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Drivers and dynamics of foliar senescence in temperate deciduous forest trees at their southern limit of distribution in Europe

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Open Research statement: data are not yet provided, and are stored in the authors' archives and available for viewing. If the paper is accepted for publication they will be permanently archived in the Zenodo repository.

26 **Abstract**

27 Research on autumn phenology is very important for understanding and simulating the future

28 growth of temperate deciduous forests. This is especially needed at the southern edge of the temperate

29 zone, where climate change impacts are particularly intense. We studied foliar senescence timing for

30 mature stands of *Fagus sylvatica* L., *Populus tremula* L., *Betula pendula* Roth, *Quercus petraea*

31 (Matt.) Liebl. and *Quercus robur* L. at the southern edge of European temperate forests. First, we

32 analysed long-term series (1997-2019) of senescence timing in southern France. Then, we compared

33 a more detailed four-year dataset (2017-2020) of senescence dynamics and its correlations to

34 meteorological conditions for stands in northern Spain and Belgium, with the latter area representing

35 the core distribution of the species. In contrast to other temperate regions, no significant delaying

36 trends in the timing of autumn phenology were detected in the long-term in southern temperate

37 forests, which were characterized by high inter-site variability. In the short-term (4 years), species-

38 specific correlations with meteorological conditions were found, with, for example, the senescence

39 of *F. sylvatica* being affected by temperature while the senescence of *Q. petraea* was affected by both

40 temperature and precipitation. Autumn dynamics differed between the core and southern areas of

41 distribution of the species in the study period. In particular, while late season conditions affected

42 senescence timing in the southern populations, the senescence dynamics of the core populations was

43 mostly influenced by the legacy of spring – early summer conditions and, overall, more affected by

44 precipitation than southern populations. Our data fill important knowledge gaps on the functioning

45 of temperate deciduous forests at the southern limit of distribution in Europe.

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Introduction

Plant phenology is the discipline that studies the recurring seasonal events of the annual life cycles of plants (*e.g.* flowering) and their connections amongst species and with the environment, from the individual to the ecosystem level (Forrest and Miller-Rushing, 2010). The study of phenology is important for increasing our understanding of temperate deciduous forests (Liu et al. 2016, Chen et al. 2018). Modifications in the timing of phenological events, due to global change, can greatly alter the functioning of such ecosystems (Fu et al. 2022; Marchin et al. 2010; Keenan et al. 2014).

Autumnal phenology has traditionally been studied less than spring phenology (Gallinat et al. 2015), as assessing key events is more difficult in autumn (*e.g.* the onset of foliar senescence and cessation of xylem formation) (Dox et al. 2020). The study of autumnal phenology and its drivers is nevertheless central to improving our comprehension of future tree growth associated with climate change and our ability to simulate it (Gallinat et al. 2015).

The onset of foliar senescence (OFS) is a key event of autumnal phenology in temperate deciduous trees, coinciding with the expression of senescence genes (Fracheboud et al. 2009, Mariën et al. 2022). At the ecophysiological level, OFS is associated with chlorophyll degradation. When the vegetative season approaches its end, the leaves undergo a combined process of gradual degradation and reallocation of nutrients to the overwintering plant structures (Estiarte and Peñuelas 2015, Estiarte et al. 2023). After OFS, foliar senescence progresses at a rate dependent on the current environmental conditions (Fracheboud et al. 2009) and becomes visible when leaves turn yellow and fall. The onset of loss of canopy greenness (OLCG), which is easier to measure than OFS, can be used as proxy of OFS, though not in the presence of significant stress (Marchin et al. 2010; Mariën et al. 2019; Mariën et al. 2021). Nevertheless, OLCG can be a valid parameter for describing, analysing and comparing the autumnal phenological dynamics of populations and single trees (Dox et al. 2022a; Jiang et al. 2022; Mariën et al. 2019).

77   The timing of foliar senescence can be influenced by several factors, ranging from tree traits to

78 environmental conditions. These factors include, in particular, genetics, the basis of inter- and

79 intraspecific variability (Weih 2009; Xie et al. 2018) and meteorological (annual scale) and climatic

80 (multi-annual scale) variables (Zhang et al. 2020). Variability in site characteristics, meteorological

81 and climatic influences, as well as the genotype of the individuals, can lead to highly variable

82 phenological behaviour within species, for example between populations in contrasting areas of the

83 species distribution. Climatic variables are particularly relevant in the long term. Among them,

84 temperature has been demonstrated to have the strongest impact on autumn phenology, especially for

85 temperate deciduous forests, while other factors (*e.g.* photoperiod) also play a key role in boreal

86 deciduous forests (Gill et al. 2015).

87   Recent studies have focused on a variety of aspects of the foliar senescence of temperate deciduous

88 trees, such as measurement methodologies (Mariën et al. 2019), the temporal relationships between

89 foliar senescence and the cessation of xylem formation (Dox et al. 2020, Dox et al 2022a), the linkage

90 between foliar senescence and drought (Mariën et al 2021, Dox et al 2022b), the relationship between

91 annual carbon assimilation and the timing of foliar senescence (Zani et al. 2020) and the impact of

92 the timing of senescence on the timing of budburst of the next year (Marchand et al. 2020). For

93 temperate deciduous forests, comprehensive studies that analyse the variability of autumnal foliar

94 phenology and its main drivers, however, are currently lacking at their southern limits, which in

95 Europe encompass areas such as northern Spain, southern France, central Italy and the Balkan

96 Peninsula. These forests are of particular interest for at least three reasons: (**i**) they are situated at the

97 frontier between Mediterranean and temperate zones, which implies unique environmental conditions

98 (Martínez-Sancho and Gutiérrez Merino 2019), (**ii**) they will be especially affected by climate change,

99 as models project lower precipitation, higher temperatures, and lower nutrient availabilities in these

100 zones over the course of this century (He and Dijkstra 2014; IPCC 2019; Peñuelas and Sardans 2021),

101 and, in addition to the other ecosystem services that they provide, (**iii**) they are important for

102 biodiversity due to the unique genetic material they possess (Anderegg et al. 2019).

Several studies exist regarding the autumn phenology trends of deciduous forest trees on a global scale in the last decades (Liu et al. 2016; Norman et al. 2017; Wang et al. 2019; Jiang et al. 2022), specifically in temperate forests (Liu et al. 2019; Hoffmann et al. 2022). For example, a trend towards the delay of autumn senescence due to increasing temperatures worldwide has been shown by Piao et al. (2007), Delpierre et al. (2016) and Fu et al. (2018). However, these studies rely mainly on remote sensing (RS). RS is an invaluable tool that is able to provide long time series of phenological data related to vast geographical areas (Dronova and Taddeo 2022). Nevertheless, European temperate forests, in particular at their southern edge, are often fragmented and immersed in heterogenous anthropic environments (EEA, 2006), which reduces the accuracy of RS data and makes site-level studies necessary, when possible, for obtaining a better resolution (Berra and Gaulton 2021).

The aims of this study can be summarised by the following questions: (**1**) Has the timing of autumnal foliar phenology become delayed in the last 25 years for European temperate deciduous forests at their southern distributional edge? Which climatic drivers are determining the interannual variability? and (**2**) Do temperate tree species have a different autumnal foliar phenology and drivers at their southern distributional limit compared to their central zone of distribution? Using field-based methods, we addressed these questions by (**i**) studying long-term time series (1997-2019) of foliar senescence for warm temperate forests of European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) in southern France, and their relationships with climatic variables; (**ii**) monitoring the seasonal pattern of canopy greenness (CG), from which we derived OLCG, for mature stands of common aspen (*Populus tremula* L.), silver birch (*Betula pendula* Roth), *F. sylvatica* and *Q. petraea* during four years (2017-2020) in northern Spain, correlating them with the seasonal meteorological conditions, and (**iii**) comparing the timing and drivers of foliar senescence obtained in (**ii**) with data on the same dynamics but for central temperate forests monitored in Belgium.

129   **Materials and Methods**

130

131   *Study species and sites*

132   Time series of phenological observations for *F. sylvatica*, *Q. robur* and *Q. petraea* from 1997 to

133   2019 were obtained from nine sites of the French national monitoring network, RENECOFOR, in

134   order to study long-term trends (for methods see Delpierre et al. 2009; Lebourgeois et al. 2010). All

135   sites are at latitudes <45°N (Fig. 1), with MAT ranging from 7.0 to 13.5 °C, MAP ranging from 850

136   to 1300 mm and altitude ranging from 30 to 1400 m a.s.l. (Table 1) and most are classified in the

137   Köppen classification (Peel et al. 2007) as temperate, with warm summers and sometimes with dry

138   summers or winters. Thirty-six trees were monitored weekly per site yearly, though some gaps in the

139   long-term series were present at some sites.

140   Mature stands of *F. sylvatica*, *P. tremula*, *B. pendula* and *Q. petraea* were selected at two

141   mountainous locations in central Catalonia, northern Spain. The stands of *F. sylvatica* and *P. tremula*

142   were located in the Montseny Natural Park and Biosphere Reserve (41°45'35"N, 2°28'04"E; 1075 m

143   a.s.l.), while the stands of *B. pendula* and *Q. petraea* were located in the Serres de Milany National

144   Park (42°11'49"N; 2°20'45"E, 1050 m a.s.l). Both sites have a warm-temperate climate with dry and

145   hot summers and mild winters (Csa of the Köppen classification of climate; Peel et al. 2007), with

146   mean annual temperature (MAT) between 10.9 and 12.2 °C and mean annual precipitation (MAP)

147   between 840 and 870 mm (means established over the experimental period: 2017-2020). The soils at

148   the sites in Montseny Natural Park and Biosphere Reserve are relatively acidic sandy soils, with

149   moderate to high amounts of organic material. The soils at the sites in Serres de Milany National Park

150   are clayey soils with high amounts of organic material; the community of *Q. petraea* is dense, but *B.*

151   *pendula* is represented only by isolated trees in pastures remaining from the clear-cutting of a large

152   stand approx. 30 years ago. Eight (co)dominant trees were selected in each stand. These trees were

153   mature individuals with good health status (*e.g.* no defoliation or damages in the crown), of similar

154 size and at a maximum distance of 30 meters from one another. Seasonal CG in summer and autumn

155 were monitored for all trees from summer 2017 to autumn 2020.

156 We compared the dynamics of southern and central temperate forests by collecting CG data for *F. sylvatica* and *B. pendula* in summer and autumn 2017-2020 from two Belgian sites: Brasschaat Park (51°20'N, 4°30'E; 15 m a.s.l.) for *F. sylvatica*, and the Klein Schietveld military domain (51°21'N, 4°37'E; 21 m a.s.l.), a Natura2000 reserve, for *B. pendula*. These two sites are 10 km apart in a topographically flat region with no features that could cause climatic differences between them. Both areas have a temperate climate, with warm but not dry summers (Cfb of the Köppen classification; Peel et al. 2007), with a MAT and a MAP of 10.5 °C and 920 mm, respectively (Table 1). Eight and 12 trees per species were monitored at the two sites.

165 *CG*

166 The loss of CG (X_t at day t) was visually estimated following the method described by Vitasse et al. (2011) as the combined rating of leaves that had changed colour (α_t, in percent) and fallen (β_t, in percent) in a canopy:

$$X_t = [\alpha_t \times (100 - \beta_t)]/100 + \beta_t$$

172 Observations were recorded weekly from the end of August until $X_t=100\%$, usually in late November or early December.

175 **Data analysis**

176 *a) Determination of senescence timing*

177 The onset of the loss of canopy greenness (OLCG) can be defined as the moment at which the colouration and fall of leaves increases sharply (or when CG decreased sharply) in autumn (Mariën et al. 2021). When such a rapid change occurs, the slope of the relationship CG *vs* time suddenly

180 becomes steeper and creates a breakpoint with the previous trend (Dox et al. 2020). We identified the

181 breakpoint using the 'segmented' R package (Muggeo 2008). This package performs multiple linear

182 regressions on a data set and calculates the breakpoint as the point of intersection between the two

183 subsequent linear regression lines with the largest change in slope. For the cases with the largest

184 statistical sample (n>10), OLCG outliers in the population were detected outside the range between

185 Q1 - 3 * IQR and Q3 + 3 * IQR and removed, where **Q1** and **Q3** are the first and third quartiles,

186 respectively, and **IQR** is the interquartile range (Benhadi-Marín 2018). OLCG was determined for

187 trees of the Spanish and Belgian populations. Two variables were available for the long-term

188 monitoring sites in France: LS10, *i.e.* the date on which 10% of the trees had at least 20% of their

189 leaves coloured or fallen (an index approximately comparable to OLCG, established at the population

190 scale), and LS90, *i.e.* the date on which 90% of the trees had at least 20% of their leaves coloured or

191 fallen (an index of an advanced state of senescence, established at the population scale).

192

b) Statistical analysis

194 All statistical analyses were performed using R v3.5.1 (R Core Team 2018).

195 Regressions of LS10 and LS90 *vs* years were performed separately for each French site and jointly

196 for all French sites to highlight possible temporal trends of the phenophases. R^2, slope and *p* value

197 were calculated for each regression. Regressions of LS10 were performed separately for each site

198 against average temperature and cumulative precipitation data for different periods (*growing season*,

199 May-September; *early spring*, March and April; *early summer*, May and June; *late summer*, August

200 and September) or for single months (May and June) as factors, to identify the environmental drivers

201 and climatic periods that had the strongest effects on the phenophases. *p* values were calculated for

202 each regression. Regressions of LS10 trends (*i.e.* slope of LS10 *vs* years) against environmental

203 variables such as MAT, MAP, altitude and aridity index (Budyko 1958) were performed to investigate

204 if and which environmental factors could determine a differential response across sites, in terms of

205 trends in autumn phenology along the studied period. R^2 and *p* values were given for each regression.

Analyses of variance (ANOVAs) were performed on OLCG of the Spanish and Belgian trees to identify interannual differences for each species and differences amongst species for each year. The data were first analysed for normality, the homogeneity of residuals ('rstatix' R package, Kassambara 2021) and the absence of extreme outliers. When these conditions were met, we performed a repeated-measures ANOVA followed by a paired *t*-test if allowed by the data structure, otherwise we applied a non-repeated-measures ANOVA followed by Tukey's post-hoc test. A Kruskal-Wallis test, followed by Dunn's post-hoc test, was applied when the data were not normally distributed. A Welch test, followed by a Games-Howell post-hoc test, was applied when the residuals were not homogeneous.

The effects of species and year on OLCG were further tested using linear models for the data from the Spanish and Belgian sites. The effect of distributional area was then aggregated to species and year in simple linear models with either two factors (species and site separately for each year), or three factors and a maximum of double interactions.

The effects of species and meteorology on OLCG for the Spanish and Belgian trees were then tested using simple linear models with average temperature or cumulative precipitation data for the different periods defined above as factors; these models were first performed with species as a second factor and successively separated by species. The means ± SD of the eight meteorological variables of temperature and precipitation for the four periods defined above are given in Table S2.

To illustrate the differences between the sites in Belgium and Spain regarding the mentioned, aggregated meteorological variables, we finally conducted a principal component analysis ordination (PCA) on their scaled and standardized values using the vegan package (v. 2.6-4).

Results

Long-term trends and impact of climatic factors based on the French sites dataset

232   Neither LS10 nor LS90 trended significantly between 1997 and 2019 when the French sites were

233 aggregated (six *F. sylvatica* sites, two *Q. robur* sites and one *Q. petraea* site) (Fig. 2). Each site had

234 highly variable trends (Table 2, Fig. S1) which were even more marked during the last 10 years of

235 observations. The trend for LS10 was significant at only three sites, while the trend for LS90 was

236 significant at other three different sites (Table 2). However, these significant trends for both LS10

237 and LS90 presented different signs among sites (Table 2). No significant correlation was found across

238 sites between LS10 trends (slope of LS10 *vs* years, Fig. S1) and environmental variables such as

239 MAT, MAP, altitude and aridity index (Fig. S2).

240   LS10 at *Quercus* sites was significantly correlated with temperature in May (negative, at two sites)

241 and June (positive, at one site) (Table 3). The correlations of LS10 with May and June temperatures

242 (more generally, with early summer temperatures) were significant for two of the six *F. sylvatica* sites

243 and tended to be significant ($0.05 < p < 0.10$) for two other sites, but with both positive and negative

244 trends (Table 3). Except at one site, these effects vanished when the temperature of the entire growing

245 season was considered (Table 3). In summary, for the study region, the long-term dataset showed

246 that: (**i**) there was neither an advance nor a delay of the onset and end of senescence in the last 25

247 years, (**ii**) temperature in the late spring – early summer had some impact on senescence onset, but

248 this impact was neither strong nor consistent across sites, and (**iii**) precipitation had no effect on long-

249 term trends of senescence timing.

250

Variability across species, years and meteorological conditions in Spain

252   At the Spanish study area, across species and years, OLCG ranged between DOY 260 and 310 (Fig.

253 3). When each species was considered separately, we observed that *F. sylvatica* and *P. tremula* had a

254 delayed OLCG in 2019, *Q. petraea* had an advanced OLCG in 2020, while OLCG for *B. pendula* did

255 not differ significantly interannually. An analysis of interspecific variation across years indicated that

256 *B. pendula* always had the earliest OLCG, while *Q. petraea* had the latest OLCG of all species in

257 2017 (Fig. 3). The linear models indicated that species-specific and year-to-year variation differences

258 explained approx. 70% of the variability of OLCG across trees (Table S1).

259 The models involving meteorological variables indicated that temperature and precipitation were

260 correlated with OLCG variation (Table 4). The best three models (explaining >54% of the variance)

261 included the temperature during the growing season (May-September), the temperature in late

262 summer (August-September) and precipitation in late summer.

263 Linear models performed separately for each species indicated that the correlation between OLCG

264 and the meteorological variables (especially with the precipitation indices) were strongest for *Q.*

265 *petraea* and weakest for *P. tremula*, but also indicated an influence of meteorological conditions on

266 the timing of senescence for all species (Table 5). As found for the aggregated models (Table 4), the

267 temperature during the growing season, the temperature in late summer and precipitation in late

268 summer were the most influential variables for OLCG across species. Temperatures throughout the

269 growing season or in late summer were, or tended to be, positively correlated with OLCG for all

270 species, so warmer conditions delayed senescence. For *B. pendula*, however, the temperature in early

271 spring (March-April) was negatively correlated with OLCG (Table 5). OLCG for *F. sylvatica* was

272 generally only affected by temperature, but both temperature and precipitation influenced OLCG for

273 *Q. petraea*, *B. pendula* and *P. tremula*. For these species, less precipitation generally delayed OLCG,

274 except for *P. tremula,* for which lower late summer precipitation advanced senescence (Table 5).

275

Variability between southern and central distributional area

277 As in Spain, the linear models indicated that both factors, species and years, contributed

278 significantly to differences in OLCG for the trees in Belgium, explaining 54% of the OLCG

279 variability (Table S1). OLCG in Belgium was between DOY 250 and 290, and significantly earlier

280 in 2018 than the other years for both *B. pendula* and *F. sylvatica* (Table 6). OLCG for *F. sylvatica*

281 was generally earlier for the Belgian than the Spanish trees when the same years were compared,

282 while for *B. pendula* the difference in OLCG between study areas varied across years (Table 6).

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Across species, the difference between distributional areas (the two countries) was significant for 2018 (p<0.001) and 2019 (p<0.001) (with earlier dates in Belgium), but not for 2017 (p=0.366) or 2020 (p=0.500). Even if the actual significance depended on the year, the linear model including country as a factor highlighted the significant effect of the distributional area when the data from the four years were analysed together (Table S1). Finally, note that the variability of OLCG due to species and year differed slightly but significantly depending on study areas, indicating that the differences in OLCG amongst species and years had different patterns in the two countries.

Linear models of OLCG and the meteorological variables for the Belgian stands, performed separately for each species, highlighted very similar dynamics for *F. sylvatica* and *B. pendula* (Table 5). The temperature during the growing season, in early spring and early summer, as well as precipitation during the growing season and in early spring, were the most influential variables. Higher temperatures throughout the growing season (and in early summer) advanced OLCG, while higher temperature in early spring delayed it. This was not (or opposite of what was) observed in Spain. For example, OLCG for *F. sylvatica* in Belgium was negatively correlated with temperature during the growing season, while the correlation was positive for the Spanish *F. sylvatica* population. Higher precipitation in early spring, however, delayed OLCG for both *B. pendula* and *F. sylvatica* in Belgium, which was also observed for *B. pendula* and *Q.petraea* in Spain.

The Belgian and Spanish sites differed mostly along the PC1 axis, which was associated with the four precipitation variables (precipitation during early spring, early summer, late summer and for the whole growing season) and with the temperature in both early spring and over the whole growing season (Figure 4). The differences by year between Belgium and Spain were spread along axis PC2, therefore driven mainly by the temperature in early and late summer. The differences between Belgium and Spain were relatively unidirectional in 2017, 2018 and 2019, albeit varying in strength, while the difference in 2020 was stronger and driven by different variables, *i.e.* mainly early spring and late summer precipitation.

309 **Discussion**

310

311 *Long-term trends*

312   A meta-analysis by Gill et al. (2015) found a general tendency towards a delay of autumnal

313 senescence for deciduous tree species in the Northern Hemisphere and that such a trend was mainly

314 due to the progressive increase in temperatures, especially in late summer. Other studies (Estrella et

315 al. 2009; Delpierre et al. 2009; Keenan and Richardson 2015) also identified higher autumnal

316 temperatures as the main factor for the progressive delay of autumnal senescence in temperate

317 deciduous forests. The autumnal dynamics of the studied temperate tree species at the southern limits

318 of their distributions, however, did not vary, or correlate with late-season temperature, during 1997-

319 2019. Temperature and autumnal dynamics were not correlated even when considering temperature

320 in September and October, as did Delpierre et al. (2009) (*data not shown*). It is possible that, in the

321 study region, the impact of inter-annual variability in meteorological conditions was larger than the

322 long-term warming trends, with no significant effect on autumn dynamics. It is known that climate

323 variability and extreme events are occurring and will occur more often in the future, and the

324 confounding effect that they create on senescence trends should be accounted for. Also, less-studied

325 drivers of senescence, such as air quality (Giovannelli et al. 2019), may play a role in the long term

326 and confound the effect of autumnal temperature. Therefore, in comparison to previous findings, our

327 study indicated that the long-term trends in senescence timing are less spatially uniform than

328 previously expected, with regional specific patterns (or lack thereof) at least in the southern part of

329 the European temperate forests. Moreover, our data also indicated high intersite variability, with

330 contrasting (unexplained) trends amongst some sites.

331   Temperatures in May and June were shown to have a potential effect on the onset of senescence in

332 the long term, though direction and significance depended on the site. Perhaps such influence is

333 related to the fact that leaves reach maturity in May and June and become a full source of carbon in

334 that period (Campioli et al. 2013). The meteorological conditions under which leaves mature can

335 influence the duration of the subsequent vegetative phase due to, for example, different

susceptibilities to environmental stressors such as photo-oxidative stress (Juvany et al. 2013). Zohner et al. (2023) recently showed a global negative correlation between late spring – early summer temperature and senescence onset for forests of the Northern Hemisphere.

Short-term trends

While for the long-term no relationship between late season temperature and senescence timing was detected, higher temperature in late summer was found to delay OLCG for *F. sylvatica*, *P. tremula* and *B. pendula* (Table 5) in Spain during the four years studied. This indicates that late summer temperature might be a limiting factor for plant functioning even at southern temperate locations, with warmer temperature in late summer likely slowing the progression of senescence because of its positive effect on photosynthesis (Fracheboud et al. 2009). Differently from *F. sylvatica* and *P. tremula*, the senescence timing of *B. pendula* was also affected by early spring and early summer temperature (Table 5). This might be related to the indeterministic growth of the canopy of *B. pendula*, which produces leaves continuously during the growing season (Maillette 1982).

The analysis of the Spanish stands further indicated a strong negative correlation between OLCG and precipitation for *Q. petraea*. Such a phenomenon could be interpreted as a strategy of compensating for the lower photosynthetic uptake in the summer due to drought stress by prolonging the vegetative period into the autumn (Zani et al. 2020). A delayed senescence following summer drought was also observed in saplings of *Q. petraea* in a drought experiment (Vander Mijnsbrugge et al 2016). The specific, strong response to precipitation by *Q. petraea* may be due to its ring-porous wood anatomy, as all other species studied are diffuse-porous. The smaller vessels produced in the late season might allow *Q. petraea* to efficiently transport water from roots to canopy and maintain a high photosynthesis rate also in late summer (Hacke et al. 2006). On the contrary, the earlier senescence associated with lower precipitation in late season observed for *P. tremula* might indicate the overall lower drought tolerance of this species (Rosso et al. 2023; Tikhomirova et al. 2023).

Comparison between edge and central distribution

The importance of the interactions in the linear model between country and species, and between country and year, indicated that both the patterns of interspecific and interannual variability differed between the two areas of distribution. Moreover, we found that the same species could have different autumnal dynamics in different areas of the distribution. Similar patterns have been documented for wood cambial phenology by Dox et al. (2022a), who found that intraspecific differences in cambial reactivation and cessation of xylem formation between Spain and Belgium were larger than the interspecific differences at the same site.

The phenological behaviour of the Spanish and Belgian populations differed in response to the meteorological drivers (Table 5). OLCG was more correlated to late-season temperatures and precipitation for the Spanish trees, while the autumnal dynamics of the Belgian trees were more responsive to conditions earlier in the season. More specifically, in Belgium, OLCG was correlated positively with March-April temperatures and negatively with May-June temperatures. Perhaps low temperature limitation in spring (March-April) affects the structure and function of the unfolding leaves and reduces their longevity, as Kikuzawa et al. (2013) observed. This effect, however, might be opposed by the negative impact that high temperatures (and potential heat stress) in May-June have on the autumnal dynamics of these populations because, as mentioned above, this period is important for leaf maturation. The influence of May-June temperature on OLCG is in agreement with the recent global analysis of Zohner et al. (2023) (*see end of section*). The strong and negative relationship between precipitation in early spring and leaf senescence timing was unexpected. Precipitation generally correlates with low insolation and lower spring temperatures, and thus a later budburst. However, later budburst is expected to prolong the leafy season, not shorten it (Fu et al. 2014; Keenan and Richardson 2015). This finding calls for further investigation. The study species showed similar responses to late season precipitation in both areas of distribution, with delayed senescence under wetter conditions for *B. pendula*. The lack of correlation between late season temperature and senescence timing in Belgium indicates that other factors can affect autumn

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phenology at higher latitudes, such as photoperiod or spring legacy effect, as suggested by Gill et al. (2005) and Mariën et al. (2021). In any case, the impact of precipitation on senescence was overall more important in Belgium than in Spain.

The separation between Belgian and Spanish data along the PC1 axis in the PCA (Fig.4) highlights the most important temperature (early spring and growing season) and precipitation (early summer and growing season) variables in affecting senescence, and reflects a geographical response pattern suggested by Hacket-Pain et al. (2016). For each year taken separately we see that the populations in Belgium and Spain were affected by early and late summer temperatures, respectively, in accordance with what we observed in the meteorological models. The inverted direction of the connection between Belgium and Spain for 2020 suggests that, for that year, the meteorological variables that drove the differences between the populations in the two countries changed in comparison to the three previous years. This could be explained by the unusually high temperature levels that the Belgian sites experienced in 2020.

As mentioned above, some of the climate influences on senescence timing observed in this study partially matched the very recent global analysis of Zohner et al. (2023), with temperatures in early and late summer being generally negatively and positively correlated with senescence timing, respectively. However, our detailed datasets showed a rather heterogeneous pattern, with early summer effects being stronger in the central temperate populations, while the late summer influences being most important for the southern temperate populations. Moreover, similarities between the long-term pattern documented here for the southern temperate French sites and the results of Zohner et al. (2023) were limited. This comparison, therefore, underlines the importance of combining larger scale studies with detailed regional studies like ours.

Methodological limitations

Despite of the clear differences observed in autumn phenology dynamics between populations in Spain and in Belgium, it is important to stress that the four-year dataset was too short to derive

relationships between autumn phenology and climate. As such, the results obtained should be considered in reference to the study period (2017-2020). The different responses recorded might also have been affected by the different meteorological conditions between Spain and Belgium during this period, in particular by the exceptional droughts and heatwaves observed in Belgium (Mariën et al. 2021, Mariën et al. 2022). On the other side, the very limited information that were available for the understudied senescence process in the southern temperate forests of Europe made our short-term dataset nevertheless insightful and useful.

Conclusions

Based on our results and objectives, we can draw the following conclusions which represent the novelty of the study.

(**i**) The long-term data series of autumnal phenology did not indicate a delay or an advance in the timing of senescence in southern temperate European forests in the last 25 years. This contrasts with previous analyses at the European level and indicates important spatial variability in senescence dynamics at the sub-continental level.

(**ii**) Despite differences among species becoming unclear in the long term, short-term autumnal phenological behaviour (4 years) can differ significantly amongst species at their southern limits of distribution, with only temperature affecting the senescence timing of *F. sylvatica* but both temperature and precipitation affecting the senescence timing of *Q. petraea*.

(**iii**) Autumn dynamics of temperate deciduous forest tree species differed between the central and southern areas of distribution between 2017 and 2020. In particular, while late season conditions affected senescence timing in the southern populations, the senescence dynamics of the core populations was mostly influenced by the legacy of spring – early summer conditions. Moreover, the impact of precipitation on senescence was overall larger at the central distributional area, while, for *F. sylvatica*, the senescence timing was later at the southern edge.

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450

451 **Figures and tables legend**

452 **Figure 1**. Map of Europe with red dots indicating the locations of the experimental and observational

453 sites: (1) Belgium and (2) northern Spain; the smaller green dots indicate the 9 RENECOFOR sites

454 in France.

455 **Figure 2.** LS10 (onset of leaf senescence as calculated at the French sites (proxy of OLCG, green))

456 and LS90 (advanced state of senescence as calculated at the French sites, brown) trends for aggregated

457 stands of *F. sylvatica* (6), *Q. robur* (2) and *Q. petraea* (1) from the south of France. Each point

458 represents the average LS10 or LS90 for one year across sites. Error bars are standard errors of the

459 means (n=5-8). Regression lines for the two variables are shown, together with their R^2, slope and *p*

460 value.

461 **Figure 3.** Histogram of OLCG (onset of loss of canopy greenness) for all the studied species and

462 years in Spain. Error bars are standard errors of the means (n = 9 for *P. tremula*; n = 8 for the other

463 species). The low case compact letter display (CLD) shows pairwise differences between years for a

464 same species; the capital CLD shows pairwise differences between species for a same year.

465 **Figure 4**. PCA of the conditions of the sites in Belgium (blue) and Spain (orange) in each year (shape)

466 based on the scaled and standardized values of the temperature and precipitation (T/P) in early spring

467 (*early Spr*; March + April), early summer (*early Sum*; May + June), late summer (*late Sum*; August

468 + September) and the full growth season (*grw Ssn*; May - October). The red arrows indicate the axis

469 for the respective meteorological environmental variable while the dashed grey lines connect

470 observations from the same year. Axis PC1 captures 62.7% of variability while axis PC2 captures

471 20.1%.

472 **Figure S1.** LS10 (green) and LS90 (brown) trends for the 9 sites in southern France analysed for the

473 period 1997-2019; each point represents the average LS10 or LS90 across trees for one year.

474 Regression lines for the two variables are shown.

475 **Figure S2.** Correlation between LS10 *vs*. Years slope and MAT, MAP, Altitude and Aridity Index

476 for the studied French sites. Each point represents the slope of the variation of LS10 throughout the

477 years studied for one specific site. Regression lines, R^2 coefficients and p-values are shown.

478 **Table 1.** Characteristics of the experimental sites involved. The Aridity Index was calculated with

479 the equation of Budyko (1958). *: per species

480 **Table 2.** Slopes, *p* values and R^2 of the correlations of LS10 and LS90 trends for the different French

481 sites analysed across the 1997-2019 period of measurements. Slopes with p<0.05 are in bold.

482 **Table 3.** p-values (+=<0.1; *=<0.05; **=<0.01) of the correlations of LS10 with different climatic

483 parameters for the different French sites analysed across the 1997-2019 period of measurements.

484 Temperature and precipitation data were aggregated for different periods (*growing season*, May-

485 September; *early spring*, March and April; *early summer*, May and June; *late summer*, August and

486 September) or for single months (May and June). Blue cells = positive correlations; red cells =

487 negative correlations.

488 **Table 4.** p-values (+=<0.1; *=<0.05; **=<0.01; ****=<0.0001) and R^2 of the linear models (OLCG

489 ~ Species * meteorological variables) with data from Spain (2017-2020).

490 *growing season*, May-September; *early spring*, March and April; *early summer*, May and June; *late*

491 *summer*, August and September

492 **Table 5**. p-values (+=<0.1; *=<0.05; **=<0.01; ***=<0.001; ****=<0.0001) and R^2 of the linear

493 models (OLCG ~ meteorological variables) with data from Spain and Belgium (2017-2020) separated

494 by species.

495 *growing season*, May-September; *early spring*, March and April; *early summer*, May and June; *late*

496 *summer*, August and September. Blue cells = positive correlations; red cells = negative correlations.

20

Table 6. Comparison between OLCG (onset of loss of canopy greenness) of *F. sylvatica* and *B. pendula* between Belgium and Spain for 2017-2020. *p* values of paired t-tests are shown. **ns**, not significant. *=<0.05; **=<0.01; ****=<0.0001

Table S1. Linear models (OLCG ~ Species * Year) with data from Spain (2017-2020) and Belgium (2017-2020) respectively, for all the studied species, and linear model (OLCG ~ Species * Year * Country) with combined data from the two countries (2017-2020), with only *F. sylvatica* and *B. pendula*. **=<0.01; ***=<0.001

Table S2. Table showing the mean ±SD of the four meteorological variables for temperature (Temp) and the cumulated values of four meteorological variables for precipitation (Precip) in early spring (March + April), early summer (May + June), late summer (August + September) and the full growth season (May - October) in both Belgium and Spain for all the four years considered here.

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Fig.1

Fig.2
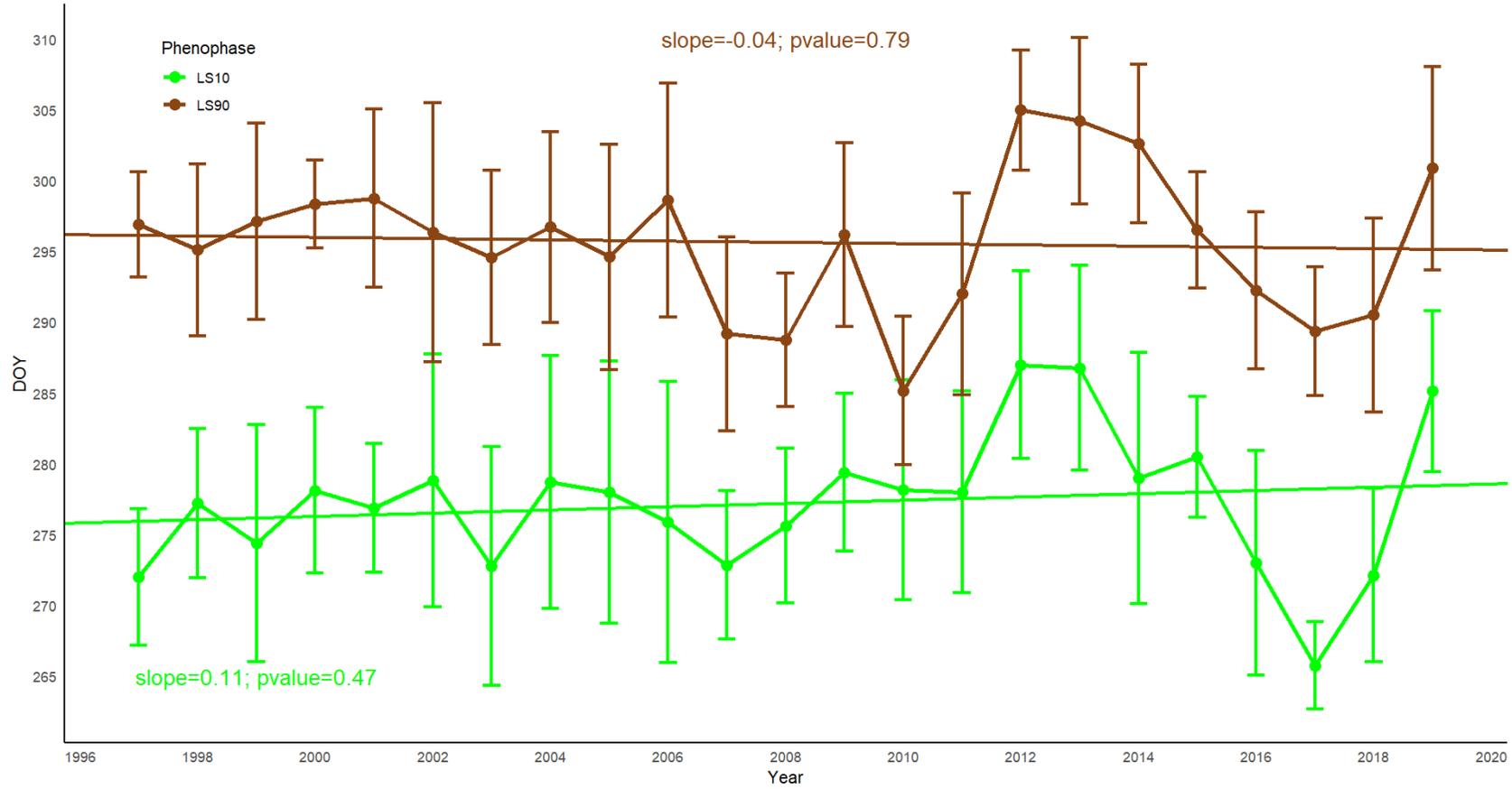
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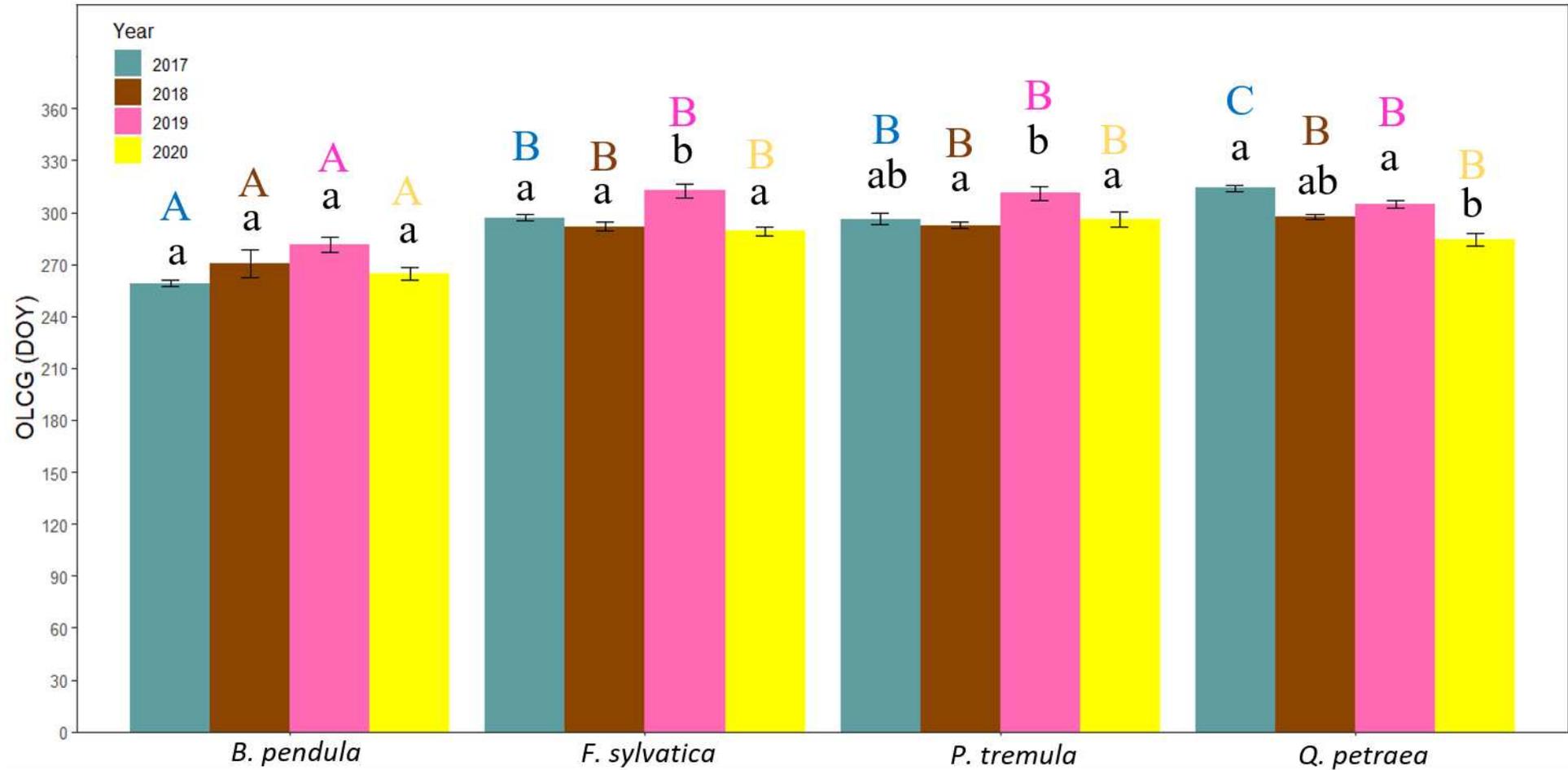
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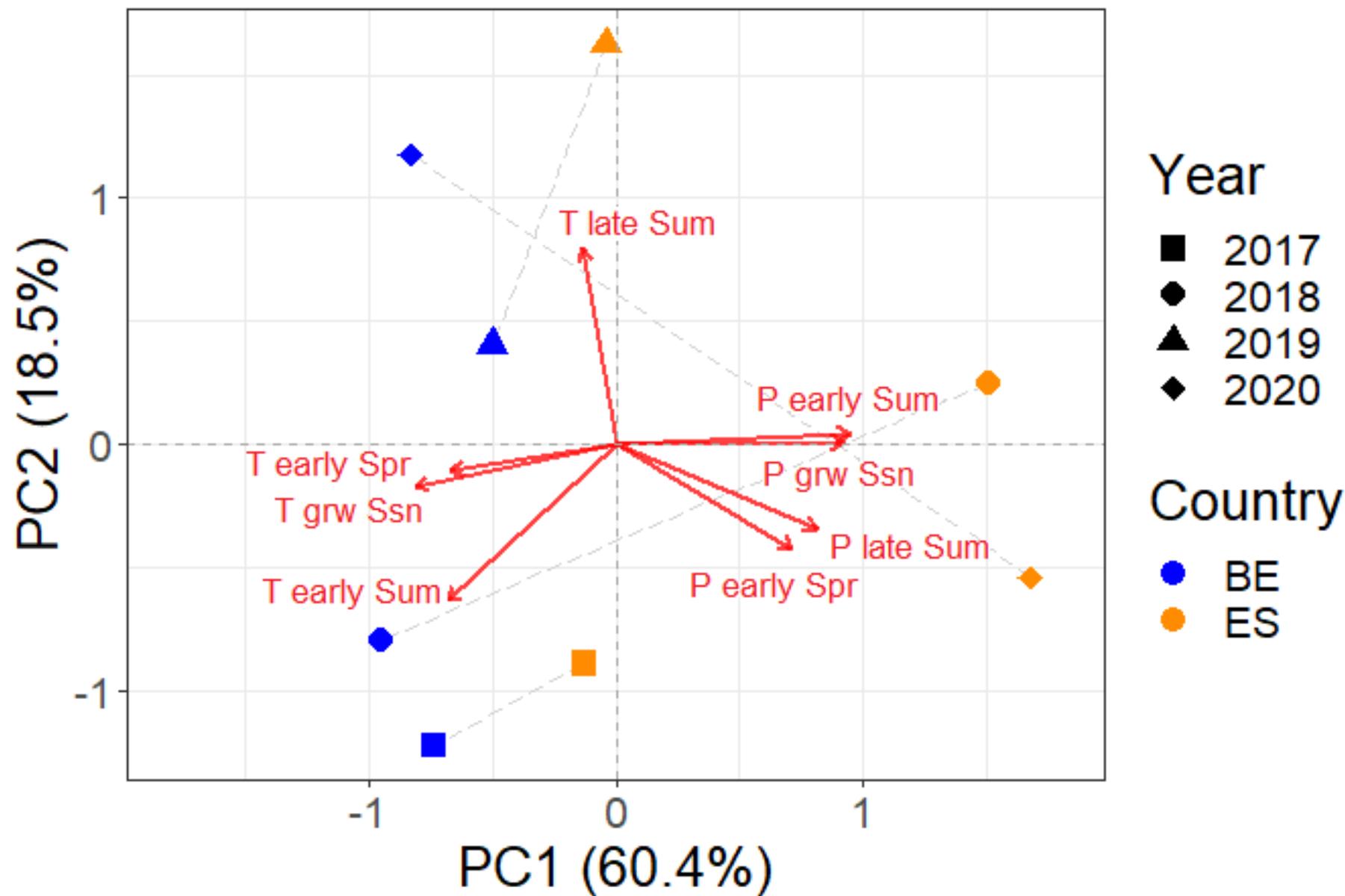
Fig.S1
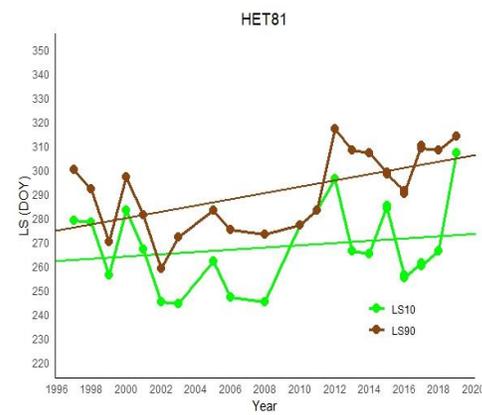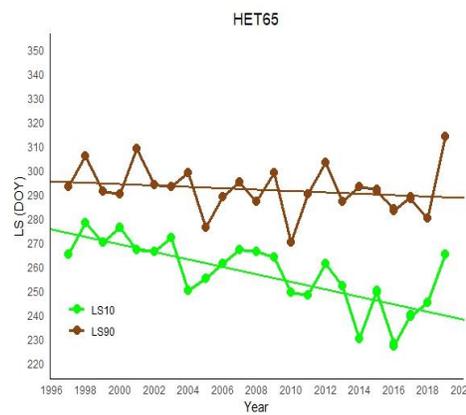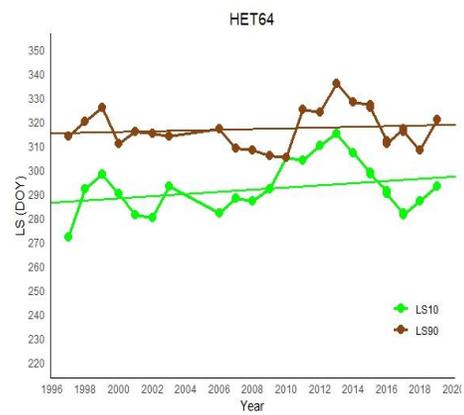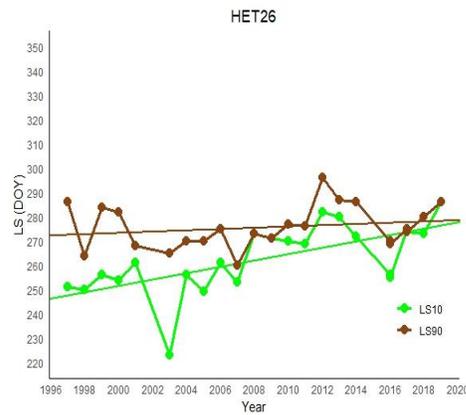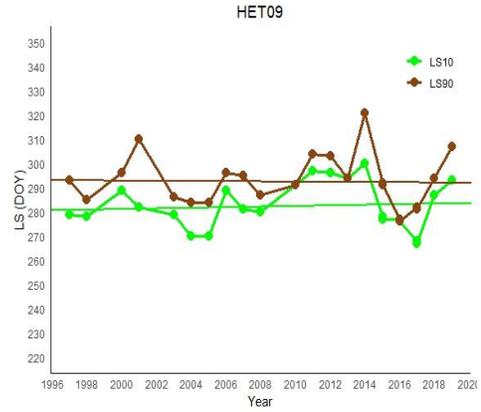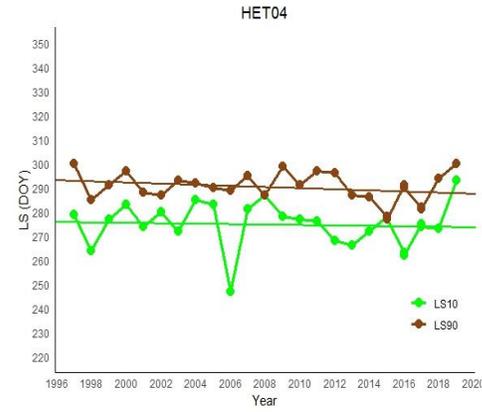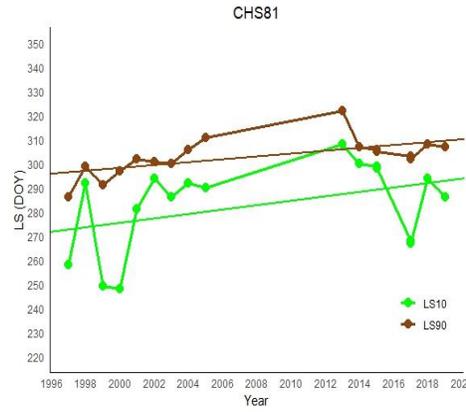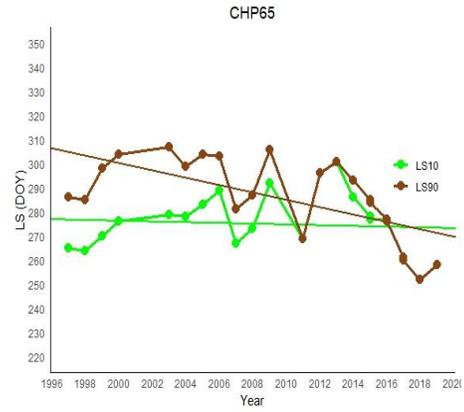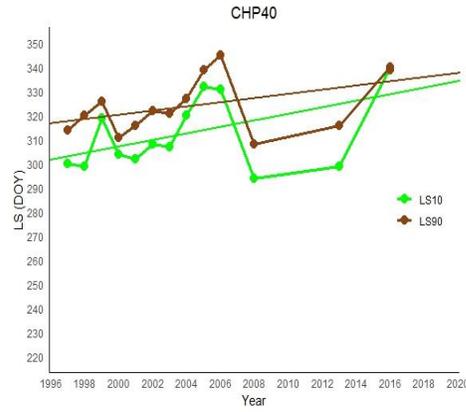
Fig.S2
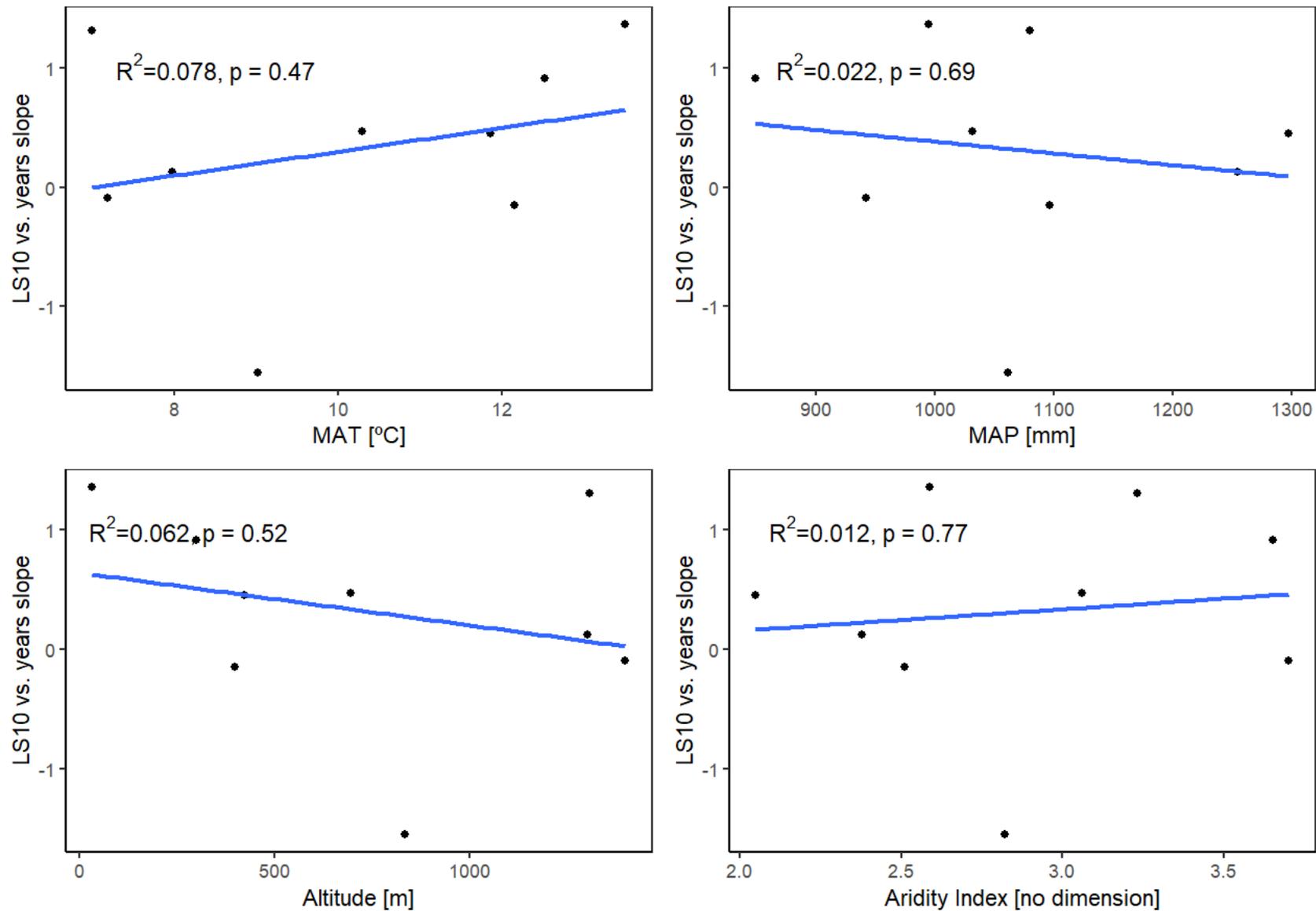
Tab.1

Site name	Country	Species	Years of experiment	Observed variables	Trees sampled*	Latitude	Longitude	Altitude	MAT	MAP	Aridity index	Koppen
Montseny	ES	P. tremula. F. sylvatica	2017-2020	CG. OLCG	8	41.76	2.468	1075	10.9	840	3.19	Csa
Serres de Milany	ES	B. pendula. Q. petraea	2017-2020	CG. OLCG	8	42.197	2.346	1050	12	873	3.58	Csa
Park of Brasschaat	BE	F. sylvatica	2017-2020	CG. OLCG	8	51.3	4.5	15	10.5	919	2.43	Cfb
Klein Schietveld	BE	B. pendula	2017-2020	CG. OLCG	12	51.35	4.617	21	10.5	919	2.43	Cfb
CHP 40	FR	Q. robur	1997-2016	LS10. LS90	36	43.737	-0.843	34	13.5	994	2.59	Csa
CHP 65	FR	Q. robur	1997-2019	LS10. LS90	36	43.202	-0.039	398	12.2	1096	2.51	Cfb
CHS 81	FR	Q. petraea	1997-2019	LS10. LS90	36	44.045	1.748	300	12.5	849	3.65	Cfb
HET 04	FR	F. sylvatica	1997-2019	LS10. LS90	36	44.13	5.799	1399	7.19	942	3.7	Csb
HET 09	FR	F. sylvatica	1997-2019	LS10. LS90	36	42.93	1.282	1302	7.98	1254	2.38	Cfb
HET 26	FR	F. sylvatica	1997-2019	LS10. LS90	36	44.917	5.294	1308	7	1079	3.23	Cwb
HET 64	FR	F. sylvatica	1997-2019	LS10. LS90	36	43.149	-0.659	423	11.9	1297	2.05	Cfb
HET 65	FR	F. sylvatica	1997-2019	LS10. LS90	36	43.026	0.436	834	9.02	1061	2.82	Cfb
HET 81	FR	F. sylvatica	1997-2019	LS10. LS90	36	43.409	2.176	697	10.3	1031	3.06	Cfb

Tab.2

Site	Main Species	Variable	Coefficient	*p* value
All Sites	**-**	LS10	0.079	0.600
		LS90	-0.072	0.650
CHP40	*Q. robur*	LS10	**1.364**	**0.048**
		LS90	0.872	0.095
CHP65	*Q. robur*	LS10	-0.152	0.700
		LS90	**-1.529**	**0.001**
CHS81	*Q. petraea*	LS10	0.916	0.108
		LS90	**0.594**	**0.010**
HET04	*F. sylvatica*	LS10	-0.092	0.741
		LS90	-0.232	0.214
HET09	*F. sylvatica*	LS10	0.126	0.687
		LS90	-0.041	0.907
HET26	*F. sylvatica*	LS10	**1.310**	**0.001**
		LS90	0.259	0.352
HET64	*F. sylvatica*	LS10	0.453	0.152
		LS90	0.153	0.533
HET65	*F. sylvatica*	LS10	**-1.556**	**0.000**
		LS90	-0.283	0.323
HET81	*F. sylvatica*	LS10	0.468	0.359
		LS90	**1.306**	**0.003**

Tab.3

Site	Meteorological values by season								Meteorological values in May and June					
	Temp growing season	Temp early spring	Temp early summer	Temp late summer	Precip growing season	Precip early spring	Precip early summer	Precip late summer	Avg Temperature May	Minimum Temperature May	Maximum Temperature May	Avg Temperature June	Minimum Temperature June	Maximum Temperature June
CHP40	+		+									*		*
CHP65									+	*	+			
CHS81									**	**	**			
HET04														
HET09		+												
HET26	*		**		+		+					*	*	**
HET64									+		+			
HET65			+						*	**				
HET81														+

Tab.4

	Temp growing season	Temp early spring	Temp early summer	Temp late summer	Precip growing season	Precip early spring	Precip early summer	Precip late summer
Species	****	****	****	****	****	****	****	****
Meteo	****	*	0.407	****	**	**	+	**
Species*Meteo	*	*	+	0.765	0.451	0.150	**	***
R^2	0.616	0.493	0.477	0.562	0.482	0.503	0.517	0.542

Tab.5

Country	Species	Temp growing season		Temp early spring		Temp early summer		Temp late summer		Precip growing season		Precip early spring		Precip early summer		Precip late summer	
		p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value	R^2
Spain	*B. pendula*	0.390	0.029	**	0.251	*	0.166	**	0.235	0.442	0.023	*	0.196	0.426	0.025	+	0.139
Spain	*P. tremula*	+	0.104	0.178	0.062	0.584	0.010	*	0.147	0.833	0.002	0.107	0.087	0.115	0.083	*	0.182
Spain	*F. sylvatica*	****	0.466	0.891	0.000	0.871	0.000	****	0.300	0.466	0.010	0.628	0.004	0.498	0.008	0.104	0.047
Spain	*Q. petraea*	****	0.700	0.700	0.006	0.127	0.084	+	0.112	***	0.357	*	0.178	****	0.581	****	0.453
Belgium	*B. pendula*	****	0.379	**	0.210	+	0.076	0.820	0.001	****	0.548	****	0.523	0.778	0.002	**	0.170
Belgium	*F. sylvatica*	****	0.350	**	0.238	*	0.139	0.748	0.003	***	0.333	***	0.351	0.404	0.020	0.272	0.034

Tab.6

Species	Year	Mean OLCG		p value	
		Belgium	**Spain**		
B. pendula	2017	284±5	259±8	0.0021	**
B. pendula	2018	246±2	253±6	0.0231	*
B. pendula	2019	273±6	284±4	0.302	ns
B. pendula	2020	273±4	263±4	0.0115	*
F. sylvatica	2017	292±5	297±5	0.0127	*
F. sylvatica	2018	263±7	295±3	< 0.0001	****
F. sylvatica	2019	293±4	315±2	< 0.0001	****
F. sylvatica	2020	283±13	286±3	0.183	ns

Tab.S1

Model variables at the study areas	Summary statistics					
SPAIN 2017-2020	**DF**	**Sum Sq**	**Mean Sq**	**F-value**	**p-value**	
Species	4	17178	4294	41.77	<0.001	***
Year	3	6449	2150	20.91	<0.001	***
Species:Year	9	2600	289	2.81	0.0054	**
Residuals	104	10691	102			**R² = 0.680**
BELGIUM 2017-2020	**DF**	**Sum Sq**	**Mean Sq**	**F value**	**p-value**	
Species	2	9706	4853	24.11	<0.001	***
Year	3	11456	3819	18.97	<0.001	***
Species:Year	5	1595	319	1.58	0.17	
Residuals	85	17108	201			**R² = 0.543**
SP + BE 2017-2020	**DF**	**Sum Sq**	**Mean Sq**	**F-value**	**p-value**	
Country	1	1336	1336	8.06	0.0053	**
Species	1	12393	12393	74.79	<0.001	***
Year	3	8889	2963	17.88	<0.001	***
Country:Species	1	1573	1573.3	9.49	0.0026	**
Country:Year	3	6818	2273	13.72	<0.001	***
Species:Year	3	171	57	0.34	0.79	
Residuals	117	19387	166			**R² = 0.593**

Tab.S2

Country	Year	Temp growing season (°C)	Temp early spring (°C)	Temp early summer (°C)	Temp late summer (°C)	Precip growing season (mm)	Precip early spring (mm)	Precip early summer (mm)	Precip late summer (mm)
Belgium	2017	16.25 ±2.3	9.15 ±0.4	17 ±2.5	16 ±2.7	431.8	95.6	84.5	163.3
	2018	17 ±3	8.9 ±5.5	17 ±0.8	17.2 ±2.4	289.1	172.8	93.2	131.7
	2019	15.8 ±3.4	9.8 ±1.8	15 ±4.6	17.1 ±2.8	371.6	118.0	115.3	115.6
	2020	16.3 ±3.2	9.8 ±3.6	15.7 ±2.5	18.7 ±2.8	385.6	92.3	94.8	156.9
Spain	2017	16.2 ±3.6	8.4 ±0.8	16 ±3.7	16.7 ±4.7	358.2	188.9	84.1	144.4
	2018	15.6 ±3.3	7.7 ±3.4	14.1 ±3.3	17.4 ±1.7	973.2	227.8	273.7	280.0
	2019	16 ±4	7.5 ±0.9	14 ±4.9	17.7 ±2.8	456.7	95.2	143.0	79.5
	2020	15.1 ±3.7	8.1 ±2.1	15 ±0.4	16.7 ±3.3	615.7	118.9	216.2	211.1