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1 What drives phenological synchrony? Warm springs advance and desynchronize flowering in  
2 oaks

3

4 Running head: Warm springs desynchronize flowering

5

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33 **Summary**

34 Annually variable and synchronous seed production, or masting, is often correlated with  
35 environmental factors and in oaks involves differential pollination success that depends on  
36 phenological synchrony in flowering. The synchronization of phenology of flowering was  
37 thought to be driven by temperature during flowering (microclimatic hypothesis). We tested  
38 an alternative, whereby phenological synchronization is driven by the timing of the onset of  
39 flowering (photoperiod-sensitivity hypothesis). This hypothesis assumes that flowering  
40 synchrony is driven by interaction between daylength and temperature, and individual  
41 variation in sensitivity to daylength as a phenological cue. We used long-term (23-26 years)  
42 records of airborne pollen in *Quercus robur*, *Q. petraea*, *Q. ilex*, and *Q. humilis*. Late pollen  
43 seasons were short, as predicted by photoperiod-sensitivity hypothesis. The onset of pollen  
44 seasons was delayed as preseason temperatures cooled over the last three decades at our  
45 Mediterranean sites, which was paralleled by shortening in pollen seasons, providing  
46 additional support for the photoperiod-sensitivity hypothesis. Global warming under the  
47 microclimatic hypothesis is predicted to lead to less frequent reproductive failures and thus  
48 decreased variability and synchrony of mast seeding. In contrast, warming under the  
49 photoperiod-sensitivity hypothesis should advance the onset of and desynchronize flowering,  
50 a pattern supported by our data. This pattern suggests that global warming will lead to more  
51 frequent vetoes and more stochastic and variable patterns of oak reproduction.

52

53 Key words: flowering onset, flowering synchrony, global warming, microclimatic variation,  
54 phenology, photoperiod sensitivity, pollen

55

56

57 **Introduction**

58 Masting, or mast seeding, is the highly variable and synchronized production of seeds  
59 by plant populations (Crone and Rapp, 2014; Kelly, 1994), that is a widespread reproductive  
60 strategy in perennial plants (Fernández-Martínez et al., 2019; Kelly and Sork, 2002;  
61 Tanentzap and Monks, 2018). The variable allocation of resources associated with masting  
62 affects plant growth, the population dynamics of plants and animals, macronutrient cycling,  
63 carbon stocks, forest regeneration, future species composition, and risk of disease in humans  
64 (Bogdziewicz et al., 2016; Clark et al., 2019; Hacket-Pain et al., 2018; Ostfeld and Keesing,  
65 2000). Masting functionally depends on economies of scale, i.e. individual plants that  
66 reproduce when other plants are also flowering have lower costs for each surviving offspring  
67 (Bogdziewicz et al., 2020c; Kelly, 1994). The proximate mechanisms driving masting, i.e.  
68 how annual variability in seed production and synchronization among individuals happen,  
69 remain poorly understood (Bogdziewicz et al., 2020a; Pearse et al., 2016).

70 Masting is frequently correlated with environmental cues such as temperature or  
71 rainfall (Bogdziewicz et al., 2020b; Koenig and Knops, 2000; Pérez-Ramos et al., 2015;  
72 Schermer et al., 2019), but little attention has been paid to the mechanisms driving these  
73 connections (Bogdziewicz et al., 2017a; Kelly et al., 2013; Koenig et al., 2015). Flowering  
74 and pollination dynamics are hypothesized to provide the mechanistic link for the observed  
75 relationship between weather and population-level seed production (Hanley et al., 2019;  
76 Koenig and Knops, 2013; Nussbaumer et al., 2018). The phenological synchrony hypothesis  
77 proposes that weather drives pollen limitation by determining the annual differences in the  
78 synchrony of flowering within a population (Koenig et al., 2015). The original formulation of  
79 the phenological synchrony hypothesis states that the phenology of flowering is driven by  
80 temperature during flowering (microclimatic hypothesis). Specifically, flowering is more  
81 synchronous in warm years when microclimatic conditions are more homogeneous,  
82 conditions that lead to lower variability in flowering time (Koenig et al., 2015). We tested an  
83 alternative hypothesis, whereby phenological synchronization is driven by the timing of the  
84 onset of flowering.

85 This alternative, known as the photoperiod-sensitivity hypothesis, assumes that  
86 flowering synchrony is driven by interaction between daylength and temperature, and  
87 individual variation in sensitivity to daylength as a phenological cue (Bogdziewicz et al.,  
88 2020a). Days in cold years are already long at the onset of warmer spring temperatures,  
89 reducing the effect of plant daylength sensitivity on flowering time and increasing population-  
90 level flowering synchrony (Fu et al., 2019c; Zohner et al., 2018). In contrast, days in warm

91 years are still short at the onset of warmer spring temperatures, preventing plants sensitive to  
92 daylength from flushing and flowering. Leaf-out and flowering in warm years thus advance  
93 only in individuals insensitive to daylength, which extends population-level flowering time  
94 and reduces synchrony. Experiments have confirmed large intraspecific variation in daylength  
95 sensitivity within populations of some species (Zohner et al., 2018). This response may  
96 consequently decrease the population-level synchrony of flowering when days are short  
97 (warm years, early spring) and increase the synchrony of flowering in late springs (cold years,  
98 late spring).

99 These two processes linking variation in weather with pollen limitation lead to  
100 contrasting predictions of the effects of global warming on flowering synchrony in plants and  
101 thus their reproductive success. Global warming under the microclimatic hypothesis should  
102 increase the frequency of years favorable for pollination, because warmer weather should  
103 generally lead to more frequent highly synchronized flowering, which in turn should reduce  
104 the interannual variability of seed production (Koenig et al., 2015). In contrast, global  
105 warming under the photoperiod-sensitivity hypothesis would lead to a lower frequency of  
106 years favorable for pollination, because warmer years would generally advance flowering in  
107 some individuals and thus desynchronize it at a population level. More frequent failures of  
108 pollination will increase the stochasticity and interannual variability of seed production  
109 (Koenig et al., 2015; Schermer et al., 2020). A better understanding of the ecophysiological  
110 processes controlling flowering phenology is thus essential for improving our understanding  
111 of the responses of trees and forests to the ongoing climate change.

112 We used long-term (23-26 years) records of airborne pollen concentrations from  
113 several locations in Europe to test the hypothesis that flowering synchrony in four oak species  
114 (*Quercus robur*, *Q. petraea*, *Q. ilex*, and *Q. humilis*) is determined by the timing of flowering  
115 onset. We used airborne pollen concentrations data as proxy of flowering times, using the  
116 length of the pollen season as an index of phenological synchrony in pollen release within the  
117 population. The link between acorn production and flowering synchrony, as measured by the  
118 length of the pollen season, has already been established in the oak populations we study here  
119 (Bogdziewicz et al., 2017a; Bogdziewicz et al., 2017b). Following relationships should hold  
120 under the photoperiod sensitivity hypothesis. First, the advanced onset of pollen production  
121 should lead to long pollen seasons. An advanced onset of pollen seasons should be in turn  
122 driven by high temperatures, as established by many studies of this topic (Fu et al., 2015; Liu  
123 et al., 2016; Peaucelle et al., 2019; Zohner et al., 2018). Second, we explored the trends  
124 (1994-2019) in timing of pollen seasons onset and their length. Here, advances in the timing

125 of pollen seasons onset driven by temperature should reduce synchrony within populations,  
126 leading to longer pollen seasons.

127

## 128 **Methods**

### 129 Study species

130 We investigated the relationships between temperature, calendar day, and airborne  
131 pollen concentrations for four oak species that are common throughout Europe. We present  
132 data for populations of two temperate oak species in Poland, *Q. petraea* and *Q. robur*, and  
133 two Mediterranean oak species in Spain, *Q. ilex* and *Q. humilis*. All species are large  
134 broadleaved trees that often dominate forests in their native ranges. They are pollinated by  
135 wind and generally self-incompatible. Flowers are produced and fertilized in spring and  
136 develop into fruits in the same year in which they were pollinated. Our previous study found  
137 that synchronous flowering was positively correlated with seed production in these  
138 populations (Bogdziewicz et al., 2017a; Bogdziewicz et al., 2017b).

139

### 140 Pollen and meteorological data

141 Data for airborne pollen for *Q. petraea* and *Q. robur* were collected at two pollen-  
142 monitoring sites in Poland for 1997-2019: Poznań (52°25'N, 16°53'E) and Rzeszów (50°01'N  
143 22°02'E). Data for *Q. ilex* and *Q. humilis* were collected at three sampling sites in Spain:  
144 Barcelona (41°23'N, 2°90'E) for 1994-2019, Bellaterra (41°30'N, 2°60'E) for 1994-2019, and  
145 Huecas in Toledo province (39°59'N, 4°13'W) for 2008-2019 (Fig. S1). Pollen grains could  
146 only be identified to genus, so the data from Poland included both *Q. robur* and the closely  
147 related species *Q. petraea*, and we analyzed the data for these two species at the community  
148 level. The pollen grains of an evergreen oak (*Q. ilex*) in Spain are distinguished from those of  
149 a deciduous species (*Q. humilis*). Other oaks in the study area included *Q. coccifera*  
150 (evergreen) and *Q. suber* (deciduous), but their densities were much lower than those of the  
151 dominating *Q. ilex* and *Q. humilis*.

152 Pollen grains were collected using Hirst traps (Hirst, 1952) specifically designed to  
153 record the concentration of atmospheric particles as a function of time. The Hirst type trap is a  
154 standard sampling method in pollen monitoring studies. For instance, in the European  
155 Aeroallergen Network, all monitoring stations use the Hirst type volumetric trap (Galan., et  
156 al. 2014). Moreover, the pollen concentrations used in this study, despite being produced in  
157 different palynological laboratories, are fully comparable, as they have been obtained  
158 following the standards of the European Aerobiology Society (Galan., et al. 2014).

159 The traps were located at a building roofs (10 – 30 m a.s.l.), and contained a built-in  
160 vacuum pump, a wind-oriented vane, and a clockwork-driven drum mounted with transparent  
161 adhesive tape that served as a medium for collecting the pollen. The sampler drum was  
162 changed weekly, and the tape was divided into seven segments (corresponding to 24-h  
163 periods). The pollen was then stained with basic fuchsine and transferred to microscope slides  
164 (Scheifinger et al., 2013). The pollen grains were identified to genus under a light microscope  
165 based on distinct morphological features. More than 10% of the total surface area of all slides  
166 was investigated following the recommendation of the European Aerobiology Society (Galán  
167 et al., 2014). We derived the length of the pollen season from the raw data for each study year  
168 as a measure of flowering synchrony (Bogdziewicz et al., 2017a; Bogdziewicz et al., 2017b;  
169 Lebourgeois et al., 2018). The length of the pollen season in Poland was determined using the  
170 95% method, whereby the season started when 2.5% of the total yearly pollen was collected  
171 and ended when 97.5% was collected (Goldberg et al., 1988). We used a cutoff of 80% for  
172 Spain due to the higher number of days with very low concentrations of pollen at the end of  
173 the season, which may have been due to the redistribution of pollen rather than additional  
174 pollen release (Bogdziewicz et al., 2017a; Fernández-Martínez et al., 2012). Data for daily air  
175 temperature and precipitation were obtained from meteorological stations within 10 km of the  
176 pollen-monitoring sites.

177

## 178 Statistical analysis

179 We began our analysis by asking whether the timing of pollen seasons onset was  
180 driven by preseason temperatures. For simplicity, we used mean daily temperatures from  
181 January to April for all sites and years; the average day of flowering onset was in April for all  
182 species (Fig. S2). Calculating these over different time periods (e.g. January – March or  
183 February – April) do not change conclusions of the analysis. We did not use more  
184 complicated approaches, like the growing degree days requirement adjusted per each site, as  
185 this may lead to illogical results when the flowering onset is very late (Fu et al., 2015, 2019c),  
186 which was the case in our dataset (unpublished). We constructed a linear mixed model  
187 (LMM), with the day of the start of the pollen season (day of the year) as a response variable  
188 and species, average preseason temperature, and their interaction as fixed effects. We next  
189 tested our prediction that advanced pollen season onset would lead to longer pollen seasons  
190 using a LMM that featured the length of the pollen seasons (in number of days) as a response  
191 variable and species, day of onset, and their interaction as fixed effects. All models included  
192 site as an intercept-only random effect to control for repeated sampling (Zuur et al., 2009).

193 We explored whether the length of the pollen season was better predicted by the  
194 timing of the season onset, as predicted by the photoperiod-sensitivity hypothesis, or by the  
195 temperature during pollen season, as predicted by the microclimatic hypothesis, by building a  
196 set of LMMs that included combinations of three predictors: the day of pollen season onset,  
197 mean temperature during the pollen season, and species. We included site as a random  
198 intercept. We then compared the models using standard Akaike information criteria (AICs)  
199 (Anderson and Burnham, 2004). We calculated the mean temperature during each pollen  
200 season as the average of daily temperatures from the first until the last day of that pollen  
201 season.

202 Finally, we used our long-term records to identify temporal trends in pollen season  
203 onset and length of the pollen season for 1994 (Spain) or 1997 (Poland) to 2019. We built two  
204 LMMs, one with the timing of the onset of the pollen season and the other with the length of  
205 the pollen season as the response. We used the interaction between year and species as a fixed  
206 effect and included site as an intercept-only random effect in both LMMs.

207 We explored models with temporal autocorrelation structures (lag-1 autocorrelation)  
208 and retained those where  $d\text{AIC} < 2$ . We fitted all models using the glmmTMB package  
209 (Brooks et al., 2017) in R using restricted maximum likelihood (REML). We tested for the  
210 statistical significance of fixed factors using the Wald type II chi-square test. Model  
211 validation by graphical inspection of residual patterns indicated normality and homogeneity.  
212 We calculated conditional (i.e. variance explained by the complete model) and marginal (i.e.  
213 variance explained by the fixed factors)  $R^2$  for the models using the sjstats package (Lüdecke,  
214 2018; Nakagawa and Schielzeth, 2017) and selected models based on the AICs using the  
215 MuMIn package (Bartoń, 2018).

216

## 217 Results

218 The timing of pollen season onset was negatively correlated with the average  
219 preseason (January-April) temperatures ( $\chi^2 = 41.09, p < 0.001$ ), which varied among species  
220 (preseason temperature  $\times$  species interaction:  $\chi^2 = 27.63, df = 2, p < 0.001$ ). Pollen season  
221 onset for *Q. robur* and *Q. petraea* advanced by 1.06 d (SE = 0.56) per 1 °C increase in the  
222 mean temperatures (Fig. 1). This effect was stronger in the Mediterranean species, advancing  
223 by 6.63 d (SE = 1.05) for *Q. humilis* and by 4.97 d (SE = 0.99) for *Q. ilex* per 1 °C increase in  
224 the preseason temperatures (conditional  $R^2 = 0.82$ , marginal  $R^2 = 0.58$ ).

225 The length of the pollen season was negatively correlated with the timing of the  
226 season onset ( $\chi^2 = 27.25, p < 0.001$ ), as predicted by the photoperiod-sensitivity hypothesis

227 (Fig. 2). A 1-d delay in flowering onset shortened the pollen season by 0.59 d (SE = 0.23) for  
228 *Q. robur* and *Q. petraea*, 0.29 d (SE = 0.15) for *Q. humilis*, and 0.62 d (SE = 0.13) for *Q. ilex*  
229 (conditional  $R^2 = 0.60$ , marginal  $R^2 = 0.20$ ).

230 The timing of pollen season onset was a better predictor of the length of the pollen  
231 season than the mean temperature during the season, supporting the photoperiod-sensitivity  
232 hypothesis (Table 1). Models that included the timing of pollen season onset and the  
233 temperature during the pollen season, or only the timing of pollen season onset, received  
234 similar AIC support ( $\Delta\text{AIC} = 1.29$ ). In contrast, the model that included temperature during  
235 the pollen season as the only predictor received little support given the data ( $\Delta\text{AIC} = 16.43$ ).  
236 In fact, when both predictors when included, the temperature was no longer significant  
237 predictor of the pollen season length ( $\beta = 0.23$ , SE = 0.59,  $p = 0.70$ ), while the onset was ( $\beta =$   
238 -0.51, SE = 0.11,  $p < 0.001$ ). These analyses indicated that the timing of flowering onset was  
239 a stronger driver of the length of the pollen season than the temperature during the pollen  
240 season.

241 We detected significant trends in both the onset of pollen seasons ( $\chi^2 = 6.70$ ,  $p =$   
242 0.009) and its duration ( $\chi^2 = 24.08$ ,  $p < 0.001$ ), which varied among the species (species  $\times$   
243 onset of flowering:  $\chi^2 = 10.86$ ,  $df = 2$ ,  $p = 0.004$ ; species  $\times$  length of the pollen season:  $\chi^2 =$   
244 13.57,  $df = 2$ ,  $p < 0.001$ ). The timing of pollen season onset for *Q. robur* and *Q. petraea* did  
245 not advance in the last decades ( $p = 0.12$ , Fig. 3). In contrast, the onset was significantly  
246 delayed by  $0.45 \text{ d y}^{-1}$  (SE = 0.15) for *Q. humilis* and by  $0.35 \text{ d y}^{-1}$  (SE = 0.15) for *Q. ilex*. The  
247 trend of delays in the pollen seasons onset shortened their length by  $1.05 \text{ d y}^{-1}$  (SE = 0.18) for  
248 *Q. ilex* (Fig. 4) but not for *Q. humilis* ( $p = 0.12$ ), in accordance with the predictions of the  
249 photoperiod-sensitivity hypothesis. The length of the pollen season did not consistently  
250 change with time ( $p = 0.64$ ) for *Q. robur* or *Q. petraea*, where no temporal trend of the onset  
251 of flowering was detected. The contrasting phenological trends in Poland and Spain were  
252 likely due to contrasting changes in temperatures the last ca. 30 years in these regions. The  
253 mean temperatures for January-April did not change in Poland but decreased in Spain (Fig.  
254 S3). We note, however, that the general trend during the last century in Spain was positive,  
255 although it slowed and reversed in the last decades (Fig. S4).

256

## 257 **Discussion**

258 Our results indicated that a late pollen seasons onset shortened their length for all  
259 species we studied, as predicted by the photoperiod-sensitivity hypothesis. The pollen season  
260 in warm years started earlier, which was correlated with long population-level flowering

261 times. Our analyses also suggested that high temperatures during the pollen seasons were not  
262 the main driver of their durations, as suggested by the microclimatic hypothesis (Koenig et  
263 al., 2015) or by studies linking flowering synchrony with pollen limitation and seed  
264 production (Bogdziewicz et al., 2017a; Bogdziewicz et al., 2017b; Lebougeois et al., 2018).  
265 Both processes can act together in driving the synchrony of flowering. However, determining  
266 whether microclimate or photoperiod sensitivity is the main driver, is important for our  
267 understanding of the processes that drive the phenological synchrony of flowering in plants,  
268 because they generate contrasting predictions of the effects of changes in global temperature  
269 on flowering synchrony and consequently seed production. Warming under the photoperiod-  
270 sensitivity hypothesis should lead to advanced flowering onsets and desynchronized  
271 flowering, a pattern supported by our data.

272 High preseason temperatures advanced onset of pollen seasons in all species, leading  
273 to long flowering seasons, supporting the predictions of the photoperiod-sensitivity  
274 hypothesis. Temperature and daylength in temperate and boreal regions interact to cause leaf-  
275 out around the optimal date (Flynn and Wolkovich, 2018; Fu et al., 2019a, 2015). The optimal  
276 timing is a trade-off between occasional late frosts and the harvesting of light (Liu et al.,  
277 2018). Daylength is hypothesized to act as a cue controlling the sensitivity of the growth of  
278 meristem cells to warm temperatures, thereby conditioning the relationship between  
279 temperature and phenology (Fu et al., 2019c). Shorter than optimal daylength reduces  
280 temperature sensitivity, thereby allowing plants to avoid precocious leaf-out that would  
281 increase the risk of frost damage. A longer than optimal daylength in turn increases  
282 temperature sensitivity, allowing leaf-out when high solar radiation is optimal for  
283 photosynthesis (Flynn and Wolkovich, 2018; Fu et al., 2019a; Malyshev et al., 2018). The  
284 sensitivity of leaf unfolding to photoperiod was recently reported to vary between species (Fu  
285 et al., 2019a). Moreover, different intraspecific sensitivities to daylength desynchronized leaf-  
286 out and subsequently flowering in several temperate species, including oaks (Zohner et al.,  
287 2018). We thus hypothesized that the negative correlation between pollen seasons onset and  
288 their length documented by our data was due to the advance of flowering in oaks insensitive  
289 to daylength, but not in individuals sensitive to daylength. Experiments and individual-level  
290 phenological observations are now required to test causality (Bogdziewicz et al., 2020a). For  
291 example, in the absence of individual plant flowering data, a long pollen season can be caused  
292 by either each tree releasing its pollen over a longer period or because trees are less  
293 synchronized with each other. In addition, experiments that simulate early (short days, high  
294 temperatures) and late (long days, high temperatures) springs in greenhouse conditions should

295 lead to desynchronization under the photoperiod-sensitivity hypothesis but not the  
296 microclimatic hypothesis.

297 The long-term changes in preseason temperature that affected the phenology of pollen  
298 production provides additional support for the photoperiod-sensitivity hypothesis. We found  
299 no trends in Poland and delayed pollen seasons onset in the Mediterranean oaks. The  
300 difference between regions in these trends of flowering paralleled the trends in preseason  
301 temperatures that decreased in Spain in the last 26 years but did not change in Poland.  
302 Importantly, the trend of delayed pollen phenology was paralleled by the shortening of the  
303 pollen seasons for *Q. ilex*, as predicted by the photoperiod-sensitivity hypothesis. The changes  
304 in pollen production phenology for *Q. humilis*, though, did not lead to trends in the length of  
305 the pollen seasons, despite the similar rate of change in the timing of the pollen season onset.  
306 We hypothesized that this result follows different sensitivity to daylength in the two oak  
307 species. Recent analyses found large interspecific variations in the effects of photoperiod on  
308 the sensitivity of plants to changes in preseason temperature (Fu et al., 2019a, 2019b; Zohner  
309 et al., 2018, 2016). In support, our models indicated that the effect of phenology of pollen  
310 season onset on the length of the pollen season was twice as large for *Q. ilex* than *Q. humilis*.

311 Our results suggest that the interspecific variation in phenological sensitivity led to  
312 species-specific effects of long-term temperature trends on flowering synchrony. Possible  
313 consequences include asymmetrical effects on pollen limitation, as predicted by the  
314 phenological synchrony hypothesis (Koenig et al., 2015; Pesendorfer et al., 2016; Wagenius  
315 et al., 2020), but also on changes in gene flow and biotic interactions (Elzinga et al., 2007;  
316 Jump and Peñuelas, 2005). The changes in flowering synchrony induced by temperature are  
317 also likely to be associated with similar changes in the phenology of leaf unfolding (Zohner et  
318 al., 2018). Leaf-out synchrony in turn affects insect herbivory (Pearse et al., 2015), which  
319 may strongly affect seed production; insect herbivory in *Q. ilex* can decrease seed set by half  
320 (Canelo et al., 2018), which can create differences in the responses of species to global  
321 warming that will have asymmetrical effects on fecundity in different plant species. Thus, a  
322 comprehensive understanding of the species-specific differences of the effects of global  
323 warming on flowering is essential for improving our understanding of the responses of forests  
324 to the ongoing climatic change (McDowell et al., 2020).

325 Our results provide support for a novel hypothesis linking variation in weather with  
326 flowering synchrony in masting oaks. Flowering synchrony drives pollen limitation in oaks,  
327 which in turn is believed to interact with the dynamics of plant resources in driving mast  
328 seeding (Koenig et al., 2015; Pesendorfer et al., 2016; Schermer et al., 2019). Desynchronized

329 flowering vetoes reproduction, which forces plants to conserve resources for subsequent  
330 years, so more frequent interference leads to more stochastic and variable patterns of  
331 reproduction (Pearse et al., 2016; Schermer et al., 2020). To the extent that phenological  
332 synchrony is involved in determining variable seed production, global warming under the  
333 microclimatic hypothesis is predicted to lead to less frequent vetoes (more frequent high  
334 flowering synchrony years), thereby decreasing masting intensity (Koenig et al., 2015). We  
335 found support for the hypothesis that predicts the opposite: global warming will lead to more  
336 frequent vetoes, i.e. more frequent desynchronized flowering. These effects will depend on  
337 the regional trends in temperature and will be asymmetrical among species, as our results  
338 demonstrate. Studies of long-term trends in fecundity have reported both increases and  
339 decreases in mean reproduction in forest species, but we do not know what drives these  
340 differences (Bogdziewicz et al., 2020c; Mutke et al., 2005; Pesendorfer et al., 2020; Redmond  
341 et al., 2012; Richardson et al., 2005). A mechanistic understanding of the links between  
342 climatic variation and plant reproduction will help to identify these drivers.

343

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353

#### 354 **Contributions**

355 MB conceived the study, run the analysis, and drafted the manuscript. All authors collected  
356 data, participated in the evaluation of the results, contributed to text editing and approved the  
357 final version.

358

#### 359 **Literature**

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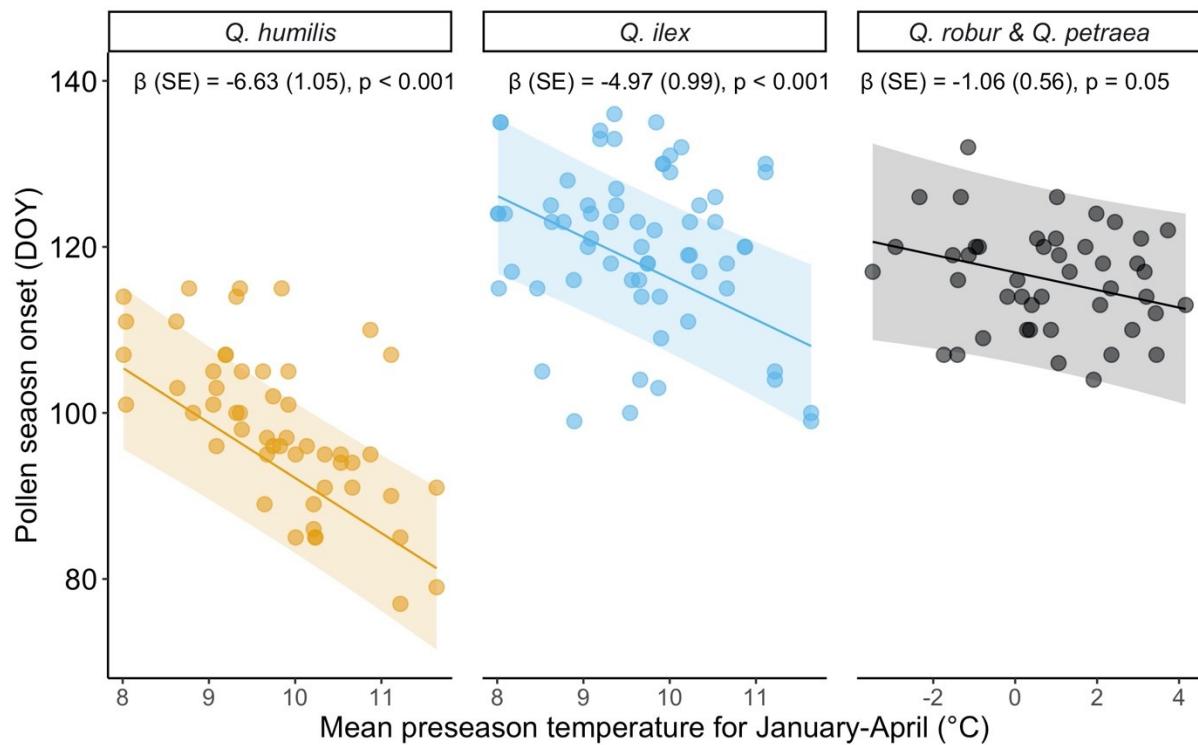
567 Table 1. Model selection. Models are ranked by Akaike's information criterion adjusted for  
568 small sample size (AICc), and w indicates model weight. Each model is a Gaussian LMM,  
569 with ar1 temporal autocorrelation structure and plot included as a random intercept.

<b>Model</b>	<b>df</b>	<b>LogLik</b>	<b>AICc</b>	<b>ΔAIC</b>	<b>w</b>
Flowering onset + species	7	-586.35	1187.4	0	0.66
Flowering onset + temperature during flowering + species	8	-585.89	1188.7	1.29	0.34
Temperature during flowering + species	7	-594.56	1203.9	16.43	0
Null model (random effect only)	4	-610.17	1228.6	41.18	0

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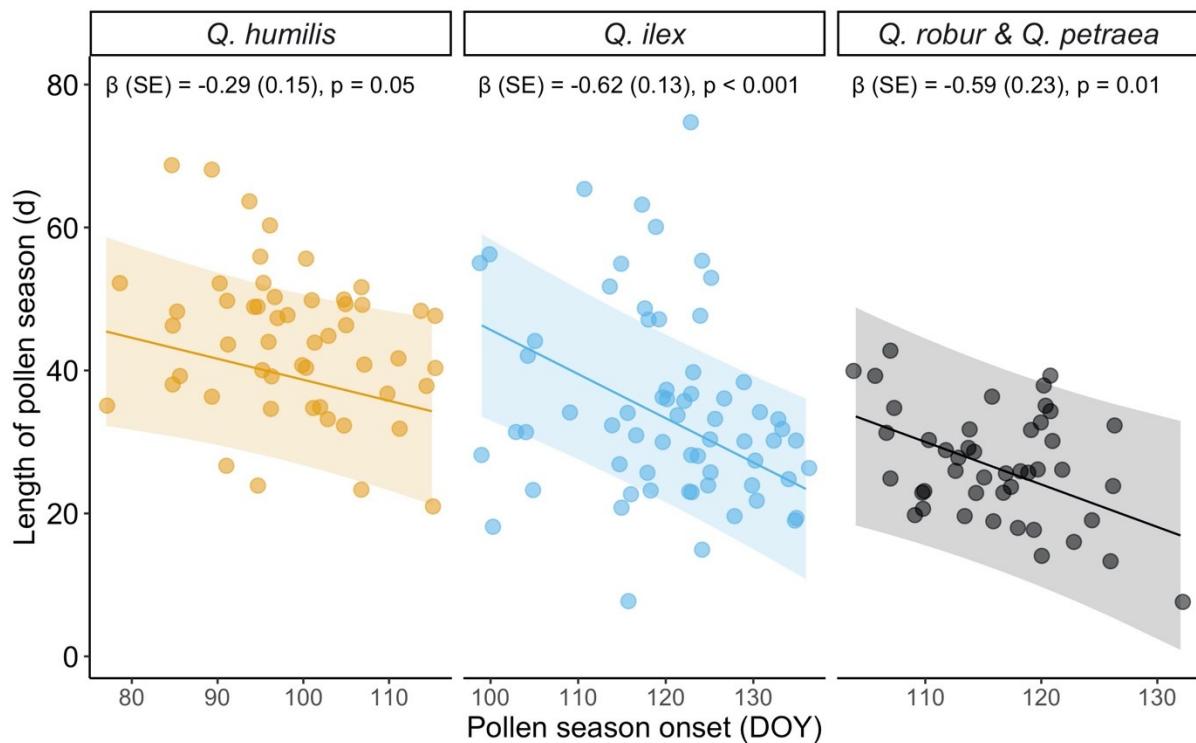
572 Figure 1. Warmer preseason temperatures advance the timing of pollen season onset (day of  
 573 the year, DOY). The lines are based on significant LMM predictions, and the shading  
 574 indicates the 95% confidence intervals,  $\beta$  shows effect sizes and associated statistics. Points  
 575 are the per-site, per-year observations, based on 22-yr in *Q. robur* (2 sites, Poland), 25-yr for  
 576 *Q. humilis* (2 sites, Spain), and 25-yr data set of pollen records in *Q. ilex* at two sites and 12  
 577 years at one site (all Spain).



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581 Figure 2. Late pollen seasons are short. The lines are based on significant LMM predictions,  
582 and the shading indicates the 95% confidence intervals,  $\beta$  shows effect sizes and associated  
583 statistics. Points are the per-site, per-year observations, based on 22-yr in *Q. robur* (2 sites,  
584 Poland), 25-yr for *Q. humilis* (2 sites, Spain), and 25-yr data set of pollen records in *Q. ilex* at  
585 two sites and 12 years at one site (all Spain).

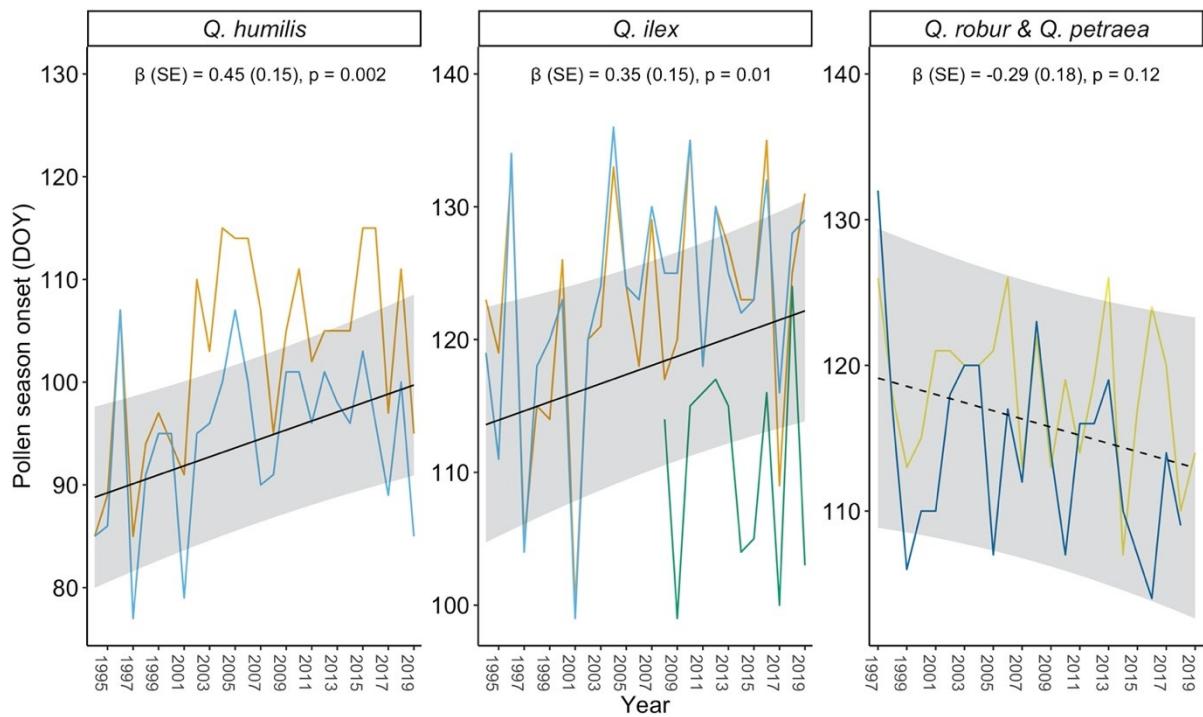
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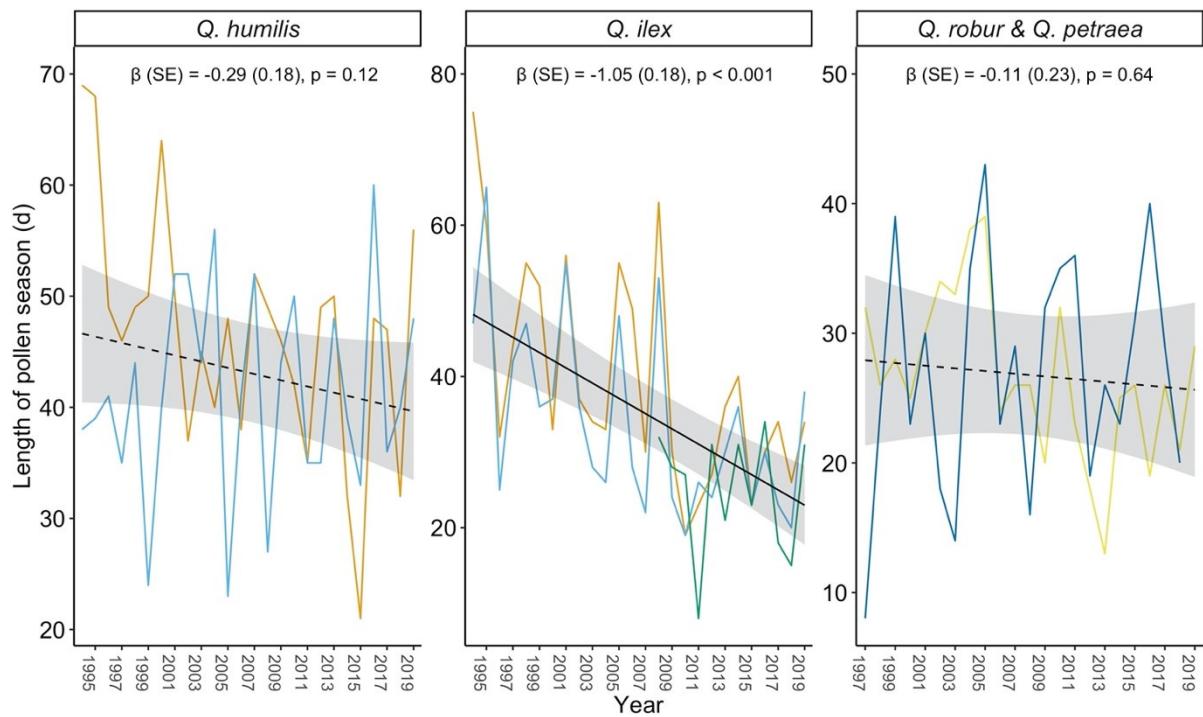
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589 Figure 3. Temporal changes in the timing of pollen season onset. The colored lines represent  
 590 sites, prediction lines are based on an LMM, and the shading indicates the 95% confidence  
 591 intervals,  $\beta$  shows effect sizes and associated statistics. The model was based on a 22-y data  
 592 set at two sites in Poland (Poznań, yellow; Rzeszów, blue) for *Q. robur* and *Q. petraea*, 25-y  
 593 data set for *Q. humilis* (two sites, Spain), and 25-y data set of pollen records at two sites  
 594 (Barcelona, orange; Bellaterra, light blue) and a 12-y data set at one site (Huecas, green) for  
 595 *Q. ilex*.



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601 Figure 5. Temporal changes in the length of the pollen seasons. The colored lines represent  
 602 sites, prediction lines are based on an LMM, and the shading indicates the 95% confidence  
 603 intervals,  $\beta$  shows effect sizes and associated statistics. The model was based on a 22-y data  
 604 set at two sites in Poland (Poznań, yellow; Rzeszów, blue) for *Q. robur* and *Q. petraea*, 25-y  
 605 data set for *Q. humilis* (two sites, Spain), and 25-y data set of pollen records at two sites  
 606 (Barcelona, orange; Bellaterra, light blue) and a 12-y data set at one site (Huecas, green) for  
 607 *Q. ilex*.



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