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Flower phenology as a disruptor of the fruiting dynamics in temperate oak species.

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Summary

- Many perennial plants display masting, *i.e.*, fruiting with strong interannual variations, irregular and synchronized between trees within the population. Here, we tested the hypothesis that the early flower phenology in temperate oak species promotes stochasticity into their fruiting dynamics, which could play a major role in tree reproductive success.
- From large field monitoring network, we compared the pollen phenology between temperate and Mediterranean oak species. Then, focusing on temperate oak species, we explored the influence of the weather around the time of bud-burst and flowering on seed production, and simulated with a mechanistic model the consequences an evolutionary shifting of flower phenology would have on fruiting dynamics.
- Temperate oak species release pollen earlier in the season than Mediterranean oak species. Such early flowering in temperate oak species results in pollen being often released during unfavorable weather conditions and resulting in frequent reproductive failure. If pollen release was delayed due to natural selection, fruiting dynamics would exhibit much reduced stochastic variation.
- We propose that early flower phenology might be adaptive by making mast-seeding years rare and unpredictable, which would greatly help controlling the dynamics of seed consumers.

Key words: masting; oak species; pollen phenology; resource budget model; stochastic mast-seeding

Introduction

Reproduction in many perennial and wind-pollinated plant species is characterized by masting, *i.e.*, synchronized and highly variable levels of seed production over the years within a population (Janzen, 1976; Kelly & Sork, 2002). Masting is known to strongly impact the demography and evolution of seed consumers (Yang *et al.*, 2010; Venner *et al.*, 2011; Gamelon *et al.*, 2013; Pélisson *et al.*, 2013; Rey *et al.*, 2015; Bogdziewicz *et al.*, 2016), with cascading effects on forest biodiversity dynamics together with major economical and societal issues (*e.g.*, forest regeneration, disease propagation) (Crawley, 2000; Ostfeld & Keesing, 2000; Frey *et al.*, 2007; Bogdziewicz & Szymkowiak, 2016). Despite the increasing number of studies addressing the issue of masting and its consequences for ecosystem functioning and service provisioning, its proximate causes remain difficult to disentangle mainly due to the diversity of candidate mechanisms possibly interacting and the strong stochasticity (in the sense of unpredictability for observers or seed consumers) in the fruiting dynamics (Crone & Rapp, 2014; Pearse *et al.*, 2016; Vacchiano *et al.*, 2018).

Fruiting of mast-seeding species, besides fluctuating strongly and synchronously over the years, is characterized by negative temporal autocorrelation (Sork *et al.*, 1993; Herrera *et al.*, 1998; Koenig & Knops, 2000; Koenig *et al.*, 2003). Such autocorrelation is classically interpreted as resulting from the resource depletion of the trees following mast-seeding years, which prevents them from producing flowers and seeds the following year (*i.e.*, resource depletion hypothesis, Monks & Kelly, 2006; Barringer *et al.*, 2013; Crone *et al.*, 2009, but see Kelly *et al.*, 2013). Consequently, the fruiting dynamics are potentially extremely asymmetrical, with lean-seeding years consistently occurring after a mast-seeding year (a deterministic component of masting due to reserve depletion of trees) while mast-seeding years may not systematically follow one lean-seeding year. This irregularity in the occurrence of mast-seeding years (called hereafter the stochastic component of masting corresponding to the fluctuations not explained by the negative temporal autocorrelation) would depend on weather conditions possibly affecting resource acquisition (Smail *et al.*, 2011), flower development, pollination and fertilization of female flowers (Cecich & Sullivan, 1999; Koenig *et al.*, 2015; Pearse *et al.*, 2015; Sabit *et al.*, 2016; Bogdziewicz *et al.*, 2017a; Schermer *et al.*, 2019) or even fruit ripening (Richardson *et al.*, 2005; Pérez-Ramos *et al.*, 2015; Chang-Yang *et al.*, 2016; Buechling *et al.*, 2016). Furthermore, such weather effect can act as ‘environmental veto’ by nearly completely preventing flower or seed

development at the tree population scale (Feret *et al.*, 1982; Cecich *et al.*, 1999; Bogdziewicz *et al.*, 2018a, 2019).

A promising avenue to understand both the proximate and evolutionary causes of masting is to identify the key tree life-history traits governing the stochastic component of masting. Flower phenology would be a serious candidate as its evolutionary change (*i.e.*, the timing of flowering at the population level that may shift independently of any climate change) could theoretically act on masting in two complementary ways: (i) by modifying the likelihood of late frost events at the vulnerable flowering stage (García-Mozo *et al.*, 2001; Augspurger, 2009) that can act as environmental veto and may strongly impede fruit set (Feret *et al.*, 1982; Cecich & Sullivan 1999; Bogdziewicz *et al.*, 2018a); (ii) by partly setting the weather conditions influencing pollen maturation and release that would play a key role in pollen limitation and then in fruiting success. In this sense, high spring temperature has recently been shown to favour phenological synchronization between trees, by reducing the flowering period, which in turn would increase pollination success and promote mast-seeding years (Koenig *et al.*, 2008, 2012, 2015; Bogdziewicz *et al.*, 2017a). High spring temperature also increases the annual amount of airborne pollen that can be mobilized for reproduction. Schermer *et al.* (2019), from analyzing the interannual variation of both airborne pollen amount and its temporal distribution, suggested that pollen limitation in European temperate oaks would rely more on the annual amount of airborne pollen than on tree synchrony.

Based on the above findings, the aim of our study was to test the hypothesis that flower phenology is a key trait driving the stochastic component of masting in two temperate oak species (*Quercus petraea* and *Q. robur*) by keeping mast-seeding years rare and unpredictable. We thus examined the consequences of an evolutionary shift in the flower phenology on their masting. For this purpose, we combined empirical and theoretical approaches. First, we tested the hypothesis that pollen phenology is early in these two temperate oak species in comparison to Mediterranean oak species (*Q. ilex* and *Q. pubescens*) and we examined the consequences of phenological differences between the two groups on the sensitivity of annual amounts of airborne pollen to spring weather conditions. Second, focusing exclusively on the two temperate oak species for which we have an extensive network of fruiting monitoring, we explored the consequences of an evolutionary change in flower phenology on fruiting dynamics. For this last point, we proceeded in two steps: (i) we determined the key weather conditions surrounding the timing of bud-burst

that should affect fruiting success (late frost and/or weather conditions affecting pollen release and diffusion), and (ii) we built a mechanistic model (resource budget model, RBM, Isagi *et al.*, 1997; Satake & Iwasa, 2000, 2002) and we simulated fruiting dynamics according to several evolutionary flower phenological strategies (*i.e.*, earlier or later phenology than currently observed).

Materials and Methods

Study species

We focused on the four oak monoecious species that are the most abundant in France: *Quercus robur* L., *Q. petraea* Liebl. L., *Q. ilex* L. and *Q. pubescens* Willd. *Q. robur* and *Q. petraea* are present from southern Scandinavia to Spain and western Russia in Europe. *Q. ilex* is the most dominant tree species in the central and western part of the Mediterranean basin. *Q. pubescens* has an intermediate distribution, co-occurring with *Q. robur* and *petraea* in central Europe and with *Q. ilex* in southern Europe. *Q. robur* and *Q. petraea* co-occur all over France except along the Mediterranean basin where they are replaced by *Q. pubescens* up to 1200 m, and *Q. ilex*, especially at lower elevation (Badeau *et al.*, 2017). The phenology of the four species show some differences. Bud-burst occurs between late April and early May for *Q. robur*, *Q. petraea* and *Q. pubescens* (Badeau *et al.*, 2017), and between April and May for *Q. ilex*, depending on the latitude (Garcia-Mozo *et al.*, 2007; Ogaya & Penuelas 2004; Misson *et al.*, 2011; Fernandez-Martinez *et al.*, 2012). The four species can have either vegetative buds with leaves only, mixed buds with male flowers, female flowers and leaves or reproductive buds with male flowers only. Male flowers are mature two weeks after bud flush and two weeks before female flowers. Leaves have reached about 75% of their final size when female flowers become receptive (Badeau *et al.*, 2017). In all four species, fertilization occurs at the end of June or early July (Pesson & Louveaux, 1984).

Phenology, pollen and fruiting data

The airborne amount of oak pollen was recorded daily using Hirst traps (Hirst, 1952) at 43 sites in France during a 22-year survey (1994-2015; Réseau National de Surveillance Aérobiologique; see Fig. 1a for a map and Table S1 for the pollen-sampling sites characteristics in the Supporting Information). Since the oak species was not recorded in the pollen dataset, we relied on the national forest inventory (IGN, France, see the forest stand dataset providing the forest cover rate

of each species) to determine within a 50-km radius at each pollen-sampling site the covering surface of each oak species. We split the pollen dataset into two sub-datasets, one called ‘temperate’ including sites where more than 80% of oaks are temperate oak species (*Q. robur* and/or *Q. petraea*, 35 sites), and the other one called ‘Mediterranean’ including sites where more than 80% of oaks are Mediterranean oak species (*Q. ilex* and/or *Q. pubescens*, 8 sites). At each site and each year, the total amount of airborne pollen was computed and divided by the percentage of the surface covered by oak trees so as to account for disparities in forest density between the sites; this corrected amount of pollen, simply called hereafter airborne pollen amount, will be used in all subsequent analyses.

We used data on the bud-burst date and the fruiting dynamics of temperate oak species from the ONF-RENECOFOR network (Ulrich, 1995) covering 30 sites for 14 years (1994-2007); see Fig. S1 for a map and Table S2 for the GPS coordinates). Among the 30 sites, nineteen are dominated by *Q. petraea*, nine by *Q. robur* and two of them are mixed oak forests (see Table S2). These sites are all different from the pollen-sampling sites. Acorn production was estimated yearly at each site on a fixed 1-acre surface where ten non-neighboring mature trees were each equipped with one 0.5 m² raised litter-fall trap; the mature acorns collected were counted exhaustively and summed for the ten trees. The bud-burst date was estimated at each site and year as the earliest date when the first 10% trees showed 20% to 50% of their buds opened (phenological stage BBCH 9, Meier *et al.*, 2009).

Meteorological data and their use

On the basis of the daily weather data extracted from the SAFRAN spatially-explicit database (8×8 km mesh size grid) (Durand *et al.*, 1993), we calculated for each of the 43 pollen and 30 acorn sampling sites the mean daily temperature (°C) and the cumulative rainfall (mm) during different periods in spring to test the effect of weather conditions on the airborne pollen amount both in temperate and Mediterranean oak species and on fruit production in temperate oak species.

At each of the 30 acorn-sampling sites of ONF-RENECOFOR network, we also computed the minimum daily temperature (to check for the possibility of late frost acting as an environmental veto -see below for threshold detection-). Following Lebourgeois *et al.*, (2008), we first modeled the bud-burst date available at each of the 30 acorn-sampling sites as a linear

function of the mean temperature of March recorded every year at these sites (see Table S3 and Fig. S2). Using this negative relationship, we then inferred the bud-burst date each year at each of the 35 pollen-sampling temperate oak sites. This allowed us to test if the weather conditions around the bud-burst date (*e.g.*, the occurrence of late frost within 30 days before, or the mean temperature one month forwards) would be linked to both airborne pollen amount and fruit production. Focusing on those identified key weather conditions around bud-burst date and using the meteorological data retrieved at each site since 1959, we further carried out simulations from RBM (see RBM modelling section) to explore the consequences of a shift in flower phenology in temperate oak species would have on fruiting dynamics.

Data analysis

We compared the ‘temperate’ and ‘Mediterranean’ oak populations for their pollen phenology. We analyzed the differences in the median date of pollen release (*i.e.*, the day when 50% of the annual airborne pollen amount has already been released) using student’s t-test.

We analyzed the sensitivity of airborne pollen amount to various spring weather variables separately for the ‘temperate’ and ‘Mediterranean’ sites as follows. First, for various spring time periods, we performed a Principal Component Analysis (PCA) on mean temperature and cumulative rainfall, and used the first Principal Component (PC1) as a synthetic weather variable reflecting both temperature and rainfall of each spring time periods (see Table S4). Second we performed Generalized Linear Mixed Models (GLMMs with Gaussian family and identity link) with log-transformed airborne pollen amount as the dependent variable and the PC1 variable - depending on the spring period considered- (see Table S4) and the lag-1 year autocorrelation of airborne pollen amount as covariates, considering the factors ‘*site*’ and ‘*year*’ as random effects. We selected the most parsimonious GLMM separately for the two forest types using the Akaike Information Criterion (AIC) (see results in Table S5).

To assess the importance of pollen phenology on masting in temperate oak species, we tested the sensitivity of fruit production to weather at different time periods around the bud-burst date, which correspond to the date when male flowers become particularly sensitive to frost up to pollen release. To ensure the robustness of the results reported, we split the whole acorn dataset into two mirror sub-datasets, each one comprising full time series of 15 acorn-sampling sites

evenly distributed over similar altitude, longitude and latitude gradients (see Fig. S1). We conducted an exploratory approach on a first sub-dataset to identify candidate periods and their weather conditions (the minimum temperature threshold below which late frost may act as environmental veto on fruiting). We fitted negative binomial GLMMs with log link to estimate fruit production with the lag-1 year autocorrelation of fruit production, the mean temperature over 30 days after bud-burst date and the occurrence of frost during several period around bud-burst date as binary factor (*i.e.*, considering frost whenever minimum daily temperature fall below a threshold value tested) as covariates, considering the factors 'site' and 'year' as random effects to increase the probability of identifying candidate periods and minimum temperature threshold (see results in Table S6). On the second sub-dataset, we tested whether the weather variables previously identified were still detected by fitting negative binomial Generalized Linear Model (GLM) with the factors 'site' and 'year' as fixed effects (see results in Table S7).

All statistical analyses were performed with the R free software environment (v.3.4.3, <http://cran.r-project.org>). We performed the PCA using the `dudi.pca` function from the *ade4* package (Dray & Dufour, 2007), and fitted the multiple additive GLMMs using the `lmer` function from *lme4* packages (Bates *et al.*, 2015).

RBM modelling

We built a Resource Budget Model (RBM), *i.e.*, an individual-based spatially explicit model accounting for the individual strategies for allocating resources into reproduction, and allowing to simulate individual flowering and fruiting dynamics within a population. We modified a previously published RBM (Venner *et al.*, 2016; Schermer *et al.*, 2019) to incorporate the effect of pollen phenology on masting in temperate oaks. According to the former RBM, interannual variations of fruit production may partly result from interannual variations of airborne pollen available for reproduction that depend on both the amount of pollen produced by trees, but also on spring temperature at the time of pollen release (see Schermer *et al.*, 2019). While in the former RBM (Schermer *et al.*, 2019), the timing of pollen release was set in April, irrespective of the year and the site, the biological realism of the RBM presented here was improved by integrating the identified key weather conditions around the actual timing of bud-burst (*i.e.*, pollen phenology see Methods S1 in the SI for further details) and we used this enhanced RBM to study the impact of a theoretical evolutionary shifted pollen phenology (*i.e.*, bud-burst date) on the fruiting dynamics of

temperate oaks. We notably explored the consequences on fruiting dynamics of a fixed 15-day shift in the bud-burst date, either advanced or delayed, depending on the model, a 15-day delayed bud-burst date corresponding to the actual pollen phenology of Mediterranean oaks (this study) and to that of ash trees (*Fraxinus spp.*) in the temperate region (Vitasse *et al.*, 2009). We further examined a 30-day delayed pollen phenology as what is observed for beech (*Fagus spp.*) in the temperate region (see Vitasse *et al.*, 2009).

The classical mathematical descriptors for masting are (i) the individual coefficient of variation of fruiting intensity (CV_i) describing the individual between-year variability in seed production; (ii) the level of synchrony among trees within the population in their fruiting interannual dynamics (classically mean of pairwise correlation between crop size of individuals within the population); (iii) the population coefficient of variation (CV_p) describing the fruiting temporal variation at the population level, and (iv) the negative temporal autocorrelation (often at 1-yr time lag) of seed production (classically ACF₁, Koenig *et al.*, 2003) (Herrera, 1998; Kelly & Sork, 2002; Buonaccorsi *et al.*, 2003). None of these descriptors, however, is able to describe the asymmetry in the fruiting dynamics (see introduction).

Here, to analyze the results of the simulations, we characterized the intensity of the fluctuations with the CV_p parameter. Complementarily, to quantify the deterministic and stochastic components of fruiting dynamics and the impact of flower phenology on these components, we analyzed temporal autocorrelation at the population scale using the standard statistic:

$$S = \sum_{t=1}^{T-1} (x_t \cdot x_{t+1}) \text{ with } x_t = z_t - \underline{z}$$

where T is the length of the fruiting series and \underline{z} , z_t and x_t correspond respectively to the average annual crop size of the population, the crop size at year t and the centered crop size at year t . This statistic corresponds to the numerator of several standard measures of autocorrelation (Wald & Wolfowitz, 1943; Dray *et al.*, 2010).

For each flower phenology, we evaluate the significance of the observed statistic (S) by comparing its value to the distribution under the null hypothesis obtained using 999 permutations of the fruiting series. To compare the different phenology scenario for their degree of stochasticity in fruiting dynamics, we computed the ‘Standardized Effect Size’ (SES, Gotelli & McCabe, 2002)

by standardizing the observed statistics (S) by the means and standard deviations estimated under the null hypothesis. Under the null hypothesis that there is no autocorrelation in the fruiting series, the distribution of SES should be centered on 0 with sd equals to 1, while SES will be all the more negative when the negative temporal autocorrelation is strong (or when the stochastic component of the masting is weak). Under the assumption that phenology has no effect on the stochastic component of masting, the distribution of SES should be similar between the different phenological scenarios.

In addition, we used a dual metric reflecting the degree of asymmetry in the fruiting dynamics as follows: (i) the probability $P_{L/M}$ for a lean-seeding year (L) to follow a mast-seeding year (M) at the population scale and (ii) the probability $P_{M/L}$ of having mast-seeding event (M) the year following a lean-seeding year (L). In the RBM outputs, mast- and lean-seeding years are defined for fruiting allocation greater than 0.7 and less than 0.3, respectively (the value 1 being, on average, the mean amount of resources acquired annually by trees that can be allocated to current reproduction or stored for future reproduction, see Methods S1). A sensitivity analysis was performed by testing various threshold values to define these two categories of fruiting level and the results remain qualitatively similar (see Fig. S3).

For each set of parameters (or sites), 100 repeated simulations of fruiting dynamics were run over 2000 years; we then computed, over the 100 last years, the population coefficient of variation (CVp) to describe masting intensity, the S and SES for analysis of temporal autocorrelation of masting (*i.e.*, its deterministic and stochastic components), then the two frequencies $P_{L/M}$ and $P_{M/L}$ for describing masting asymmetry. We could then compare various scenarios differing in their flower phenology for the degree of asymmetry in their associated fruiting dynamics.

We carried out additional simulations to analyze the relative contribution of the two modeled meteorological effects (by integrating only one of the two mechanisms at a time, *i.e.*, either the ‘environmental veto’ effect related to late frosts or the effect of weather conditions on pollen aerial diffusion) on the fruiting dynamics under the different phenological scenarios. Finally, to address the issue of decoupled investment made by trees into male and female flowers in pollen limitation and fruiting dynamics (see Crone & Rapp, 2014), we carried out sensitivity analyses considering that the relative allocation of male and female flowering resources could

deviate from a strict equilibrium of 0.5. We ran analyses in two complementary ways, considering that (i) trees may have their own, consistent allocation ratio into male flowering (defined for each tree by randomly sampling in a Gaussian distribution with 0.5(0.1) mean (sd)) or (ii) each tree may vary from one year to the next in their relative allocation into male and female flowers (defined for each tree and each year by sampling the ratio in a Gaussian distribution with 0.5 (0.1) mean (sd)).

Data availability

Data supporting the results are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p8cz8w9k3>

Results

Pollen phenology in temperate and Mediterranean oaks

In oak species growing in the temperate region, pollen is released mainly from the second half of April to early May, which occurs earlier in the season as latitude decreases (see Fig. S4). Mediterranean oak species, despite being located south of the temperate oak forests (Fig. 1a), release their pollen mainly in May (Fig. 1b), that is, about 2 weeks later on average than temperate oaks (two sample Student's t-test: $t = 17.42$; $df = 676$; $p < 0.001$; 95%*C.I.*[12.96;16.25]).

Depending on the region (temperate or Mediterranean), pollen release thus occurs under contrasted weather conditions due to phenological differences between oak species (Fig. 2a). In the temperate region, the annual airborne pollen amount was positively related to April temperature, following a logistic relationship (Table S8 for results of the GLMMs selection, and Table S9 for results of the model selection between the logistic and linear models) in line with a recent study (Table S5; Schermer *et al.*, 2019). Conditions for pollen release seem optimal for mean April temperature above 13°C (value determined by a threshold model; Huber, 1964, see Fig. S5), which occurred in 11% and 100% of the sites and years for temperate and Mediterranean oak species, respectively (Fig. 2b).

Impact of a shift in the pollen phenology on fruiting dynamics in temperate oaks

In the temperate region, the early timing in pollen release makes reproduction sensitive to late frost (-5°C or less) whenever occurring within 30 days before the bud-burst date (Fig. 3a, Tables S6 and S7) and to the mean temperature over 30 days after bud-burst date (*i.e.*, spring temperature impacting airborne pollen amount, see Fig. S6) (Fig. 3b and Tables S6, S7 and S9).

Our RBM simulations suggest that fruiting dynamics of temperate oak tree populations would be sensitive to evolutionary shifting pollen phenology (Figs. 4 and 5). Although fruiting dynamics remain greatly fluctuating under all phenological scenarios (Fig. 4), the population coefficient of variation (CVp) would decrease under later phenology (Fig. 5a) while the negative temporal autocorrelation would become more pronounced (Fig. 5b) and hence, variation in the fruiting dynamics more deterministic. A shift toward earlier pollen phenology would be accompanied by more pronounced asymmetry of fruiting dynamics (Fig. 5c, d): the probability for a lean-seeding year to follow a mast-year remained unchanged and high (*i.e.*, mainly between 0.8 and 1) irrespective of the phenology simulated (Fig. 5c). On the contrary, the probability of having a mast- after a lean-seeding year was very variable according to the different phenological scenarios and was lowest for earliest phenologies (Fig. 5d).

By considering weather factors in isolation in the modelling, we revealed that the veto-like effect of late frost would play only a minor role in fruiting dynamics under current phenology, while the weather conditions that influence pollen spread, as they stand, would retain a key role (Fig. S7b). If oak phenology was earlier by 15 days, the negative effect of late frost would then emerge (Fig. S7a). Later flower phenologies would almost systematically meet optimal conditions for reproduction, without severe weather conditions unfavourable to flower survival or pollen diffusion (Fig. S7c, d).

Overall, our results suggest that if temperate oak evolved toward delayed phenology (independently of any climate change), their fruiting dynamics would still fluctuate but in much less stochastic way and mast-seeding years should then become more predictable (*i.e.*, mainly driven by negative temporal autocorrelation). These results were obtained considering that trees invested equal energy into male and female flowers; our findings remained robust to departure from that assumption (see Fig. S8).

Discussion

While the timing of pollen release is delayed with increasing latitude within temperate oak species, our results evidenced that these species have much earlier pollen phenology (15-day difference) than Mediterranean oaks. In the four species studied, fertilization consistently takes place at the same period (late June, early July) (Pesson & Louveaux, 1984) and at a much later date than pollination, suggesting that the phenology of temperate oak species could theoretically be later than it actually is. In temperate oak forests, we show that the early pollen phenology observed in the field is often associated with weather conditions that are unfavourable to pollen maturation and/or aerial diffusion, which could explain why reproductive failure is common. Our results suggest that such advanced pollen phenology would give trees a selective advantage by generating strong stochastic component in fruiting dynamics, which is possibly decisive for effective control of seed consumer demography.

The early spring pollen maturation of temperate oak species could be seen as maladaptive owing to the sub-optimal weather conditions encountered at the time of pollen release (around 10% years have mean temperature above 13°C over 30 days after bud-burst date (Fig. 3b and Fig. S6)), and to the probability to suffer frost damage at flowering (*i.e.*, 5% of years with minimum temperature below -5°C occurring within 30 days before the bud-burst date). Such early pollen phenology might lead to frequent, massive fruiting failure and explain why the fruiting dynamics of some oak species are very sensitive to spring weather conditions (Pearse *et al.*, 2014; Koenig *et al.*, 2015; Bogdziewicz *et al.*, 2017a; Caignard *et al.*, 2017; Nussbaumer *et al.*, 2018; Schermer *et al.*, 2019). On the contrary, Mediterranean oak pollen, because of the warmer climatic conditions encountered and their delayed pollen phenology, experience weather conditions most often favorable for pollen maturation and release (Fig. 2), and very rare exposure to late intense frost (Fig. S9b). The evolutionary divergence in pollen phenology between these oak species would then sustain the diversity of their responses to spring weather conditions and partly explain why finding common determinants of masting is so difficult in the genus *Quercus* (Sork *et al.*, 1993).

From an evolutionary perspective, pollen phenology could be seen as a key life history trait that partly controls the degree of stochasticity in fruiting dynamics in temperate oak species. Based on our RBM, we show that contrasting yet realistic variations in oak flower phenology (*i.e.*, within the range of other wind-pollinated forest species) would all still generate large fluctuations

in fruiting (Fig. 4). However, the stochastic component of masting was increased only when simulating earlier pollen phenology (Fig. 5b,d), which generated conditions often unfavourable to reproduction. As proposed from theoretical work (Rees *et al.*, 2002), disturbance in fruiting dynamics is probably essential to efficiently control the dynamics of seed consumer populations and maximize tree fitness. Oak acorns are a pulsed resource for various consumers that affect their population dynamics (insects: Venner *et al.*, 2011; birds: McShea, 2000; rodents: Wolff, 1996; ungulates: Gamelon *et al.*, 2017). Among consumers, insects specialized in this resource are probably the most problematic for the following reasons: (i) insects are able to respond demographically very quickly to the fluctuations of the resource (Bogdziewicz *et al.*, 2018b), (ii) acorn consumption by insects severely reduce seed germination success and seedling survival (Andersson, 1992; Yi *et al.*, 2019; Muñoz *et al.*, 2014, Leiva *et al.*, 2018); (iii) several weevil species commonly coexist on the same individual trees and display widely diverse life history traits (Venner *et al.*, 2011; Péliesson *et al.*, 2012, 2013; Rey *et al.*, 2015) making it difficult for the trees to control the dynamics of the whole insect community. Efficient control of such insect diversity is probably tightly linked to strong stochastic component in the fruiting dynamics. In temperate oaks species, our results suggest that early phenology would play this pivotal role in inducing weather conditions most often detrimental to yearly reproduction, and in consequence, making mast-seeding years unpredictable for seed consumers, thus maximizing tree fitness. Our results are therefore in line with the recent proposal by Bogdziewicz *et al.*, (2019) that the weather conditions causing frequent fruiting failure are traditionally perceived as negative for plants while they would help maximizing their lifetime reproductive success.

Under the current phenology of temperate oaks species, fruiting failure is explained much more widely by climatic conditions that are often unfavourable to pollen maturation or diffusion (*i.e.*, the month following the bud-burst date) than by the occurrence of late frost (the month preceding the bud-burst date) which are relatively rare and which would only have minor effects on fruiting dynamics (see Fig. 3a and Fig. S9b). Although very early phenology would make fruiting dynamics even more stochastic (*e.g.*, by reinforcing the ‘environmental veto’ effect of late frost), it would likely be too costly in terms of fitness either by generating too rare mast-seeding years or by impairing leaf growth (see below).

Mediterranean oak species are also exposed to greatly diverse seed consumers whose control is also expected to require stochastic fruiting dynamics. Although not studied here, the

fruiting dynamics of Mediterranean oak species are probably as variable and stochastic as those of temperate oak species (Bogdziewicz *et al.*, 2017b). The late flower phenology of Mediterranean oaks seems to promote weather conditions mainly favorable to pollination (Fig. 2b). In consequence, the stochastic component of masting is likely to be independent of weather-driven-pollination failure but would rather be due to severe drought in spring or summer resulting in frequent and very high fruit abortion rate (Fernandez-Martinez *et al.*, 2012; Pérez-Ramos *et al.*, 2015 for a review; Bogdziewicz *et al.*, 2017b, Pearse *et al.*, 2015). In Mediterranean oaks species, the late flower phenology could be a way of not adding noise to the already very stochastic fruiting dynamics and, consequently, keeping frequency of mast-seeding years at a minimum threshold. Overall, the proximate mechanisms of oak masting (*i.e.*, including environmental veto due to late frost or water stress, weather conditions impacting flower maturation and pollen diffusion) would likely depend on the species, local ecological conditions and/or local adaptation (Koenig *et al.*, 2016). Considering this last point, the evolution of flower phenology could be rapid - as it is tightly linked to leaf phenology that itself is quickly evolving (Franjić *et al.*, 2011) - and could thus be responsible for the short term change in the weight of late frost and weather conditions at the time of pollen release in masting.

Our study, in line with previous work (Koenig *et al.*, 2015; Bogdziewicz *et al.*, 2017b), underlines the need to elucidate the interdependency between fruiting strategies (*i.e.*, the interannual dynamics of fruiting, possibly masting) and the phenology of perennial plants. For example, in oaks, flower maturation is organically linked to leaf maturation because most buds are compound buds (*i.e.*, containing leaves and flowers), leaf and flower phenologies are thus tightly related (Koenig *et al.*, 2012). The evolution of flower phenology might thus be a by-product of, and driven by leaf phenology that would be predominantly selected to maximize carbon gain through photosynthesis; in this sense, the early flower phenology of temperate oak (and the stochasticity induced in masting) would be an exaptation. Most likely, the phenology of temperate oaks would result from a trade-off between the advantage of being early to trigger stochastic fruiting dynamics and to lengthen the canopy duration, and the advantage of being late to avoid exposing the nascent leaves to late frost.

More generally, integrative work on phenology and masting is worth being developed through comparative approaches of the dynamics of fruiting and phenology of flowers and leaves in wind-pollinated perennial plant species. For example, in species with separate flower and leaf

buds, pollen phenology could be even earlier, and fruiting dynamics more stochastic, than in other, more constrained species. From a more theoretical perspective, it might be worth combining several models including those ones considering ecophysiological traits for their impact on plant phenology (Chuine & Beaubien, 2001), those mechanistic ones of the fruiting dynamics (Isagi *et al.*, 1997; Abe *et al.*, 2016; this work) – *e.g.*, the evolution of traits affecting resource allocation in reproduction- and those ones dedicated to simulate seed consumer dynamics (Rees *et al.*, 2002; Tachiki & Iwasa, 2013), to link explicitly the proximate causes of masting to fitness consequences and plant regeneration success. Coupling these approaches is all the more urgent as phenology is greatly affected by climate change in a vast number of plant species, which could impact their fruiting dynamics, the success of regeneration and ultimately the assembly of perennial plant species in forest ecosystems and the ecosystem services associated (Cleland *et al.*, 2007).

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Author Contribution

ES, SV and M-C V conceived, led the study and wrote the paper. ES and GO assembled the pollen dataset. ES, IC, SDe, VB assembled the dataset of bud-burst dates in temperate oak trees. ES and SV analysed field data and performed modelling. SDr analysed autocorrelation within simulated fruiting dynamics. IC, SDe, J-M G, VB and I LR gave fruitful comments during the research process. All authors revised the manuscript.

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Figure legends

Fig. 1: Comparison of the pollen phenology between the temperate and Mediterranean oak forests. **(a)** Spatial distribution of the 43 pollen-sampling sites. Temperate oak forests are defined when including 80% or more *Quercus petraea* and/or *Q. robur* (35 sites, see orange circles) while Mediterranean oak forests include 80% or more *Q. ilex* and/or *Q. pubescens* (8 sites, green triangle) relative to the whole oak forest area comprised within a 50km-radius around each pollen-sampling site. The GPS coordinates and the forest cover rate of each oak species of all pollen-sampling site are indicated in Supporting Information Table S1. **(b)** Cumulative frequency distribution of the median date of oak pollen release for the 'temperate' (orange line) and 'Mediterranean' (green line) oak forests. The median date was calculated each year (from 1994 to 2015) at each site as the day when 50% of the annual pollen amount has already been released. Dates are in Julian days, that is, the number of days elapsed since January 1st (day 1) of each year.

Fig. 2: Comparison of the sensitivity of airborne pollen amount to mean of temperatures at time of pollen release between temperate and Mediterranean oak forests. **(a)** Mean annual airborne pollen amount as a function of mean of temperatures at time of pollen release for both Mediterranean (*Quercus ilex* and/or *Q. pubescens*, green circles) and temperate oaks (*Q. petraea* and/or *Q. robur*, orange circles). Mean of temperatures were computed in April for temperate oaks and between mid-April and mid-May for Mediterranean oaks to account for the 15-day delayed pollen phenology (see Fig. 1). Data shown are mean(+SE) of annual airborne pollen amount ranked according to increasing temperature and grouped by sets of 10 consecutive values to compute mean(+SE) (see Supporting Information Fig. S10a,b showing the same relationship with ungrouped data). Shaded areas show the 95% confidence interval of the model estimates. **(b)** Cumulative frequencies of the April temperatures (orange line) and temperatures between mid-

April and mid-May (green line) at each site and year for temperate and Mediterranean oaks, respectively. The orange vertical dotted line shown in panels (a) and (b) is the 13°C threshold value above which the pollen amount of temperate oaks reaches high values, independent of mean April temperature (see Fig. S5 for the deviance profile from the ‘threshold model’ (Huber, 1964)).

Fig. 3: Sensitivity of fruiting intensity to temperature around bud-burst date in temperate oak forests (*Quercus petraea* and/or *Q. robur*). **(a)** Annual acorn production along the minimum temperatures occurring within 30 days before the bud-burst date. The vertical line corresponds to the -5°C threshold value under which frost is detected causing fruiting failure (see Supporting Information Tables S6 and S7 for results). **(b)** Mean annual acorn production as a function of mean temperatures over 30 days after bud-burst date (*i.e.*, at the time of pollen release, see Fig. S6 for a similar relationship between airborne pollen amount and mean temperature over 30 days after bud-burst date) (Table S9). The mean (+SE) acorn amounts shown were computed within groups of ten consecutive *site-year* values once being ranked according to their mean temperature (see Fig. S11 showing the same relationship with ungrouped data). Shaded area shows the 95% confidence interval of the model estimates.

Fig. 4: Examples of population fruiting dynamics simulated by our RBM over 100 years depending of pollen phenology: (a) earlier; (b) current; (c) later; and (d) very later phenologies. The ‘Population crop size’ axis corresponds to the index of the mean amount of resource allocated into fruiting at the population level. For each pollen phenology scenario, the values of CVp (population Coefficient of Variation), autocorrelation SES (Standardized Effect Size) and the probabilities $P_{L/M}$ of having a lean-seeding year (L) the year following a mast-seeding event (M) and $P_{M/L}$ of having a mast-seeding event (M) the year following a lean-seeding year (L) were indicated (see legend of Fig. 5 for details on phenology or masting parameters).

Fig. 5: Impact of an evolutionary shift in flower phenology on the fruiting dynamics of temperate oak species. Four flower phenologies were tested for their impact on fruiting dynamics from simulation with Resource Budget Model. The current phenology correspond to the phenology recorded in the field at the 30 fruit sites. The early flower phenology corresponds to a 15-day advance in the bud-burst date, while the late and very late pollen phenologies correspond to a 15-day (as the one observed for Mediterranean oak species, see Fig. 1b) and 30-day lag (as observed for beeches in some temperate forest communities) in the bud-burst date, respectively. Here are

shown the cumulative frequency distribution of sites for **(a)** the population coefficient of variation of fruiting (CV_p), **(b)** the autocorrelation ‘Standardized Effect Size’ (SES) which reflects both the deterministic and stochastic components of masting, **(c)** the probability $P_{L/M}$ of having a lean-seeding year (L) after a mast-seeding year (M), and **(d)** the probability $P_{M/L}$ of having a mast-seeding event (M) the year following a lean-seeding year (L), which together describe the degree of asymmetry of the masting. The polygons display the 95% credible interval (*i.e.*, including 95% of the simulations).

Supporting Information

Additional supporting information may be found in the online version of this article.

Methods S1 Detailed description of the Resource Budget Model.

Table S1 Characteristics of the pollen-sampling sites.

Table S2 Characteristics of the acorn-sampling sites.

Table S3 Response of bud-burst date to March mean daily temperature.

Table S4 Proportion of variance explained by the various synthetic weather variables reflecting both temperature and rainfall.

Table S5 Response of airborne pollen amount to spring weather variables depending on temperate and Mediterranean regions.

Table S6 Exploring the sensitivity of fruiting intensity to weather conditions around the bud-burst date.

Table S7 Testing the sensitivity of fruiting intensity to weather conditions around the bud-burst date.

Table S8 Model selection between the various models explaining the airborne pollen amount in the temperate region.

Table S9 Model selection between the logistic model and polynomial regression models for predicting airborne pollen amount or fruit production from spring weather conditions in the temperate region.

Fig. S1 Spatial distribution in the temperate region of the 30 acorn-sampling sites.

Fig. S2 Relationship between bud-burst date and March mean daily temperature in the temperate region.

Fig. S3 Sensitivity analysis of the Resource Budget Model outputs.

Fig. S4 Relationships between the median date of oak pollen release and the latitude.

Fig. S5 Deviance profile from the ‘threshold model’ applied to the logistic relationships between mean airborne pollen amount and mean April temperature in the temperate region.

Fig. S6 Logistic relationship between the mean amount of airborne pollen and mean temperature over 30 days after bud-burst date in the temperate region.

Fig. S7 Analyse of the relative contribution of the late frost and the mean temperature impacting pollen aerial diffusion in the fruiting dynamics under 4 different simulated pollen phenological scenarios.

Fig. S8 Sensitivity analysis of the Resource Budget Model outputs to the Female flower Allocation.

Fig. S9 Distribution of the March minimum temperatures depending on temperate and Mediterranean regions.

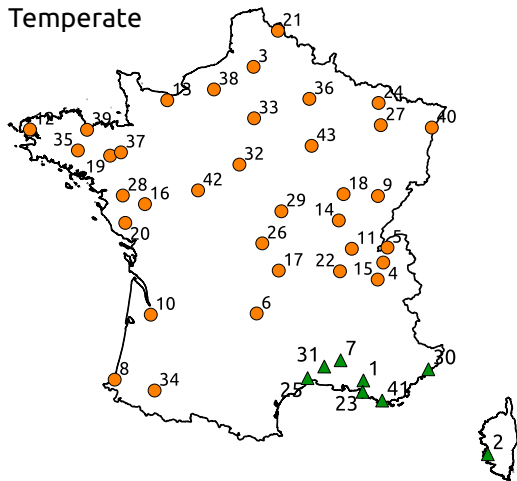
Fig. S10 Relationships between airborne pollen amount and spring temperatures depending on temperate and Mediterranean regions.

Fig. S11 Response of both airborne pollen amount and acorn production to temperatures over 30 days after bud-burst date in the temperate region.

(a)

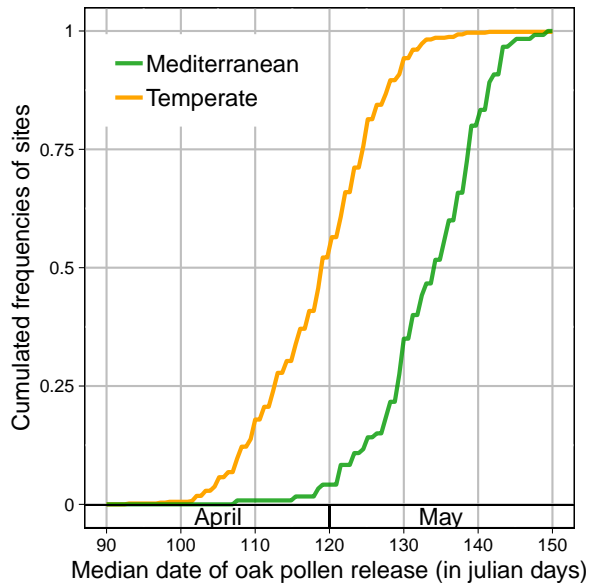
▲ Mediterranean

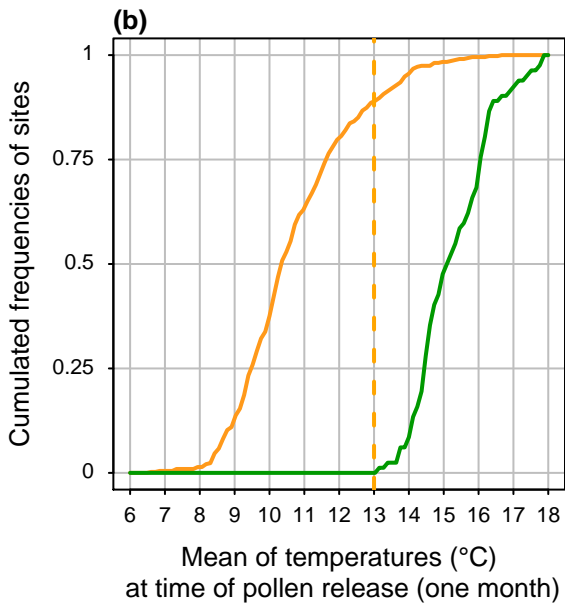
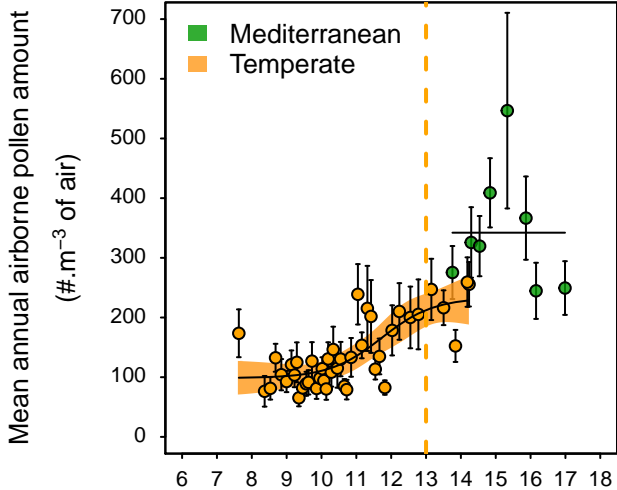
● Temperate

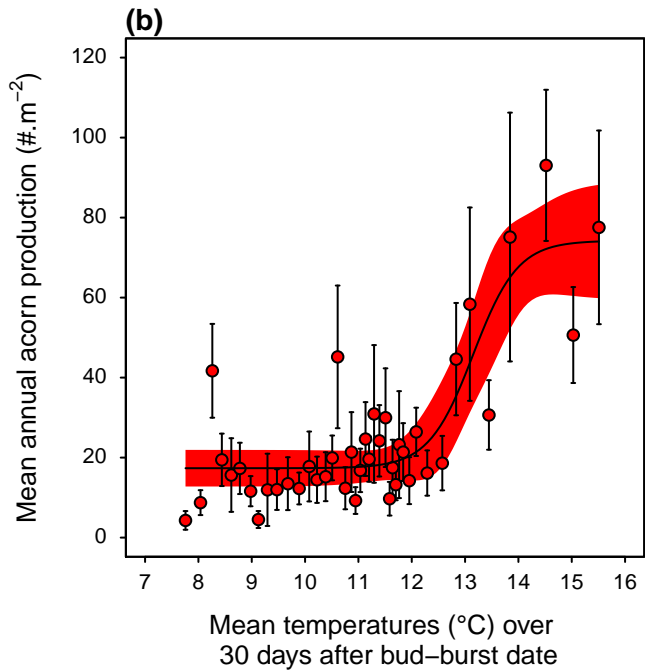
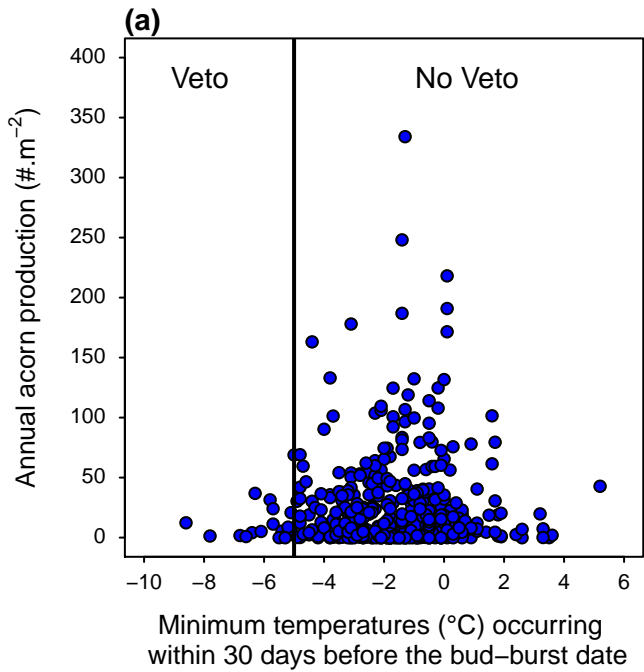


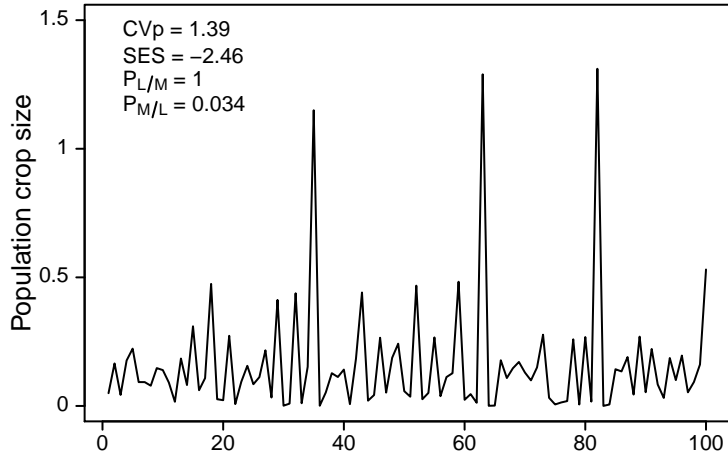
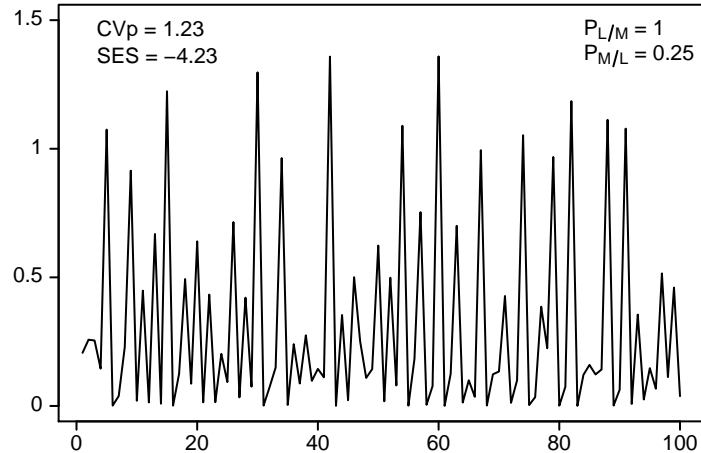
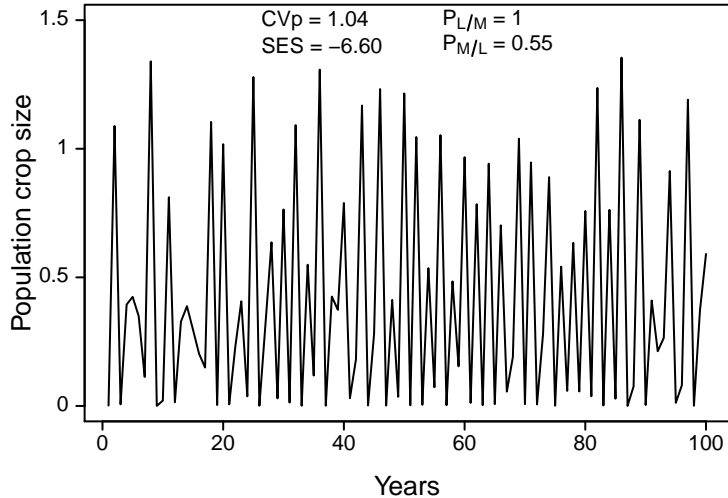
(b)

— Mediterranean
— Temperate







a) Early pollen phenology**b) Current pollen phenology****c) Late pollen phenology****d) Very late pollen phenology**