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

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ABSTRACT

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

1. Introduction

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

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synchronization among individuals happen, remain poorly understood (Bogdziewicz et al., 2020a; Pearse et al., 2016).

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

This alternative, known as the photoperiod-sensitivity hypothesis, assumes that flowering synchrony is driven by interaction between daylength and temperature, and individual variation in sensitivity to daylength as a phenological cue (Bogdziewicz et al., 2020a). Days in cold years are already long at the onset of warmer spring temperatures, reducing the effect of plant daylength sensitivity on flowering time and increasing population-level flowering synchrony (Fu et al., 2019c; Zohner et al., 2018). In contrast, days in warm years are still short at the onset of warmer spring temperatures, preventing plants sensitive to daylength from flushing and flowering. Leaf-out and flowering in warm years thus advance only in individuals insensitive to daylength, which extends population-level flowering time and reduces synchrony. Experiments have confirmed large intraspecific variation in daylength sensitivity within populations of some species (Zohner et al., 2018). This response may consequently decrease the population-level synchrony of flowering when days are short (warm years, early spring) and increase the synchrony of flowering in late springs (cold years, late spring).

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

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

2. Methods

2.1. Study species

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

2.2. Pollen and meteorological data

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

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

The traps were located at a building roofs (10 – 30 m a.s.l.), and contained a built-in vacuum pump, a wind-oriented vane, and a clockwork-driven drum mounted with transparent adhesive tape that served as a medium for collecting the pollen. The sampler drum was changed weekly, and the tape was divided into seven segments (corresponding to 24-h periods). The pollen was then stained with basic fuchsine and transferred to microscope slides (Scheifinger et al., 2013). The pollen grains were identified to genus under a light microscope based on distinct morphological features. More than 10% of the total surface area of all slides was investigated following the recommendation of the European Aerobiology Society (Galán et al., 2014). We derived the length of the pollen season from the raw data for each study year as a measure of flowering synchrony (Bogdziewicz et al., 2017a, b; Lebourgeois et al., 2018). The length of the pollen season in Poland was determined using the 95% method, whereby the season started when

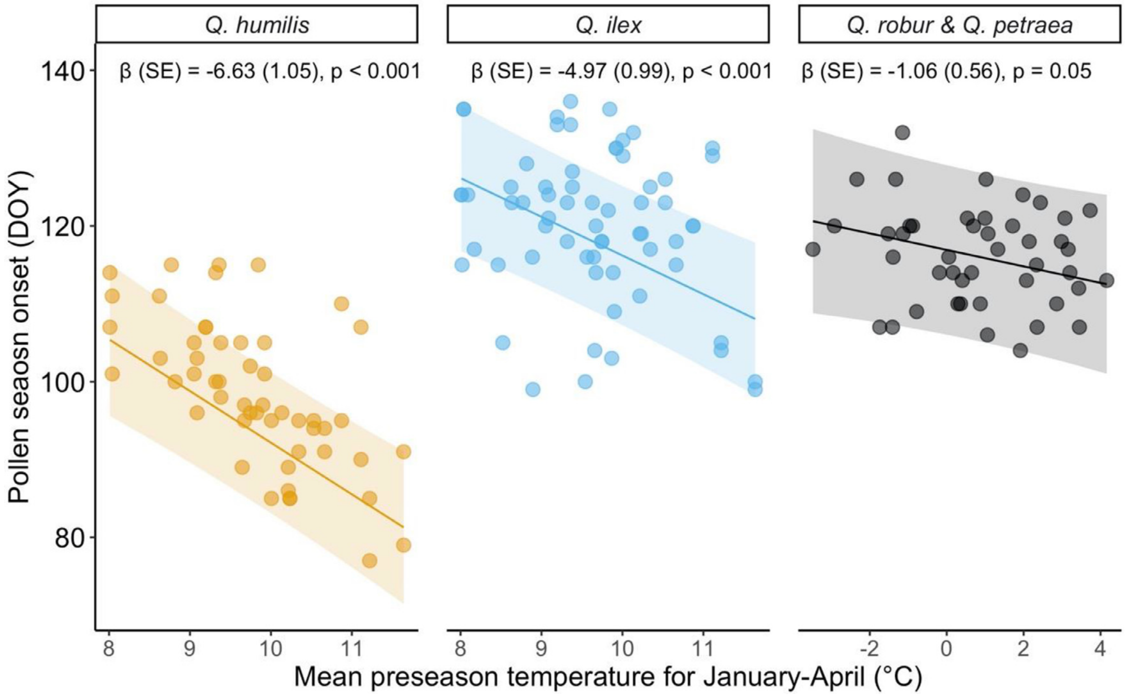

Fig. 1. Warmer preseason temperatures advance the timing of pollen season onset (day of the year, DOY). The lines are based on significant LMM predictions, and the shading indicates the 95% confidence intervals, β shows effect sizes and assocaited statistics. Points are the per-site, per-year observations,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

2.5% of the total yearly pollen was collected and ended when 97.5% was collected (Goldberg et al., 1988). We used a cutoff of 80% for Spain due to the higher number of days with very low concentrations of pollen at the end of the season, which may have been due to the redistribution of pollen rather than additional pollen release (Bogdziewicz et al., 2017a; Fernández-Martínez et al., 2012). Data for daily air temperature and precipitation were obtained from meteorological stations within 10 km of the pollen-monitoring sites.

2.3. Statistical analysis

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

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

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

We explored models with temporal autocorrelation structures (lag-1 autocorrelation) and retained those where dAIC $<$ 2. We fitted all models using the glmmTMB package (Brooks et al., 2017) in R using restricted maximum likelihood (REML). We tested for the statistical significance of fixed factors using the Wald type II chi-square test. Model validation by graphical inspection of residual patterns indicated normality and homogeneity. We calculated conditional (i.e. variance explained by the complete model) and marginal (i.e. variance explained by the fixed factors) R^2 for the models using the sjstats package (Lüdecke, 2018; Nakagawa and Schielzeth, 2017) and selected models based on the AICs using the MuMIn package (Bartoń, 2020).

3. Results

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

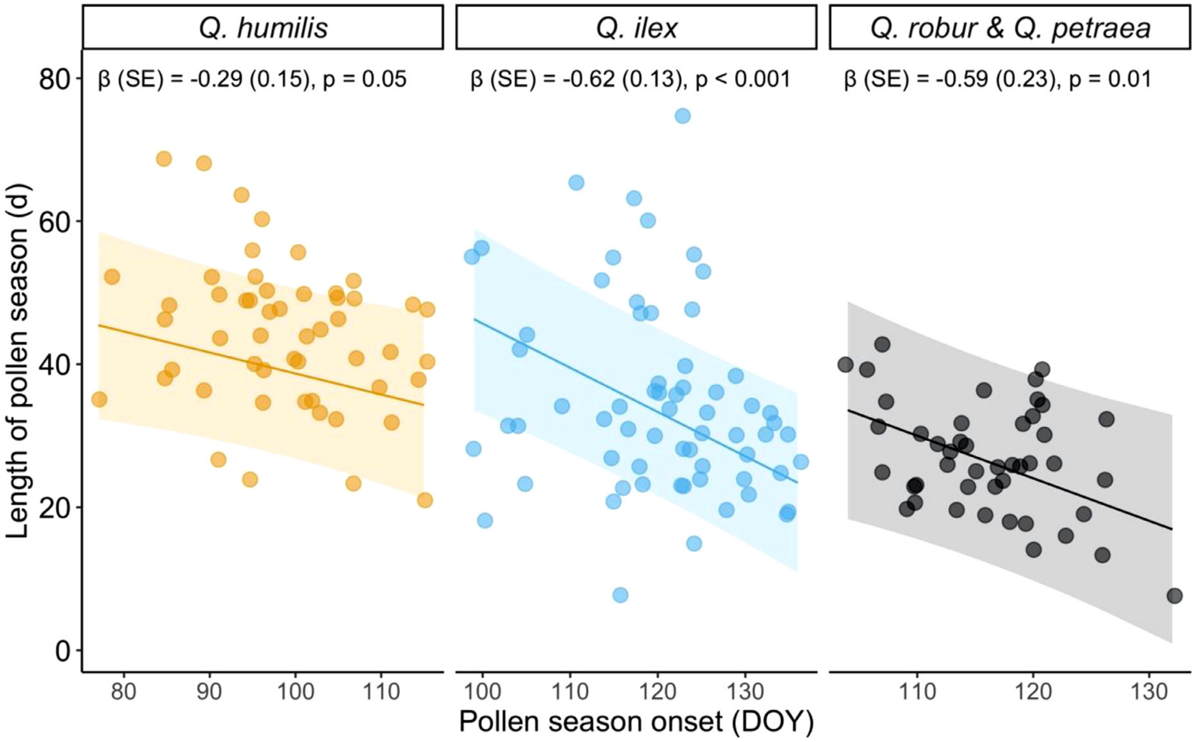

Fig. 2. Late pollen seasons are short. The lines are based on significant LMM predictions, and the shading indicates the 95% confidence intervals, β shows effect sizes and assocaited statistics. Points are the per-site, per-year observations, based on 22-yr in *Q. robur* (2 sites, Poland), 25-yr for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

The length of the pollen season was negatively correlated with the timing of the season onset ($\chi^2 = 27.25, p < 0.001$), as predicted by the photoperiod-sensitivity hypothesis (Fig. 2). A 1-d delay in flowering onset shortened the pollen season by 0.59 d (SE = 0.23) for *Q. robur* and *Q. petraea*, 0.29 d (SE = 0.15) for *Q. humilis*, and 0.62 d (SE = 0.13) for *Q. ilex* (conditional $R^2 = 0.60$, marginal $R^2 = 0.20$).

The timing of pollen season onset was a better predictor of the length of the pollen season than the mean temperature during the season, supporting the photoperiod-sensitivity hypothesis (Table 1). Models that included the timing of pollen season onset and the temperature during the pollen season, or only the timing of pollen season onset, received similar AIC support (ΔAIC = 1.29). In contrast, the model that included temperature during the pollen season as the only predictor received little support given the data (ΔAIC = 16.43). In fact, when both predictors when included, the temperature was no longer significant predictor of the pollen season length (β = 0.23, SE = 0.59, $p = 0.70$), while the onset was (β = −0.51, SE = 0.11, $p < 0.001$). These analyses indicated that the timing of flowering onset was a stronger driver of the length of the pollen season than the temperature during the pollen season.

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

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

Model	df	LogLik	AICc	ΔAIC	w
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

4. Discussion

Our results indicated that a late pollen seasons onset shortened their length for all species we studied, as predicted by the photoperiod-sensitivity hypothesis. The pollen season in warm years started earlier, which was correlated with long population-level flowering times. Our analyses also suggested that high temperatures during the pollen seasons were not the main driver of their durations, as suggested by the microclimatic hypothesis (Koenig et al., 2015) or by studies linking flowering synchrony with pollen limitation and seed production (Bogdziewicz et al., 2017a, b; Lebourgeois et al., 2018). Both processes can act together in driving the synchrony of flowering. However, determining whether microclimate or photoperiod sensitivity is the main driver, is important for our understanding of the processes that drive the phenological synchrony of flowering in plants, because they

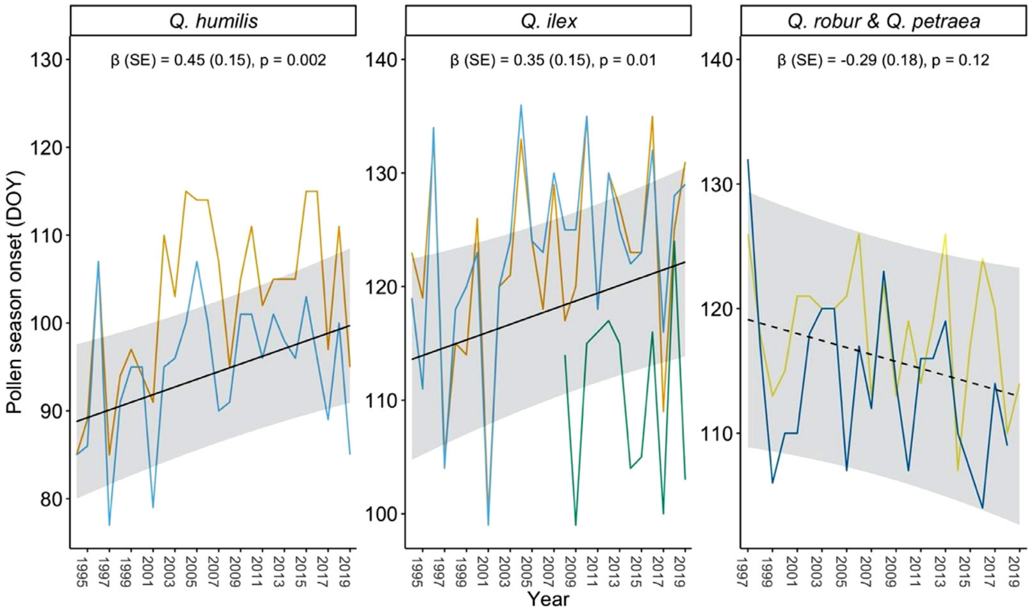

Fig. 3. Temporal changes in the timing of pollen season onset. The colored lines represent sites, prediction lines are based on an LMM, and the shading indicates the 95% confidence intervals, β shows effect sizes and assocaited statistics. The model was based on a 22-y data set at two sites in Poland (Poznań, yellow; Rzeszów, blue) for *Q. robur* and *Q. petraea*, 25-y data set for *Q. humilis* (two sites, Spain), and 25-y data set of pollen records at two sites (Barcelona, orange; Bellaterra, light blue) and a 12-y data set at one site (Huecas, green) for *Q. ilex*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

generate contrasting predictions of the effects of changes in global temperature on flowering synchrony and consequently seed production. Warming under the photoperiod-sensitivity hypothesis should lead to advanced flowering onsets and desynchronized flowering, a pattern supported by our data.

High preseason temperatures advanced onset of pollen seasons in all species, leading to long flowering seasons, supporting the predictions of the photoperiod-sensitivity hypothesis. Temperature and daylength in temperate and boreal regions interact to cause leaf-out around the optimal date (Flynn and Wolkovich, 2018; Fu et al., 2019a, 2015). The optimal timing is a trade-off between occasional late frosts and the harvesting of light (Liu et al., 2018). Daylength is hypothesized to act as a cue controlling the sensitivity of the growth of meristem cells to warm temperatures, thereby conditioning the relationship between temperature and phenology (Fu et al., 2019c). Shorter than optimal daylength reduces temperature sensitivity, thereby allowing plants to avoid precocious leaf-out that would increase the risk of frost damage. A longer than optimal daylength in turn increases temperature sensitivity, allowing leaf-out when high solar radiation is optimal for photosynthesis (Flynn and Wolkovich, 2018; Fu et al., 2019a; Malyshev et al., 2018). The sensitivity of leaf unfolding to photoperiod was recently reported to vary between species (Fu et al., 2019a). Moreover, different intraspecific sensitivities to daylength desynchronized leaf-out and subsequently flowering in several temperate species, including oaks

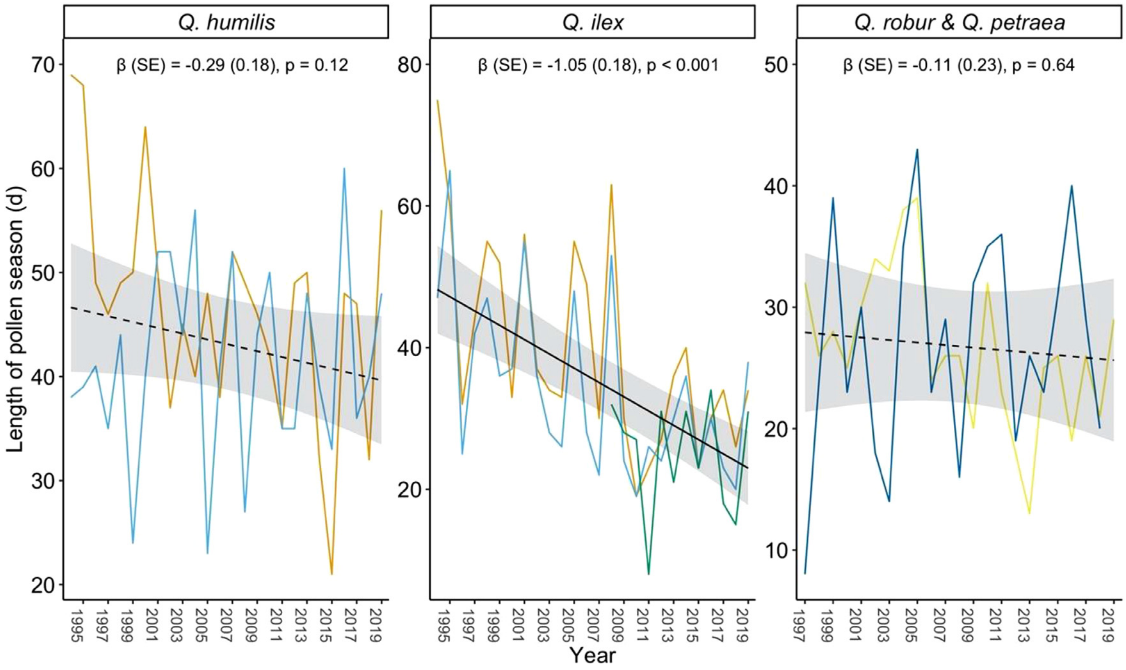

Fig. 4. Temporal changes in the length of the pollen seasons. The colored lines represent sites, prediction lines are based on an LMM, and the shading indicates the 95% confidence intervals, β shows effect sizes and assocaited statistics. The model was based on a 22-y data set at two sites in Poland (Poznań, yellow; Rzeszów, blue) for *Q. robur* and *Q. petraea*, 25-y data set for *Q. humilis* (two sites, Spain), and 25-y data set of pollen records at two sites (Barcelona, orange; Bellaterra, light blue) and a 12-y data set at one site (Huecas, green) for *Q. ilex*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Zohner et al., 2018). We thus hypothesized that the negative correlation between pollen seasons onset and their length documented by our data was due to the advance of flowering in oaks insensitive to daylength, but not in individuals sensitive to daylength. Experiments and individual-level phenological observations are now required to test causality (Bogdziewicz et al., 2020a). For example, in the absence of individual plant flowering data, a long pollen season can be caused by either each tree releasing its pollen over a longer period or because trees are less synchronized with each other. In addition, experiments that simulate early (short days, high temperatures) and late (long days, high temperatures) springs in greenhouse conditions should lead to desynchronization under the photoperiod-sensitivity hypothesis but not the microclimatic hypothesis.

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

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

Our results provide support for a novel hypothesis linking variation in weather with flowering synchrony in masting oaks. Flowering synchrony drives pollen limitation in oaks, which in turn is believed to interact with the dynamics of plant resources in driving mast seeding (Koenig et al., 2015; Pesendorfer et al., 2016; Schermer et al., 2019). Desynchronized flowering vetoes reproduction, which forces plants to conserve resources for subsequent years, so more frequent interference leads to more stochastic and variable patterns of reproduction (Pearse et al., 2016; Schermer et al., 2020). To the extent that phenological synchrony is involved in determining variable seed production, global warming under the microclimatic hypothesis is predicted to lead to less frequent vetoes (more frequent high flowering synchrony years), thereby decreasing masting intensity (Koenig et al., 2015). We found support for the hypothesis that predicts the opposite: global warming will lead to more frequent vetoes, i.e. more frequent desynchronized flowering. These effects will depend on the regional trends in temperature and will be asymmetrical among species, as our results demonstrate. Studies of long-term trends in fecundity have reported both increases and decreases in mean reproduction in forest species, but we do not know what drives these differences (Bogdziewicz et al., 2020c; Mutke et al., 2005; Pesendorfer et al., 2020; Redmond et al., 2012; Richardson et al., 2005). A mechanistic understanding of the links between climatic variation and plant reproduction will help to identify these drivers.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Contributions

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

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108140.

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