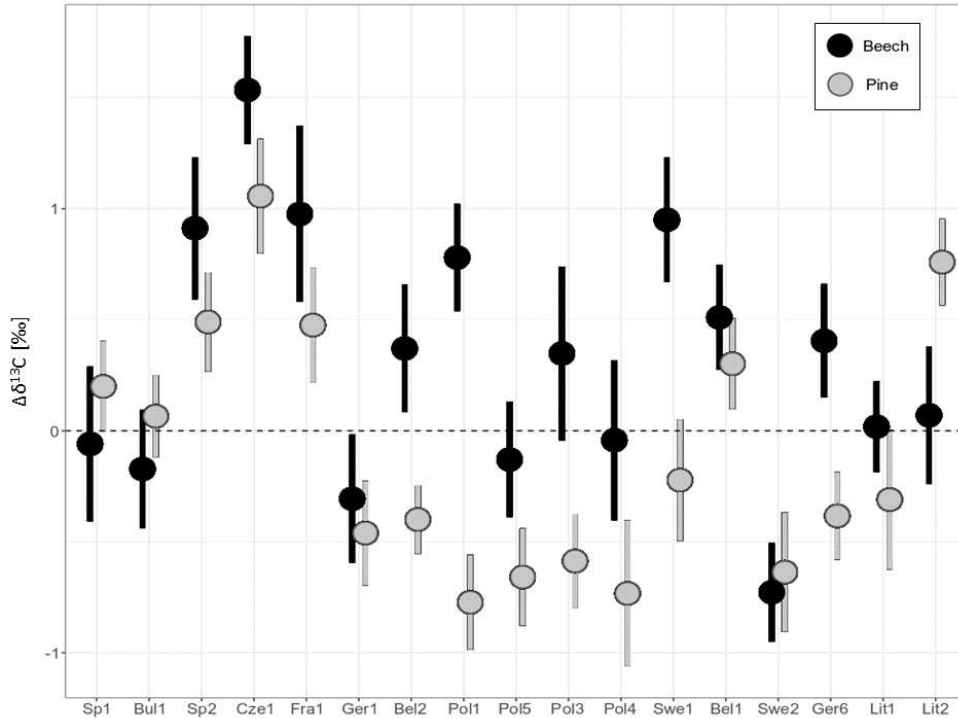
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250

251 Looking at the drivers behind the temporal and spatial patterns of mixture effects (Table 4), we found that
252 beech $\Delta \delta^{13}C$ was not influenced by any of the site or stand characterization variables, but that SPEI had a
253 significant positive effect. Between-site variability of pine $\Delta \delta^{13}C$ was linked to WB_{VP} and to mean age of
254 the stand (the $\Delta \delta^{13}C / WB_{VP}$ relationship becoming less negative as age increased). No annual climatic
255 variable successfully explained the species-mixture effect on pine (Table 4).

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265 **Table 4** *Parameter estimates, p-values and r-squared for the linear mixed models adjusted on the 1993-2014 series of raw*
266 $\delta^{13}C_{pure\ stands}$ – raw $\delta^{13}C_{mixed\ stands}$. *For both models, we used site as the random intercept. Marginal R-squared (R^2m) represents*
267 *the variance explained by fixed factors. Conditional R-squared (R^2c) represents the variance explained by both fixed and random*
268 *factors (whole model). WB_{VP} is the average water balance over the vegetation period (precipitation + potential available soil*
269 *water – potential evapotranspiration) calculated over the period 1950-2014*

Species	R^2m	R^2c	Fixed effects	parameters	p-values
Scots pine	0.2373	0.5433	Intercept	-.5322	.16
			WB_{VP}	-.0062	<.01
			Age	.0029	.56
			SPEI $_{June-September}$	-.0264	.37
			Age x WB_{VP}	.0001	<.01
European beech	0.0289	0.4381	Intercept	.3472	.01
			WB_{VP}	-.0005	.36
			SPEI $_{June-September}$	.0820	.02

270

271

272 There was no significant difference in correlation coefficients between the $\delta^{13}C_{raw}$ time series for beech
273 and pine in pure and mixed stands (Figure 6), thus indicating that species mixture did not change the
274 synchrony of the two species' reactions to environmental fluctuations.
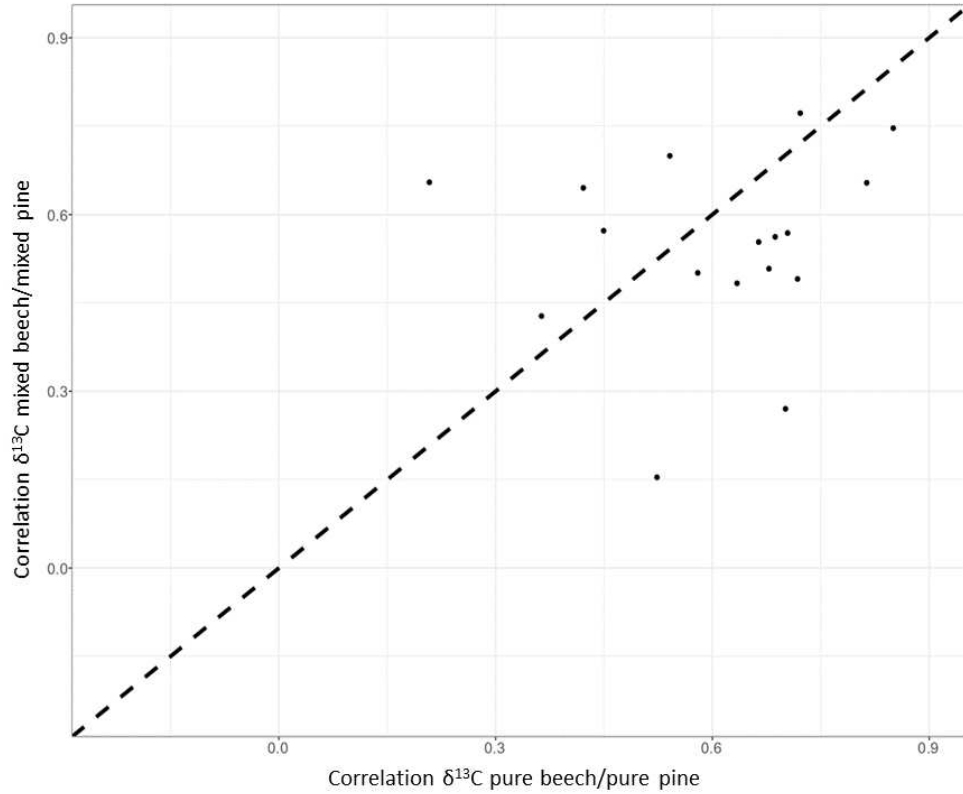
275

276   ***Fig. 6*** *Relationship between correlation coefficients of the species δ13C$_{raw}$ series in pure and mixed stands*

277

278   There was no significant mixture effect on either resistance or resilience, for either of the species
279   (Table 5, Figure 7).

280   ***Table 5*** *Parameter estimate, standard error and p-values for the models testing for species-mixture effects on resilience component*
281   *indices. Pure is the value estimated for pure stands, mixed - pure is the difference between mixed and pure stands*

Resilience components	Species	Stand	Estimate	Std. err.	p-value
Resistance index	Beech	Pure	-.442	.290	.15
		Mixed - pure	-.211	.253	.42
		Mixed	-.652	.290	.04
	Pine	Pure	-.537	.177	.01
		Mixed - pure	-.122	.172	.49
		Mixed	-.659	.177	.00
Resilience index	Beech	Pure	.397	.208	.07

	Mixed - pure	-.300	.239	.23
	Mixed	.097	.208	.646
Pine	Pure	.189	.122	.14
	Mixed - pure	-.126	.172	.48
	Mixed	.063	.122	.61

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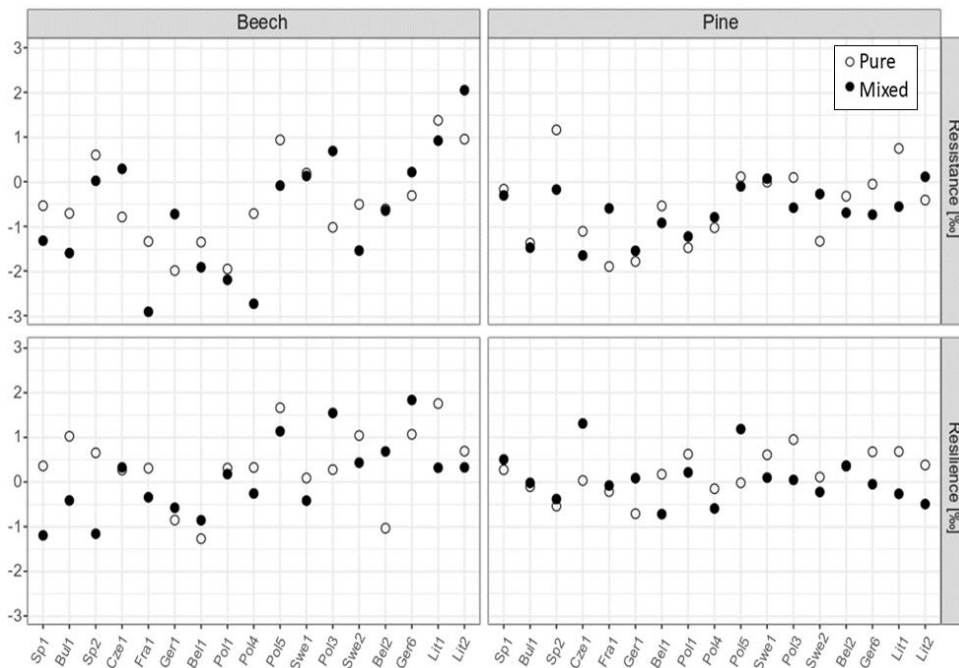
Fig. 7 *Resilience component indices (Resistance: upper panel, Resilience: lower panel) for pure (++) and mixed (==) stands of both species (Beech: left panel, Pine: right panel). Study sites are shown in increasing order of average water resources (WB$_{VP}$) over the 1950-2014 period*

287

3.3. Temporal constancy

Temporal stability and sensitivity values are shown in Table S3. No significant difference of temporal stability between pure and mixed stands was found (Table 6). Climatic variables (average WB$_{VP}$ and average temperature over the period 1993-2014) did not explain the variability of temporal stability between sites. Older pine stands tended to be more stable than younger ones.

No mixture effect was found on sensitivity (Table 6). No climatic or site characterization effect was found to explain variability in sensitivity (Table 6).

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Table 6 *Parameter estimates, p-values and R-squared for the linear mixed models adjusted for temporal stability and sensitivity values. Site is used as the random intercept. Marginal R-squared (R²m) represents the variance explained by fixed factors. Conditional R-squared (R²c) represents the variance explained by both fixed and random factors (whole model)*

	R^2m	R^2c	Species	Fixed effects	parameters	p-values
Temporal stability	0.0458	0.2716	Beech	Intercept	45.2748	.00
				Stand composition (mixed)	-3.9306	.36
	0.3415	0.4464	Pine	Intercept	26.2478	.00
				Age	.3133	.00
				Stand composition (mixed)	4.0479	.31
Sensitivity	0.0056	0.1625	Beech	Intercept	.6650	.00
				Stand composition (mixed)	-.0668	.65
	0.0389	0.5919	Pine	Intercept	.6251	.00
				Stand composition (mixed)	-.1748	.10

4. Discussion

3.2. Spatial and temporal variation of $\delta^{13}C$ in pure stands

Carbon isotope composition in tree rings was systematically higher in pine than in beech (Figure 3), pointing to greater intrinsic water use efficiency for pine compared to beech; this is consistent with previous studies (Daux et al. 2018; Hemmings et al. 1998; Szczepaneck et al. 2006). Several explanations for these differences are possible. Firstly, because of differences in physiological or morphological characteristics (such as higher light availability associated with lower light interception in pine stands due to a less dense canopy), the carbon uptake (*A*) is higher in pine, thus leading to increased $\delta^{13}C$. Daux et al. (2018) recently discarded this explanation as a cause for the observed difference in isotopic composition between beech and pine because conifers usually have lower *A* than broadleaved trees. However, Medlyn et al. (1999) report a higher potential electron rate and maximum rate of Rubisco activity for pine compared to beech, suggesting that this general rule of lower *A* for conifers than for broadleaves might not hold true for pine and beech. The difference in $\delta^{13}C$ levels between the two species could also be explained by lower stomatal conductance (g_s) in pine. Lower g_s could originate either as a direct effect of morphological characteristics (e.g. lower stomatal density, smaller stomata), or as an indirect effect of ecological functioning. Indirect effects include *(i)* lower leaf area index in pine stands leading to higher evapotranspiration from the soil and the understory (Daux et al. 2018); and *(ii)* lower access to belowground water reserves due to shallower rooting (Daux et al. 2018). These indirect effects tend to reduce water availability in pine stands. However, if indirect effects do indeed prevail, we would expect the difference in $\delta^{13}C$ between species to be lower or, even, to disappear when water availability is higher.

321   We did not observe any such pattern leading us to think that the difference in $\delta^{13}C$ between species is
322   probably due to an effect either of light interception or of difference in stomatal characteristics of beech
323   and pine.

324   We predicted that more severe water-limiting periods (low SPEI) would result in less negative $\delta^{13}C_{cor}$
325   values for both species thus explaining a significant part of the temporal variation of $\delta^{13}C_{cor}$ (Roden et al.
326   2005; Saurer et al. 1995; Warren et al. 2001). This turned out to be the case in our study as our data
327   showed that pine and beech $\delta^{13}C_{cor}$ were significantly influenced by water availability during the last part
328   of the vegetation period (Table 2). These results are consistent with previous studies and with physiological
329   models of the response of isotopic discrimination and water use efficiency during carbon assimilation
330   under soil drought conditions (Farquhar et al. 1989). Saurer et al. (2008) found that $\delta^{13}C$ chronologies of
331   pine and beech were negatively correlated with precipitation on non water-limited sites, while Gonzalez
332   de Andres et al. (2018) found a negative influence of water balance (P – PET over the summer) on $\delta^{13}C_{cor}$
333   for climatically contrasting sites

334   We also highlighted a drought effect on pine $\delta^{13}C_{cor}$ by analysing the tree's reaction to characteristic years
335   (Table 3, Figure 7). For beech, this effect was non-significant, but by a very slight margin. However, Figure
336   7 showed that on drier sites, beech was almost systematically affected by drought. We conclude that the
337   larger amount of water available on wetter sites is enough to dampen the drought effect. This difference
338   in drought reaction between dry and wet sites was not observed for pine. We attribute this to the fact that
339   Scots pine is a "drought-avoiding" species, which closes its stomata quickly during water shortages to avoid
340   damage to the conductive system (Cochard 1992; Martínez-Vilalta et al. 2004). This drought avoidance
341   strategy is common in conifers (especially *Pinus* species), which tend to have lower embolism resistance
342   than angiosperms (Martínez-Vilalta et al. 2004; Choat et al. 2012). Beech, on the other hand, is more
343   anisohydric (Pflug et al. 2018; Schäfer et al. 2017). However, we found no significant difference in
344   resistance values between the two species when considering the whole dataset. This could indicate that,
345   while pine reacts quicker than beech to drought, both species end up being affected in a similar way during
346   extreme events.

347   Beech resilience, for its part, appears to be influenced by average site water availability and stand age
348   (increasing level of resilience with increasing site WB_{VP} and decreasing age). One possible explanation for
349   the WB_{VP} effect is that higher water reserves in sites with higher WB_{VP} could dampen the effects of a
350   punctual drought. We did not find any lasting effect of drought on tree functioning as both species were
351   able to return to pre-drought levels of carbon isotope composition after the extreme event.

352   The $\delta^{13}C_{cor}$ time-series for both species were coherent within a site (Figure 4, Table S5); this indicates that,
353   as expected, both species faced similar environmental fluctuations, and that their response to those
354   temporal fluctuations was similar. There were, however a few exceptions. In most cases, those exceptions
355   were linked to the long-term trend in the $\delta^{13}C_{cor}$ time-series of one of the two species, thus decoupling
356   pine and beech $\delta^{13}C_{cor}$ values. For instance, such an effect can be seen in the decreasing trend in beech
357    $\delta^{13}C_{cor}$ series at Bel2 or in the drop in beech $\delta^{13}C_{cor}$ values around 1995-2003 at Bel1 (Figure 4). The
358   considerable length of those trends suggest that they are not of climatic origin but are probably rather due
359   to changes in stand characteristics (e.g. changes in access to light, management effect) or to tree
360   weakening (dieback), which could have influenced the physiological functioning of the trees. Such long-
361   term effects aside, short-term (climatic) variations seem similar for both species. In addition, as previously
362   explained, we found that inter-annual variations in $\delta^{13}C_{cor}$ values for both species were influenced by the

363   same climatic variable: a climatic water balance (Table 2) and that their reaction to climatic events were

364   similar (Table 3). Any species-mixture effect on carbon isotope composition stability would therefore not

365   be caused by asynchrony in species response to environmental conditions, unless mixing induced a

366   decoupling of the species reaction to environmental fluctuations in pure and mixed stands.

367   Contrary to what we had hypothesized, spatial variation of pine $\delta^{13}C_{cor}$ was not driven by the

368   average site water availability. We suppose this is due to the non-linear pattern of variation in average δ

369     $^{13}C_{cor}$ along the water availability gradient (Figure 3). Indeed, because of this non-linearity, the relationship

370   between the average $\delta^{13}C_{cor}$ and WB_{VP} was non-significant, even though dry sites clearly displayed higher

371     $\delta^{13}C_{cor}$ values. On the other hand, the hypothesis of higher $\delta^{13}C_{cor}$ levels in drier sites was verified for beech

372   stands (Figure 3, Table 2).

373   However, it is important to note that spatial and temporal variations of carbon isotope

374   composition are not independent of each other. Indeed, we found that for beech, due to the SPEI/WB_{VP}

375   interaction, the WB_{VP} effect on $\delta^{13}C_{cor}$ disappeared during extremely wet years (SPEI >3), but held in other

376   situations. Saurer et al. (1995) found a similar increase in $\delta^{13}C_{cor}$ values for pine and beech on drier sites in

377   Switzerland. The absence of any significant influence of the interaction term "SPEI $_{June\text{-}September}$ x WB_{VP}" on

378   pine $\delta13C_{cor}$ suggests the existence of local adaptation mechanisms as well as long-term genetic

379   divergence within species; this means ecotypes vary in functional traits, as previously proposed by Weigt

380   et al. (2015) and Härdtle et al. (2013). We also found that the inter-annual variation in $\delta^{13}C$ was influenced

381   by stand variables (basal area for pine, and basal area and slope for beech). Basal area in both pine and

382   beech stands (and lower WB_{VP} in beech stands), could have been "aggravating factors" as they induce a

383   higher sensitivity of $\delta^{13}C_{cor}$ to annual water balance (more negative $\delta^{13}C_{cor}$/SPEI slope). The aggravating

384   effect of basal area can probably be linked to increased competition among trees for soil water, and low

385   WB_{VP} is likely to be correlated to higher sensitivity to annual variations in the water balance. Surprisingly,

386   stand slope did not have such an aggravating effect on the $\delta^{13}C_{cor}$/SPEI relationship in the pure beech

387   stands. Indeed, a site with a more pronounced slope should be more sensitive to inter-annual variations

388   in the water balance (because of increased runoff), yet this was not the case. Slope aspect undoubtedly

389   plays a significant role in this slope/ $\delta^{13}C_{cor}$ relationship.

390   An important point to make is that, as explained earlier, $\delta^{13}C_{cor}$ did not respond similarly to annual

391   water balance at all the sites (Figure S1). None of the site, stand or climate characterisation variables were

392   able to explain this variability in the $\delta^{13}C_{cor}$/SPEI relationship. SPEI$_{June – Septembre}$ was chosen because *(i)*

393   during this period, the $\delta^{13}C_{cor}$/SPEI relationship is most intense, and *(ii)* the last third of the growth ring is

394   likely made during this period. However, using only one annual climatic water balance variable (SPEI$_{June –}$

395     $_{Septembre}$), despite the fact that the different sites did not respond in the same manner to annual water

396   balance, may be one reason why the models do not perfectly capture the inter-annual variability of $\delta^{13}C_{cor}$.

397   It is also interesting to note that, despite the noise associated with $\delta^{13}C_{cor}$/SPEI variability, the annual water

398   balance had a significant effect, both alone and through interactions with other variables on $\delta^{13}C_{cor}$, thus

399   highlighting the importance of water availability in the processes at play.

400

401 **3.3.   Species-mixture effects on $\delta^{13}C$**

402   One major result of our study is that species-mixture effect on $\delta^{13}C$ differed between the two

403   species and that the difference depended on average water availability level (Fig. 5 and Table 4.). We relate

the difference in species-mixture effect to the differences in behavior the two species displayed in pure plots.

On *wet sites* (sites with a consistently positive water balance, sites with permanent available belowground water resources) species-mixture effect on $\delta^{13}C$ should be close to zero on average, that is if the species-mixture effect is indeed mainly due to water-related mechanisms. If the species-mixture effect differs from zero, then other mechanisms should be considered. A key mechanism influencing $\delta^{13}C$ values, and therefore $\Delta \delta^{13}C$, is the access to light (Ehleringer et al. 1986; Farquhar et al. 1989). Our results showed a high variability of $\Delta \delta^{13}C$ in wet sites (Bel2, Swe2, Ger6 and Lit2), which could be due to a species-mixture effect on light availability. We used delta height (the difference between the height of the cored target-species trees in mixed stands and the mean height of the mixed stand) to investigate the potential effect of light interception on $\Delta \delta^{13}C$. However, light interception did not fully explain $\Delta \delta^{13}C$ deviation from zero on very humid sites. Indeed, some sites for which access to light did not differ between pure and mixed stands also displayed significant $\Delta \delta^{13}C$ deviation from zero and vice versa (we found differences in access to light but no significant $\Delta \delta^{13}C$ deviation from zero). On *moderately wet sites* (average WB_{VP} close to zero), the same consideration holds (species mixture effect close to zero), on the condition that the addition of a second species does not influence water availability (increased belowground competition in mixed stands compared to pure ones). If this is the case, species-mixture effect could be negative for one or both species, depending on their ecophysiological characteristics. On this type of site, we found a high variability in beech $\Delta \delta^{13}C$, suggesting the influence of non-water-related mechanisms as stated earlier. For pine, $\Delta \delta^{13}C$ was consistently negative. Indeed, the models adjusted on data from pure stands showed that the two species displayed systematic differences in their $\delta^{13}C$ levels. This systematic difference is indicative of a difference in the compromise strategies of the two species between carbon uptake and water loss. If this is the case, we could conclude that, in moderately wet sites (theoretically non-stress sites), adding beech would induce a stress on pine consistently to previous findings (Gonzalez de Andres et al. 2018). On *dry sites*, species mixture effect can be positive (see Forrester and Bauhus 2016) (i) if species mixture has an influence on water availability, (ii) if this influence is large enough to affect carbon isotope composition, and (iii) if potential negative species-mixture effects (competition) are lower than the positive effects. We found that species-mixture effect tends to be positive for both species on dry sites (SP2, CZE1, FRA1) but, as we move towards *extremely dry sites* (SP1, BUL1), this positive effect seems to disappear. This is probably indicative of the fact that the positive species-mixture effect on water availability is not strong enough to compensate for the increasing environmental constraint. While this seems contradictory to the expected trend in species mixture effect along the gradient of environmental conditions (such as the one proposed by Forrester and Bauhus 2016), a possible decrease in the positive effects of species mixture in extremely harsh situations is not a new idea (Maestre and Cortina 2004; Tielborg and Kadman 2000). Holmgren and Scheffer (2010) theorized the idea of a positive species-mixture effect with a bell-curved shape along a gradient of environmental stress.

Our models for pine highlighted the role average site water balance plays in the species-mixture effect (Table 4). Average site water balance effect depended on the mean age of pine in pure and mixed stands since, in older stands, the slope of the $\Delta \delta^{13}C/WB_{VP}$ relationship was less negative. We should eliminate two unlikely causes of age effect in mature stands such as the ones used in this study: (i) vegetation growing close to the forest floor using air with increased $^{12}C/^{13}C$ ratio due to respiration (McCarroll et al. 2004), and (ii) variation of bark refixation of respired CO_2 as bark is usually too thick in mature stands for bark refixation to play a major role (McCarroll et al. 2004). It is possible, however, that this age effect was

447 confounded with the effect of height, considering that using mean stand height instead of age as a variable
448 only slightly decreases the performance of the model. Our results showed that species mixture had a less
449 contrasted effect between wet and dry sites for beech than for pine. This is likely due to beech's more
450 intense competitive nature (Gonzalez de Andres et al. 2018). Our model also highlighted an annual water
451 balance (SPEI) effect on beech Δ δ^{13}C, which suggests that complementarity effects mainly express
452 themselves during wet years. Our results also indicate that species-mixture effect on pine is not influenced
453 by either annual climatic variable (SPEI, temperature). This suggests that, when considering a large scale,
454 variations in complementarity for pine are driven mostly by spatial fluctuations, but very little by temporal
455 variations in environmental factors.

456   It is interesting to note that, with data from the same network, del Rio et al. (2016) highlighted a
457 positive species-mixture effect on growth at the population level for beech, and a negative one for pine.
458 Water-related mechanisms could be good explanatory candidates for between-site variability in over-
459 yielding, given the patterns of species-mixture effect on δ^{13}C found in the present study.

460   It is important to note that our models explain only a small part of the system variability, especially
461 for beech. This is at least partly because variability in time-series of wood isotopic composition cannot be
462 exclusively associated with water-related mechanisms, since non-water-limiting years were included in
463 the series. Indeed, variability in wood isotopic composition is the result of a complex balance of water-
464 and non-water-related mechanisms (e.g. mechanisms influencing the rate of net photosynthesis). Another
465 possible explanation for the small part of the total variability explained by our models may be that our
466 analyses of the species-mixture processes were mostly based on a linear approach (see, for instance, the
467 framework proposed by Forrester and Bauhus (2016)). The species-mixture effect presented in this study
468 may be indicative of a more complex structure with threshold points (Figure 5). These threshold points
469 could correspond to the level of average site water availability where beech starts to regulate its water
470 consumption (Figure 3), thus reducing competition and inducing a switch from negative to positive species-
471 mixture effect in pine.

472   The lack of any significant mixture effect on tree response to drought stress across the gradient
473 (Table 5, Figure 7) indicates that species mixture does not influence the drought reaction of either species.
474 Pure plots displayed higher δ^{13}C levels under more intense water-limiting conditions, and mixed stands
475 also had a similar behavior. This is consistent with the growing body of literature on the subject, which
476 reports that species mixture does not always improve reaction to drought (Bonal et al. 2017; Forrester et
477 al. 2016; Grossiord et al. 2014), although this may indeed be the case in certain situations (Grossiord et al.
478 2015; Lebourgeois et al. 2013; Pretzsch et al. 2013). Our study is representative of the inconsistent results
479 in the literature for mixed stands' reaction to drought (Figure 7) since we were not able to find any distinct
480 pattern in the differences between pure and mixed beech resistance or resilience. Indeed, while most sites
481 showed a strong difference in index values between pure and mixed stands, the effect could be positive
482 or negative. For pine, however, the difference between indices in pure and mixed stands was less
483 pronounced, aside from a few exceptions (SP2, FRA1, SWE2 and LIT1). Inspection of Figure 7 suggests that
484 two of these sites have higher resistance values in pure stands, while the opposite is observed for the
485 other two (mixed stands had lower δ^{13}C values during drought). Such differences in species-mixture effect
486 could be due to differences in competition levels between pure and mixed stands (e.g. increased
487 competition for water in mixed stand). However, density alone cannot explain species-mixture effect since
488 the difference of resistance between pure and mixed stands had the same direction (lower resistance in
489 mixed stands) for site SP2 (lower BA in the mixed stand) and for site LIT1 (higher BA in the mixed stand).

490   Competition for light could explain part of the effect since light is known to influence tree carbon isotope
491   composition (Francey et al. 1985). We used differences in mean height between the trees of the two
492   species to explore such aboveground competition, but found no consistent relationship with resistance.

493   There was no significant difference in the correlation between the two species in mixed and pure
494   stands, indicating that species mixture did not induce a decoupling of the species reaction to
495   environmental fluctuations. Therefore, positive or negative species-mixture effects on productivity or on
496   the stability of productivity were not caused by an asynchronous species response to environmental
497   fluctuations, contrarily to what Loreau and de Mazancourt (2008) and Hector et al. (2010) found.

498

499   3.4.   Temporal constancy

500   We did not find any significant effect of stand composition on temporal stability (TS) of ecosystem
501   properties (Table 6). A species-mixture effect could be caused either by a differential response (sensitivity
502   to different parameters or differential temporality of the response) of each species to environmental
503   changes (Loreau and de Mazancourt 2008; Hector et al. 2010), or by reduced competition in mixed stands
504   compared to pure ones (leading to a higher mean level of the ecosystem property in question, Tilman
505   1999). The similar behaviour of beech and pine in our study (sensitivity to the same climatic variable (SPEI),
506   strong correlation between species $\delta^{13}C_{raw}$ time-series) is coherent with an absence of significant species-
507   mixture effect on temporal stability.

508   Differential species response to environmental changes can also reduce inter-annual variability
509   (sensitivity) of the ecosystem properties through a reduction in competition. We did not find any
510   significant effect of stand composition on sensitivity (Table 6) because of the similarity in species response
511   to environmental fluctuations. Species mixture therefore did not influence either sensitivity or temporality
512   of carbon isotope composition at the species level.

513   The diversity-stability relationship is not a trivial one. Contrasting results have been reported, from the
514   total absence of a stabilizing effect in single-trophic communities (Jiang and Pu 2009) to higher stability in
515   mixed forests (Jucker at al. 2014). It is currently becoming more and more accepted that diversity improves
516   stability at the community level but decreases stability, or does not affect it, at the species level. Del Rio
517   et al. (2016) recently highlighted the stabilizing/destabilizing pattern for productivity in mixed pine/beech
518   stands across Europe. Although water is often considered a main factor of resource-driven effects, we
519   found no clear stabilizing/destabilizing species-mixture effect on water-related processes at the species
520   level.

521

522   4. Conclusion.

523   We conclude from the present study that Scots pine and European beech present different levels of
524   average $\delta^{13}C$ values indicative of the compromise between CO_2 assimilation and H_2O loss, but that the
525   spatial and temporal variations in their $\delta^{13}C$ values are similar.

526   Species mixture leads to contrasted effects on beech and pine carbon isotope composition (a slightly
527   positive effect for beech and no significant effect for pine) when the whole gradient of water availability
528   is taken into account. The global pattern of species-mixture effect along this gradient is consistent with

529 some theories (such as the framework proposed by Forrester and Bauhus 2016): an increasingly positive
530 species-mixture effect on drier sites until the drought constraint becomes too great for the species-mixture
531 effect to compensate. However, we found that this pattern is not linear and that the species-mixture effect
532 appears at certain threshold points. Intrinsic species characteristics concerning water-related processes
533 play a critical role in species-mixture effect, especially at moderately wet sites. A combination of the
534 difference in the two species' CO_2/H_2O compromise and average environmental conditions in terms of
535 water availability therefore determines the balance between competition and complementarity in mixed
536 stands. No species-mixture effect on drought resistance was found, in accordance with the growing body
537 of literature on this topic.

538

546
Author's contributions
548 G.d.S, D.B. and Q.P. conceived the ideas and designed methodology; all authors contributed to data
549 collection; G.d.S, D.B. and Q.P. analysed the data and led the writing of the manuscript; All authors
550 contributed to the drafts and gave final approval for publication.

551

552
553 **Conflict of interest** The authors declare that they have no conflict of interest.

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Country	Stand	Triplet name	Longitude	Latitude	Elevation (m)	M	P$_{VP}$	SWA	WB$_{VP}$
Spain	PB	Sp1	03°10'19.00"	42°05'57.00"	1293	46	351	98	-347.0
	PP							30	-415.0
	M							108	-337.0
Bulgaria	PB	Bul1	23°21'03"	41°53'43"	1187	47	331	90	-262.3
	PP							90	-262.3
	M							90	-262.3
Spain	PB	Sp2	02°15'44.23"	42°10'18.09"	1116	61	371	84	-248.8
	PP							84	-248.8
	M							84	-248.8
Czech Republic	PB	Cze1	16°36'08.78"	49°18'14.40"	440	35	384	146	-136.5
	PP							146	-136.5
	M							146	-136.5
France	PB	Fra1	07°29'13.60"	48°58'41.80"	275	48	474	82	-107.0
	PP							65	-124.0
	M							91	-94.0
Germany	PB	Ger1	11°14'12.49"	48°34'57.95"	430	38	382	273	7.5
	PP							158	-107.5
	M							158	-107.5
Belgium	PB	Bel1	5°27'00"	50°01'48.00"	545	57	439	172	-44.8
	PP							172	-44.8
	M							151	--44.8
Poland	PB	Pol1	14°36'17.51"	53°20'07.40"	60	37	347	280	5.1
	PP							280	5.1
	M							280	5.1
Poland	PB	Pol4	20°13'45.84"	50°01'27.60"	208	36	471	215	-3.1
	PP							229	10.9
	M							286	67.9
Poland	PB	Pol5	20°19'37.26"	50°01'36.00"	213	36	463	286	45.6
	PP							229	-11.4
	M							286	45.6
Sweden	PB	Swe1	13°35'35.00"	56°09'12.00"	120	39	421	135	6.9
	PP							143	14.9
	M							194	65.9
Poland	PB	Pol3	20°41'08.90"	50°59'27.96"	383	37	419	280	32.2
	PP							280	32.2
	M							280	32.2
Sweden	PB	Swe2	14°11'46.00"	55°42'33.00"	25	47	359	272	149.3
	PP							272	149.3
	M							272	149.3
Belgium	PB	Bel2	04°19'29.60"	50°45'06.10"	160	49	540	122	159.6
	PP							122	159.6
	M							122	138.6
Germany	PB	Ger6	12°44'08.30"	48°11'12.47"	400	31	675	184	200.5
	PP							184	200.5
	M							184	200.5
Lithuania	PB	Lit1	22°24'24.01"	55°04'47.30"	25	45	415	715	567.8
	PP							715	567.8

	M							715	567.8
Lithuania	PB	Lit2	21°32'23.44"	55°27'02.80"	20	48	431	715	632.4
	PP							715	632.4
	M							715	632.4

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Table S2 Stand characteristics of the 17 sites sorted by average water balance calculated over the vegetation period (March-September - WB$_{VP}$) for all stand types (pure beech, pure pine and mixed). Characteristic are given for each stand at each site

Site ID	Site name	Species	Stand type	Age (Years)	Basal area (m^2.ha^{-1})
1042	Sp1	Beech	Pure	40	33
		Beech	Mixed	40	14
		Pine	Pure	40	55
		Pine	Mixed	40	39
1047	Bul1	Beech	Pure	65	41
		Beech	Mixed	65	37
		Pine	Pure	65	54
		Pine	Mixed	65	42
1041	Sp2	Beech	Pure	50	52
		Beech	Mixed	50	21
		Pine	Pure	50	40
		Pine	Mixed	50	11
1049	Cze1	Beech	Pure	45	36
		Beech	Mixed	45	13
		Pine	Pure	45	43
		Pine	Mixed	45	26
1040	Fra1	Beech	Pure	60	26
		Beech	Mixed	60	15
		Pine	Pure	60	41
		Pine	Mixed	60	17
1033	Ger1	Beech	Pure	53	23
		Beech	Mixed	50	16
		Pine	Pure	65	25
		Pine	Mixed	50	17
1057	Bel1	Beech	Pure	150	27
		Beech	Mixed	100	20
		Pine	Pure	150	11
		Pine	Mixed	130	10

1035	Pol1	Beech	Pure	54	38
		Beech	Mixed	54	12
		Pine	Pure	54	42
		Pine	Mixed	54	26
1044	Pol4	Beech	Pure	57	18
		Beech	Mixed	57	23
		Pine	Pure	57	30
		Pine	Mixed	57	13
1045	Pol5	Beech	Pure	55	25
		Beech	Mixed	55	16
		Pine	Pure	55	34
		Pine	Mixed	55	16
1054	Swe1	Beech	Pure	84	33
		Beech	Mixed	106	20
		Pine	Pure	56	32
		Pine	Mixed	106	20
1037	Pol3	Beech	Pure	69	31
		Beech	Mixed	72	24
		Pine	Pure	80	41
		Pine	Mixed	72	19
1053	Swe2	Beech	Pure	65	52
		Beech	Mixed	65	17
		Pine	Pure	65	48
		Pine	Mixed	65	29
1063	Bel2	Beech	Pure	115	28
		Beech	Mixed	115	17
		Pine	Pure	115	40
		Pine	Mixed	115	29
1070	Ger6	Beech	Pure	64	23
		Beech	Mixed	60	11
		Pine	Pure	73	34
		Pine	Mixed	60	28

1051	Lit1	Beech	Pure	90	26
		Beech	Mixed	90	20
		Pine	Pure	90	35
		Pine	Mixed	90	43
1052	Lit2	Beech	Pure	102	43
		Beech	Mixed	102	18
		Pine	Pure	102	41
		Pine	Mixed	102	41

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Table S3 *Characteristics of the cored trees. Sites are ranked according to the average water balance over the vegetation period for all stand types (pure beech, pure pine and mixed)*

Site name	Species	Stand type	Mean height (m)	Mean diameter (cm)	δ¹³C (‰) Mean	Sd	Temporal stability	Sensitivity (‰)
Sp1	Beech	Pure	18.1	17.0	-23.7	0.5	45.54	0.07
	Beech	Mixed	16.4	13.1	-23.7	0.6	36.91	0.19
	Pine	Pure	17.0	22.7	-22.6	0.5	60.98	0.13
	Pine	Mixed	18.1	24.6	-22.7	0.5	44.87	0.13
Bul1	Beech	Pure	25.5	22.1	-23.5	0.6	36.55	1.74
	Beech	Mixed	28.3	22.4	-23.6	0.6	40.91	1.68
	Pine	Pure	27.8	30.5	-22.9	0.7	32.55	1.74
	Pine	Mixed	28.3	33.9	-22.9	0.7	32.12	1.16
Sp2	Beech	Pure	22.6	30.0	-24.0	0.5	51.41	0.45
	Beech	Mixed	15.8	25.6	-25.1	0.5	52.49	0.20
	Pine	Pure	10.1	24.4	-22.7	0.6	35.62	0.48
	Pine	Mixed	14.4	26.8	-23.3	0.5	46.01	0.37
Cze1	Beech	Pure	20.8	20.7	-25.2	0.8	49.53	0.48
	Beech	Mixed	21.0	26.7	-24.5	0.5	79.67	0.43
	Pine	Pure	21.3	24.8	-22.8	0.8	53.76	0.83
	Pine	Mixed	21.1	23.9	-22.4	0.4	27.53	1.28
Fra1	Beech	Pure	21.7	24.8	-25.2	0.5	41.00	0.64
	Beech	Mixed	25.1	21.1	-24.8	0.6	23.88	0.38
	Pine	Pure	23.4	30.8	-24.1	0.5	53.49	0.92
	Pine	Mixed	25.4	27.1	-23.9	0.4	44.67	0.68
Ger1	Beech	Pure	22.5	22.6	-25.6	0.7	31.68	1.19
	Beech	Mixed	25.5	23.5	-25.7	0.8	46.47	0.15
	Pine	Pure	22.6	32.6	-24.2	0.6	34.80	0.61
	Pine	Mixed	25.8	25.6	-24.4	0.7	48.45	0.16
Bel1	Beech	Pure	28.0	44.7	-26.8	0.7	48.71	0.75
	Beech	Mixed	29.2	44.6	-26.5	0.5	41.11	0.37
	Pine	Pure	33.3	48.3	-24.0	0.3	80.21	0.24
	Pine	Mixed	28.4	61.8	-24.1	0.3	85.85	0.48

Pol1	Beech	Pure	24.1	29.7	-25.3	1.1	24.83	0.46
	Beech	Mixed	27.2	22.7	-24.9	1.0	24.28	1.11
	Pine	Pure	26.1	27.4	-23.0	0.6	29.53	0.11
	Pine	Mixed	27.3	27.6	-24.6	0.8	37.02	0.06
Pol4	Beech	Pure	26.9	24.9	-25.5	0.9	40.76	0.57
	Beech	Mixed	18.3	30.3	-25.5	0.6	22.05	0.48
	Pine	Pure	26.9	33.9	-23.4	0.7	38.44	0.76
	Pine	Mixed	23.1	32.9	-23.9	0.6	52.38	0.29
Pol5	Beech	Pure	24.2	29.7	-25.2	0.5	48.67	0.03
	Beech	Mixed	27.0	32.4	-25.3	0.5	45.26	1.40
	Pine	Pure	25.2	33.9	-24.0	0.6	63.04	0.09
	Pine	Mixed	25.9	32.0	-24.4	0.4	41.76	0.65
Swe1	Beech	Pure	23.3	45.9	-25.2	0.6	39.62	1.08
	Beech	Mixed	20.9	36.8	-26.2	0.4	64.10	0.15
	Pine	Pure	22.3	31.4	-24.2	0.6	40.89	0.62
	Pine	Mixed	23.1	42.1	-23.8	0.4	66.31	0.53
Pol3	Beech	Pure	27.4	30.9	-25.3	0.7	58.24	0.21
	Beech	Mixed	28.4	29.0	-25.1	0.4	28.57	0.42
	Pine	Pure	27.0	32.7	-23.4	0.4	54.34	1.21
	Pine	Mixed	26.2	30.4	-23.6	0.4	67.62	0.55
Swe2	Beech	Pure	25.3	42.3	-26.6	0.4	73.44	0.13
	Beech	Mixed	27.1	37.2	-25.9	0.6	42.83	0.70
	Pine	Pure	24.7	35.4	-24.9	0.7	37.80	0.64
	Pine	Mixed	25.6	57.9	-24.2	0.3	73.72	0.42
Bel2	Beech	Pure	22.7	31.0	-25.6	0.5	54.94	0.67
	Beech	Mixed	27.4	32.2	-25.3	0.5	52.37	0.69
	Pine	Pure	22.2	40.3	-24.1	0.4	59.17	0.00
	Pine	Mixed	19.5	38.3	-24.1	0.4	64.24	0.03
Ger6	Beech	Pure	19.4	25.6	-25.7	0.9	33.30	1.04
	Beech	Mixed	20.5	18.8	-25.5	0.8	27.18	0.25
	Pine	Pure	21.6	20.9	-24.0	0.5	59.52	0.64
	Pine	Mixed	17.5	22.2	-24.3	0.4	65.14	0.30

Lit1	Beech	Pure	32.3	28.3	-26.7	0.8	35.31	1.13
	Beech	Mixed	29.8	28.2	-26.7	0.7	40.75	0.91
	Pine	Pure	26.5	36.6	-24.4	0.6	38.37	1.54
	Pine	Mixed	33.2	42.6	-24.3	0.5	48.66	0.46
Lit2	Beech	Pure	25.9	30.6	-26.7	0.5	56.15	0.65
	Beech	Mixed	27.7	26.6	-26.6	0.8	34.04	0.68
	Pine	Pure	34.3	44.6	-23.5	0.5	56.53	0.07
	Pine	Mixed	31.1	39.4	-26.6	0.8	49.62	0.10

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845 **Fig. S1** *Heat map showing the intensity of the linear relationship (R^2 of the models) between $\delta^{13}C_{cor}$ and SPEI at each site, for*
846 *beech (A) and pine (B) in pure stands. SPEI was calculated for periods of one to six months, ending between March and October.*
847 *The insert in the top left corner of each panel indicates the level of the R^2 values*
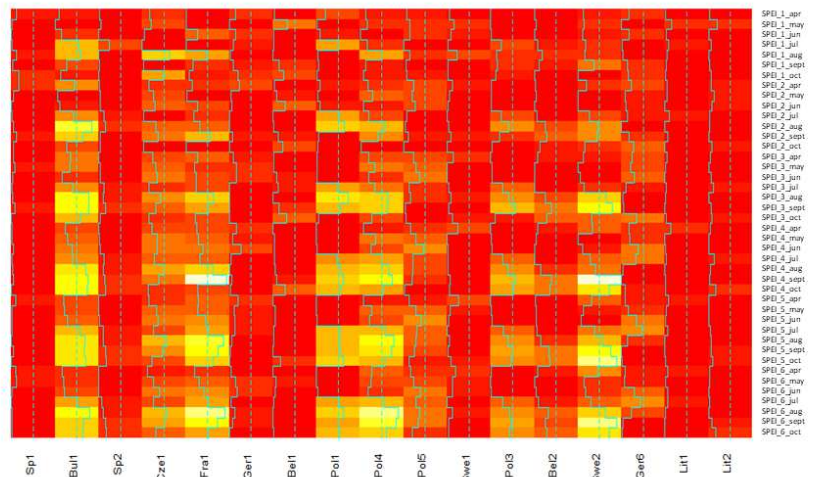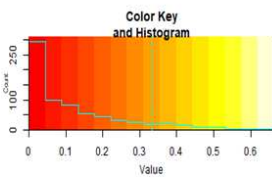
848 *(A)*
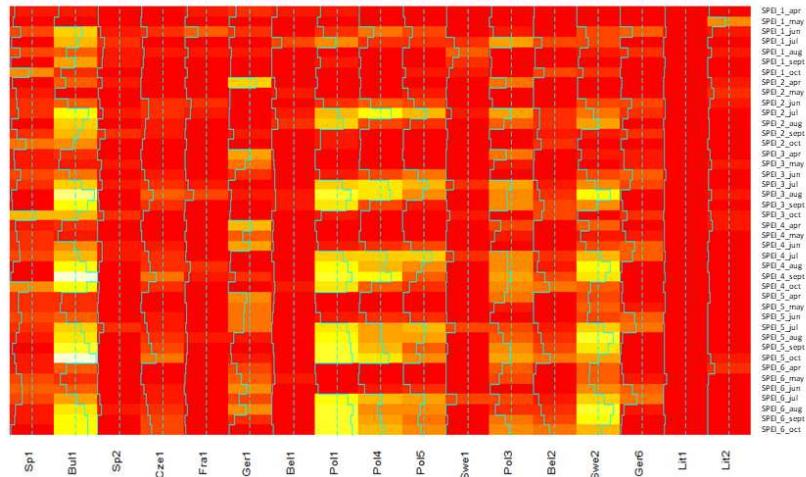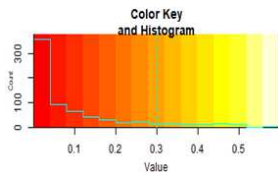
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850 *(B)*

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	Time series of $\delta^{13}C_{cor}$ for each species in the pure stands	Difference in average $\delta^{13}C_{cor}$ values between species in the pure stands	Species reaction to drought	Species mixture effects	Temporal constancy
Elevation [m]	X	X	X	X	X
Slope [degrees]	X	X		X	X
Age [year]	X	X	X	X	X
BA [m^2.ha^{-1}]	X	X	X		X
Mean height [m]	X	X	X		X
Height ratio (Height $_{target\ species\ in\ mixed\ stand}$/Mean height $_{mixed\ stand}$) [-]				X	
BA ratio [(BA $_{pure\ stand}$ – BA $_{mixed\ stand}$)/Mean BA $_{pure/mixed\ stands}$] [-]				X	
WB$_{VP}$ [mm]	X	X	X	X	X
SPEI $_{June\ –\ September}$ [-]	X			X	
Annual June - September Temperature [°C]	X			X	
Annual June - September Temperature averaged for 1993-2014 [°C]		X	X		X
Species					X
Stand composition (pure/mixed)			X		X

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858 ***Table S5*** *Correlation coefficient between δ13C$_{cor}$ time series of beech and pine in the pure stands for each site. Sites are shown by*
859 *increasing value of mean water resources in pure stands (WB$_{VP}$ calculated on the approximate vegetation period (March-*
860 *September) and averaged over the 1950-2014 period*

Site	Correlation
Sp1	0.70
Bul1	0.72
Sp2	0.45
Cze1	0.70
Fra1	0.69
Ger1	0.58
Bel1	0.52
Pol4	0.36
Pol1	0.85
Swe1	0.81
Pol5	0.54
Pol3	0.68
Swe2	0.66
Bel2	0.21
Ger6	0.63
Lit1	0.72
Lit2	0.42

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862 ***Table S6*** *Results of paired t-tests for the significance of the difference between average δ^{13}C values for pure stands of each species*
863 *within each site. P-values indicate the significance of the deviation from zero (mean δ^{13}C$_{beech}$ – mean δ^{13}C$_{pine}$). Sites are shown by*
864 *increasing value of mean water resources in pure stands (WB$_{VP}$ calculated on the approximate vegetation period (March-*
865 *September) and averaged over the 1950-2014 period*

Site	Mean δ^{13}C$_{beech}$ – Mean δ^{13}C$_{pine}$	p-values
Sp1	-1.0897	<.001
Bul1	-0.6833	.002
Sp2	-1.2430	<.001
Cze1	-2.0693	<.001
Fra1	-0.8837	<.001
Ger1	-1.3444	<.001
Bel1	-2.4247	<.001
Pol4	-1.6442	<.001
Pol1	-0.2462	.381
Swe1	-0.9799	<.001
Pol5	-0.9064	<.001
Pol3	-1.5122	<.001
Swe2	-1.6868	<.001
Bel2	-1.2829	<.001
Ger6	-1.1803	<.001
Lit1	-2.3095	<.0001
Lit2	-3.2289	<.001

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Site	Type of year	Year	SPEI	P - PET	$(P - PET)_{mean}$
	Preceding	1997	2.13	-205.98	
Sp1	Dry	2005	-2.26	-608.77	-457.12
	Following	2014	0.22	-410.09	
	Preceding	1995	0.80	-231.39	
Bul1	Dry	2000	-2.12	-522.33	-316.58
	Following	2014	2.03	-67.75	
	Preceeding	1997	0.67	-230.99	
Sp2	Dry	2009	-2.25	-551.86	-368.83
	Following	2011	-0.28	-335.71	
	Preceeding	2001	1.48	-64.97	
Cze1	Dry	2003	-2.07	-386.80	-194.58
	Following	2010	1.64	-49.97	
	Preceeding	2000	1.00	-55.19	
Fra1	Dry	2003	-2.20	-404.01	-171.86
	Following	2007	0.99	-56.39	
	Preceeding	1995	1.38	-78.82	
Ger1	Dry	2003	-2.38	-459.44	-213.04
	Following	2007	0.96	-114.84	
	Preceeding	2001	1.74	27.16	
Bel1	Dry	2003	-1.61	-293.56	-97.23
	Following	2004	1.71	25.08	
	Preceeding	1993	1.28	-70.83	
Pol1	Dry	1994	-1.59	-329.64	-164.71
	Following	2007	2.34	49.27	
	Preceeding	2001	1.88	91.03	
Pol4	Dry	2006	-1.69	-313.69	-142.59
	Following	2010	1.64	50.04	
	Preceeding	1993	-0.28	-187.09	
Pol5	Dry	1994	-1.80	-338.78	-147.32
	Following	2010	1.86	80.22	
	Preceeding	1993	1.60	94.35	
Swe1	Dry	1997	-1.86	-272.61	-58.20
	Following	2007	2.30	218.12	
	Preceeding	1993	0.40	-124.97	
Pol3	Dry	1994	-1.41	-322.03	-151.92
	Following	2001	2.15	119.17	
	Preceeding	1993	1.46	42.43	
Swe2	Dry	2003	-1.68	-235.02	-84.26
	Following	2007	2.20	144.76	
	Preceeding	2000	1.35	104.76	
Bel2	Dry	2003	-1.83	-224.48	-39.30
	Following	2004	1.62	141.72	
	Preceeding	1993	1.34	158.18	
Ger6	Dry	2003	-2.48	-324.01	-16.61
	Following	2010	0.37	56.26	
	Preceeding	1993	0.91	22.77	
Lit1	Dry	1994	-1.47	-258.96	-92.92
	Following	2007	1.73	140.62	
	Preceeding	1998	1.29	146.06	

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| Lit2 | Dry | 2006 | -1.55 | -233.73 | -39.92 |
| | Following | 2007 | 1.34 | 153.80 | |

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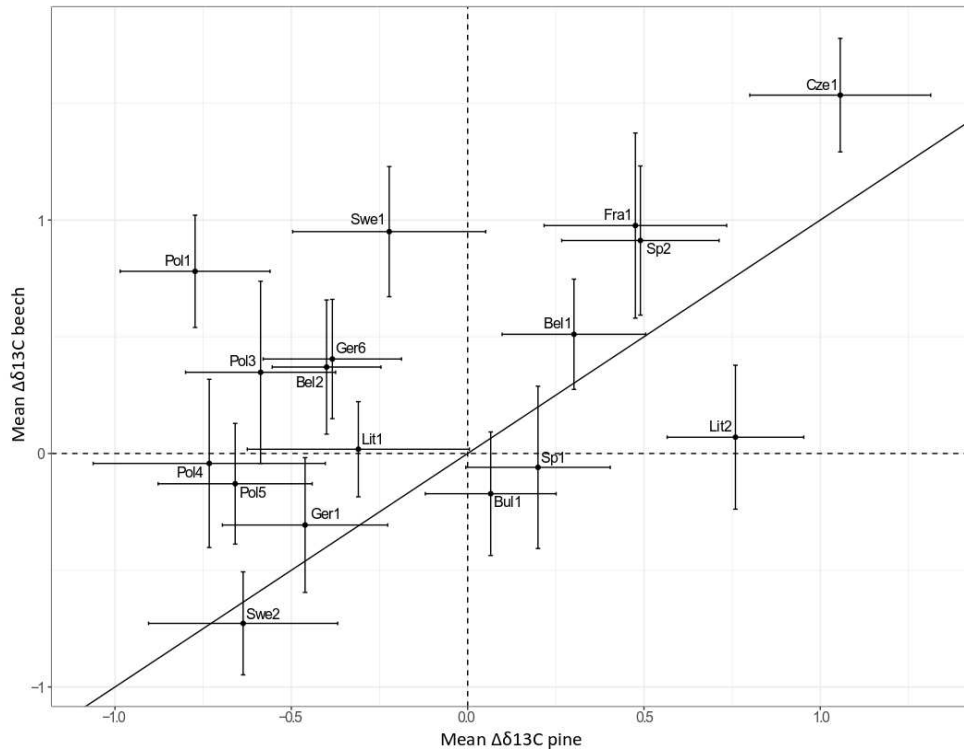
Fig. S2 *Relationship between the mean differences in δ¹³C between pure and mixed stands (δ¹³C$_{pure}$ − δ¹³C$_{mixed}$) for beech (Y axis)*
878 *and pine (X axis). Vertical and horizontal bars represent 95% confidence intervals. Horizontal and vertical dashed lines indicate*
879 *zero and the solid line indicates the 1:1 relationship*

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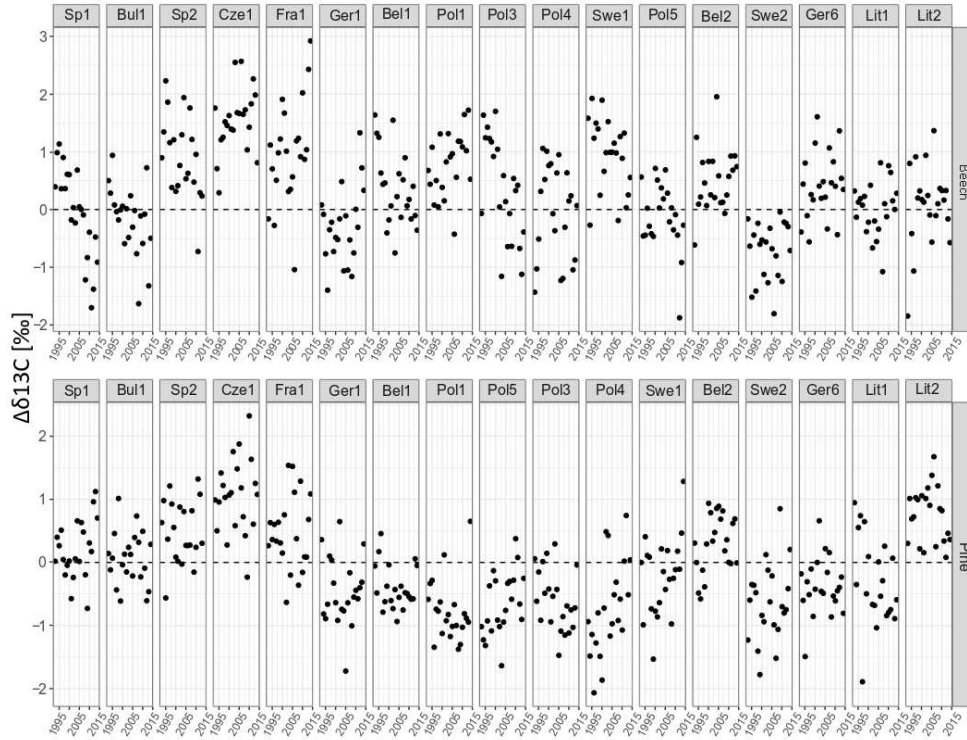
Fig. S3 *Series of raw $\delta^{13}C_{pure\ stands}$ – raw $\delta^{13}C_{mixed\ stands}$ ($\Delta\ \delta^{13}$C) for both species. Positive values indicated lower (more negative)*
$\delta^{13}C_{raw}$ values in mixed stands. Horizontal dashed lines indicate zero. Sites are ranked in increasing order of average WB_{VP}
(calculated aver the 1950-2014 period) between pure and mixed stands for each species