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

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Summary

- Many perennial plants display masting, that is, 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 a 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 budburst and flowering on seed production, and simulated with a mechanistic model the consequences that an evolutionary shifting of flower phenology would have on fruiting dynamics.
- Temperate oak species release pollen earlier in the season than do Mediterranean oak species. Such early flowering in temperate oak species results in pollen often being released during unfavorable weather conditions and frequently results in reproductive failure. If pollen release were delayed as a result of 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 in controlling the dynamics of seed consumers.

Introduction

Reproduction in many perennial and wind-pollinated plant species is characterized by masting, that is, synchronized and highly variable amounts of seed production over the years within a population (Janzen, 1976; Kelly & Sork, 2002). Masting is known to impact the demography and evolution of seed consumers strongly (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 because of 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 as a result of 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 (hereafter called 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 a weather effect can act as an 'environmental veto' by nearly completely preventing flower or seed development at the tree population scale (Feret *et al.*, 1982; Cecich & Sullivan 1999; Bogdziewicz *et al.*, 2018a, 2019).

A promising avenue to understanding 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 which may shift independently of any climate change) could theoretically act on masting in two complementary ways: by modifying the likelihood of late frost events at the vulnerable flowering stage (García-Mozo *et al.*, 2001; Augspurger, 2009), which can act as environmental veto and may strongly impede fruit set (Feret *et al.*, 1982; Cecich & Sullivan 1999; Bogdziewicz *et al.*, 2018a); and by partly setting the weather conditions influencing pollen maturation and release which would play a key role in pollen limitation and then in fruiting success. In this sense, high spring temperature has recently been shown to favor 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), after 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 these 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 *Quercus 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 (*Quercus ilex* and *Quercus 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: first, we determined the key weather conditions surrounding the timing of budburst that should affect fruiting success (late frost and/or weather conditions affecting pollen release and diffusion);

and then 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 most abundant oak monoecious species 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 parts 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 elevations (Badeau *et al.*, 2017). The phenologies of the four species show some differences. Budburst 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 2 wk after bud flush and 2 wk before female flowers. Leaves have reached *c.* 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 yr survey (1994–2015; Réseau National de Surveillance Aérobiologique; see Fig. 1a for a map; see Supporting Information Table S1 for the pollen-sampling site characteristics). As the oak species was not recorded in the pollen dataset, we relied on the national forest inventory (Institut Géographique National, 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 > 80% of oaks are temperate oak species (*Q. robur* and/or *Q. petraea*, 35 sites), and the other one called 'Mediterranean', including sites where >80% of oaks are Mediterranean oak species (*Q. ilex* and/or *Q. pubescens*, eight sites). At each site and each year, the total amount of airborne pollen was computed and divided by the percentage of the surface
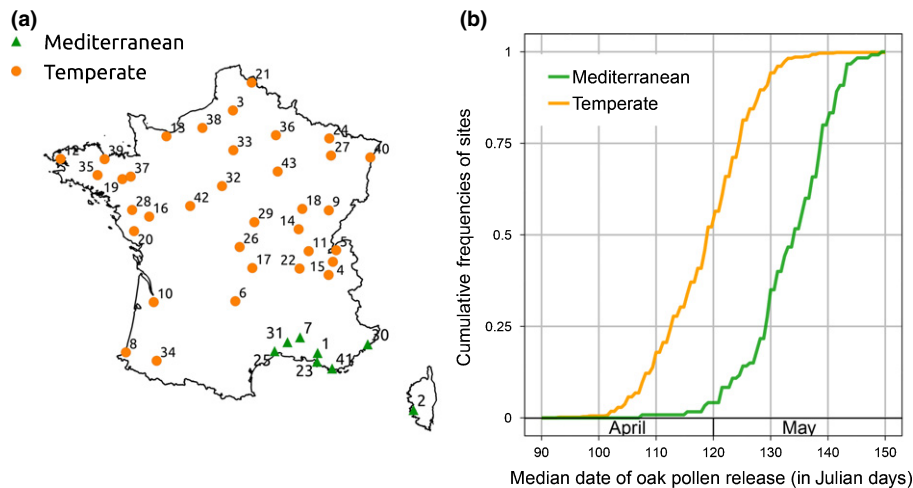
Fig. 1 Comparison of the pollen phenology between the temperate and Mediterranean oak forests. (a) Spatial distribution of the 43 pollen-sampling sites. Temperate oak forests are defined to include 80% or more *Quercus petraea* and/or *Quercus robur* (35 sites; see orange circles) and Mediterranean oak forests include 80% or more *Quercus ilex* and/or *Quercus pubescens* (eight sites; green triangles) relative to the whole oak forest area comprised within a 50 km radius around each pollen-sampling site. The GPS coordinates and the forest cover rate of each oak species of all pollen-sampling sites 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 by which 50% of the annual pollen amount has already been released. Dates are in Julian days, that is, the number of days elapsed since 1 January (day 1) of each year.

covered by oak trees so as to account for disparities in forest density between the sites; this corrected amount of pollen (hereafter airborne pollen amount) will be used in all subsequent analyses.

We used data on the budburst date and the fruiting dynamics of temperate oak species from the ONF-RENECOFOR network (Ulrich, 1995) covering 30 sites for 14 yr (1994–2007) (see Fig. S1 for a map and Table S2 for the GPS coordinates). Among the 30 sites, 19 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 (0.405 ha) surface where 10 nonneighboring 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 10 trees. The budburst date was estimated at each site and year as the earliest date at which the first 10% of trees had 20–50% of their buds open (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 amount of airborne pollen in both temperate and Mediterranean oak species and on fruit production in temperate oak species.

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

budburst date available at each of the 30 acorn-sampling sites as a linear function of the mean March temperature recorded every year at these sites (see Table S3; Fig. S2). Using this negative relationship, we then inferred the budburst date each year at each of the 35 pollen-sampling temperate oak sites. This allowed us to test if the weather conditions around the budburst date (e.g. the occurrence of late frost within 30 d before, or the mean temperature 1 month afterwards) were linked to both amount of airborne pollen and fruit production. Focusing on these identified key weather conditions around budburst date and using the meteorological data retrieved at each site since 1959, we carried out further simulations using the RBM (see RBM modeling section) to explore the effect of a shift in flower phenology in temperate oak species 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 by which 50% of the annual airborne pollen 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 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 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 yr 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 (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 budburst date, from the date on which male flowers become particularly sensitive to frost right 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 an environmental veto on fruiting). We fitted negative binomial GLMMs with log link to estimate fruit production with the lag-1 yr autocorrelation of fruit production, the mean temperature over 30 d after budburst date and the occurrence of frost during several periods around budburst date as binary factor (i.e. considering frost whenever minimum daily temperature falls 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 Table S6). On the second sub-dataset, we tested whether the weather variables previously identified were still detected by fitting a negative binomial generalized linear model (GLM) with the factors 'site' and 'year' as fixed effects (see 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 in the ADE4 package (Dray & Dufour, 2007), and fitted the multiple additive GLMMs using the 'lmer' function in the LME4 package (Bates *et al.*, 2015).

RBM modeling

We built an RBM, that is, an individually based, spatially explicit model accounting for the individual strategies for allocating resources into reproduction, and allowing us 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 and spring temperature at the time of pollen release (see Schermer *et al.*, 2019). Whereas in the former RBM (Schermer *et al.*, 2019), the timing of pollen release was set to 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 budburst (i.e. pollen phenology; see Methods S1 for further details) and we used this enhanced RBM to study the impact of a theoretical

evolutionarily shifted pollen phenology (i.e. budburst date) on the fruiting dynamics of temperate oaks. Notably we explored the impact on fruiting dynamics of a fixed 15 d shift in the budburst date, either advanced or delayed, depending on the model, and a 15 d delayed budburst 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 d delayed pollen phenology, as observed for beech (*Fagus* spp.) in the temperate region (see Vitasse *et al.*, 2009).

The four classical mathematical descriptors for masting are: the individual coefficient of variation of fruiting intensity (CVi) describing the individual between-year variability in seed production; the degree of synchrony among trees within the population in their fruiting interannual dynamics (classically the mean of pairwise correlation between crop size of individuals within the population); the population coefficient of variation (CVp) describing the fruiting temporal variation at the population level; and 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 the Introduction).

Here, to analyze the results of the simulations, we characterized the intensity of the fluctuations with the CVp 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:

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

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 evaluated 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 SDs 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 = 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: the probability $P_{L/M}$ for a lean-seeding year (L) to follow a mast-seeding year (M) at the population scale; and the probability $P_{M/L}$ of having a 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 > 0.7 and < 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 yr; we then computed, over the last 100 years, the CVp to describe masting intensity, the S and SES for analysis of temporal autocorrelation of masting (i.e. its deterministic and stochastic components), and the two frequencies $P_{L/M}$ and $P_{M/L}$ for describing masting asymmetry. We were then able to 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 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 each tree may vary from one year to the next in its 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 (doi: 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, occurring 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 wk later on average than temperate oaks (two-

sample Student's *t*-test: $t = 17.42$, df $= 676$, $P < 0.001$, 95% CI: 12.96–16.25).

Depending on the region (temperate or Mediterranean), pollen release thus occurs under contrasting weather conditions owing 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 (see Table S8 for results of the GLMM selection; see 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 $> 13°C$ (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 of pollen release makes reproduction sensitive to late frost ($-5°C$ or less) whenever it occurs within 30 d before the budburst date (Fig. 3a; Tables S6, S7), and to the mean temperature > 30 d after budburst date (i.e. spring temperature impacting airborne pollen amount; see Fig. S6) (see also Fig. 3b; Tables S6, S7, S9).

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

By considering weather factors in isolation in the modeling, we revealed that the veto-like effect of late frost would play only a minor role in fruiting dynamics under current phenology, whereas the weather conditions that influence pollen spread, as they stand, would retain a key role (Fig. S7b). If oak phenology was 15 d earlier, 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 unfavorable to flower survival or pollen diffusion (Fig. S7c,d).

Overall, our results suggest that if temperate oak evolved towards delayed phenology (independently of any climate change), their fruiting dynamics would still fluctuate, but in a much less stochastic way, and mast-seeding years should then become more predictable (i.e. mainly driven by negative

(a)

(b)
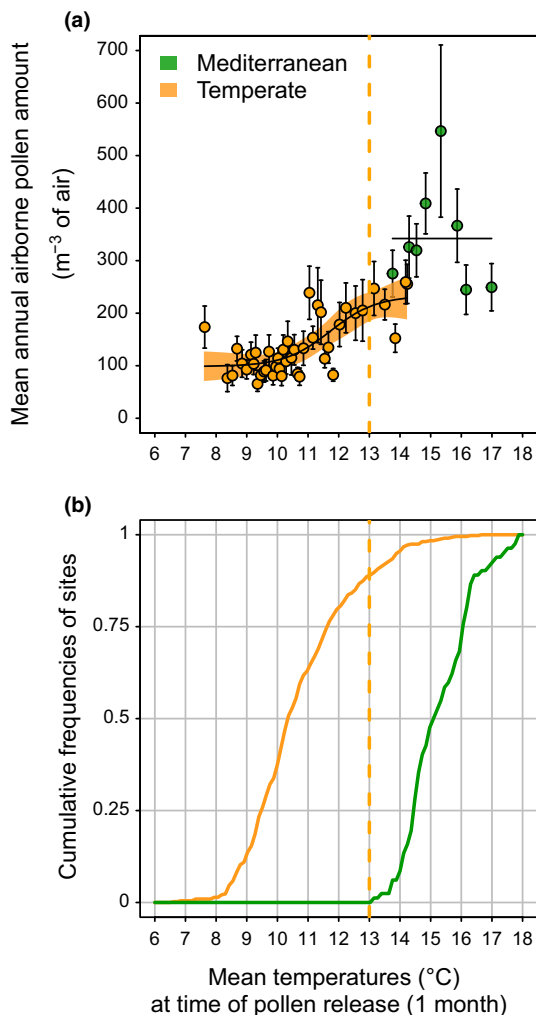
Fig. 2 Comparison of the sensitivity of airborne pollen and mean temperature at time of pollen release between temperate and Mediterranean oak forests. (a) Mean annual airborne pollen amount as a function of mean temperature at time of pollen release for both Mediterranean (*Quercus ilex* and/or *Quercus pubescens*; green circles) and temperate oaks (*Quercus petraea* and/or *Quercus robur*; orange circles). Mean temperatures were computed in April for temperate oaks and between mid-April and mid-May for Mediterranean oaks to account for the 15 d delayed pollen phenology (see Fig. 1). Data shown are means ± 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, which shows the same relationship with ungrouped data). Shaded areas show the 95% confidence interval of the model estimates. (b) Cumulative frequencies of 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 (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)).

temporal autocorrelation). These results were obtained considering that trees invested equal amounts of energy into male and female flowers; our findings remain robust to departures from that assumption (see Fig. S8).

Discussion

Whereas the timing of pollen release is delayed with increasing latitude within temperate oak species, our results revealed that these species have much earlier pollen phenology (15 d difference) than Mediterranean oaks. In the four species studied, fertilization consistently takes place during 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 unfavorable 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 a 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 suboptimal weather conditions encountered at the time of pollen release (*c.* 10% of years have mean temperature > 13°C over 30 d after budburst date (Figs 3b, S6)) and to the probability of suffering frost damage at flowering (i.e. 5% of years with minimum temperature < −5°C occurring within 30 d before the budburst 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). By contrast, Mediterranean oak pollen, because of the warmer climatic conditions encountered and their delayed pollen phenology, experience weather conditions that are usually favorable to pollen maturation and release (Fig. 2), with 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 that are often unfavorable 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
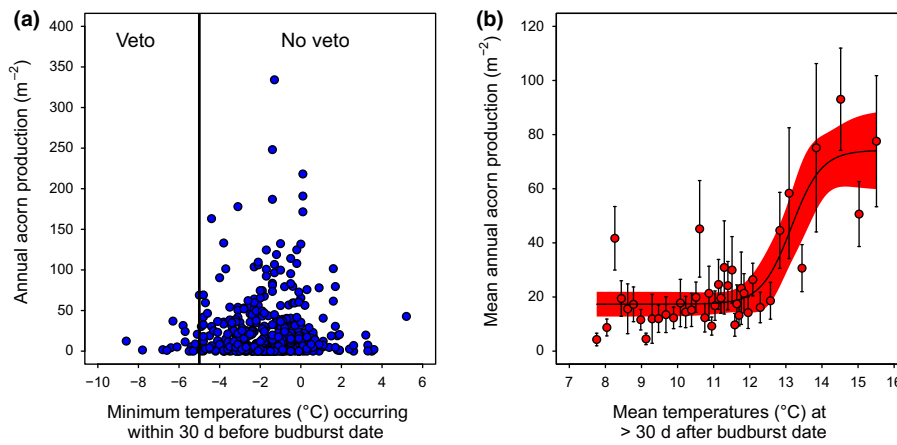
Fig. 3 Sensitivity of fruiting intensity to temperature around budburst date in temperate oak forests (*Quercus petraea* and/or *Quercus robur*). (a) Annual acorn production along the minimum temperatures occurring within 30 d before budburst. The vertical line corresponds to the −5°C threshold value 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 at > 30 d after budburst (i.e. at the time of pollen release; see Fig. S6 for a similar relationship between airborne pollen amount and mean temperature at > 30 d after budburst date) (Table S9). The mean (± SE) acorn amounts shown were computed within groups of 10 consecutive site × year values once being ranked according to their mean temperature (see Fig. S11, which shows the same relationship with ungrouped data). Shaded area shows the 95% confidence interval of the model estimates.
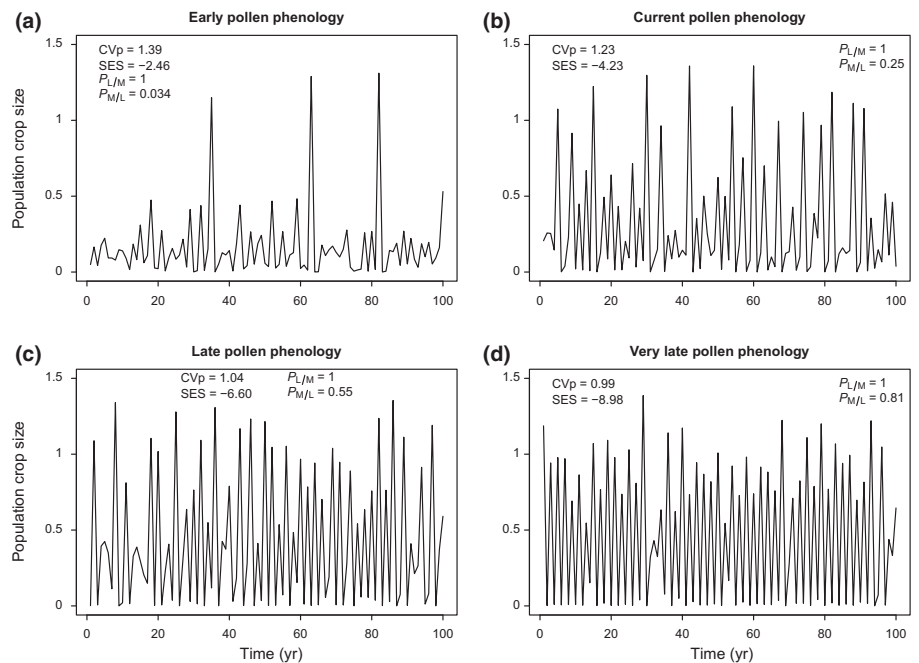

Fig. 4 Examples of population fruiting dynamics simulated by our resource budget model over 100 yr depending of pollen phenology: (a) earlier; (b) current; (c) later; and (d) very late. The 'population crop size' axis corresponds to the index of the mean amount of resource allocated to fruiting at the population level. For each pollen phenology scenario, the values of the population coefficient of variation (CVp), autocorrelation standardized effect size (SES) 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) are indicated (see legend of Fig. 5 for details on phenology or masting parameters).

problematic for the following reasons: insects are able to respond demographically very quickly to the fluctuations of the resource (Bogdziewicz *et al.*, 2018b); acorn consumption by insects severely reduces seed germination success and seedling survival (Andersson, 1992; Muñoz *et al.*, 2014; Leiva *et al.*, 2018; Yi *et al.*, 2019); and several weevil species commonly coexist on the same individual trees and display widely diverse life-history traits (Venner *et al.*, 2011; Pélisson *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 oak species, our

results suggest that early phenology would play this pivotal role in inducing weather conditions most often detrimental to yearly reproduction, thus making mast-seeding years unpredictable for seed consumers, and hence 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, but would help to maximize their lifetime reproductive success.

Under the current phenology of temperate oak species, fruiting failure is explained much more widely by climatic conditions that are unfavorable to pollen maturation or diffusion (i.e. the month following the budburst date) than by the occurrence of late frost
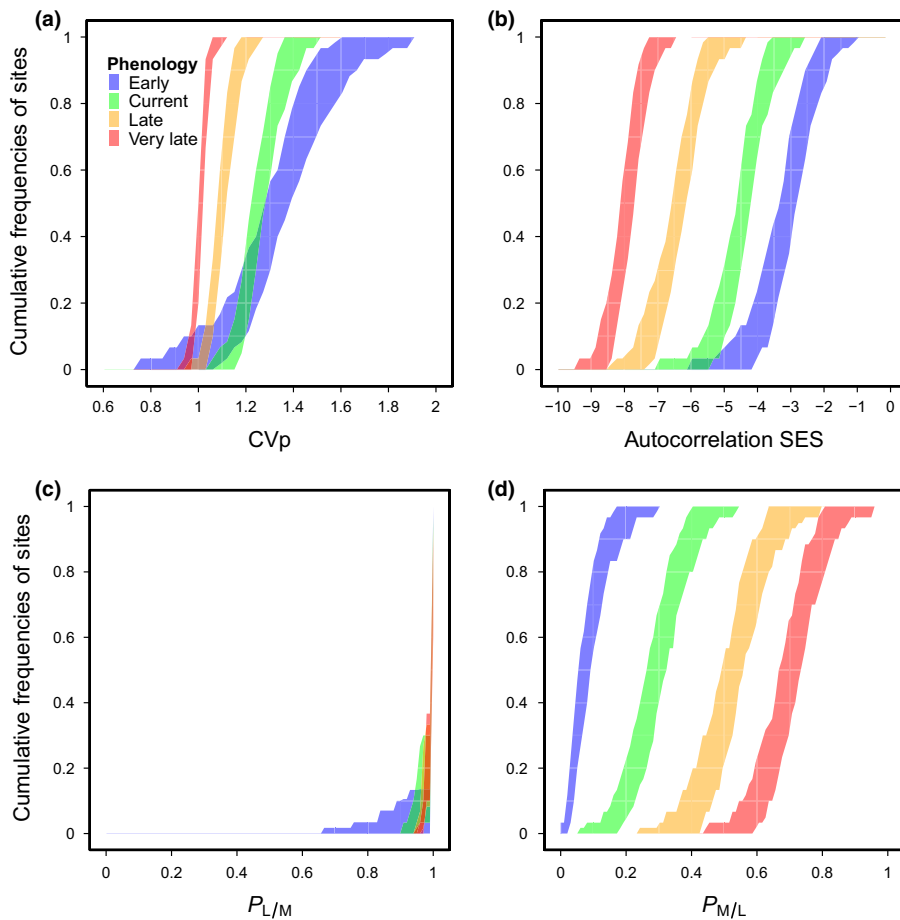
Fig. 5 Impact of an evolutionary shift in flower phenology on the fruiting dynamics of temperate oak species. Four flower phenologies were tested for their impact on fruiting dynamics through simulation with the resource budget model. The current phenology corresponds to the phenology recorded in the field at the 30 fruit sites. The early flower phenology corresponds to a 15 d advance in the budburst date, and the late and very late pollen phenologies correspond to a 15 d (as observed for Mediterranean oak species; see Fig. 1b) and a 30 d lag (as observed for beeches in some temperate forest communities) in the budburst date, respectively. (a–d) Cumulative frequency distribution of sites for: (a) the population coefficient of variation of fruiting (CVp); (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). Together these describe the degree of asymmetry of the masting. The polygons display the 95% credible interval (i.e. including 95% of the simulations).

(the month preceding the budburst date), which is relatively rare and which would only have minor effects on fruiting dynamics (see Figs 3a, 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 probably be too costly in terms of fitness, either by producing too rare mast-seeding years or by impairing leaf growth (see later).

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, instead being a result of 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); Pearse *et al.*, 2015; Bogdziewicz *et al.*, 2017b). In Mediterranean oak species, the late flower phenology could be a way of not adding noise to the already very stochastic fruiting dynamics and, consequently, keeping the frequency of mast-seeding years at a minimum threshold. Overall, the proximate mechanisms of oak masting (i.e. including environmental veto as a result of late frost or water stress, weather conditions impacting

flower maturation and pollen diffusion) would probably 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, which is itself 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 oak species, 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 tradeoff 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, it would be useful to develop integrative work on phenology and masting 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 considering ecophysiological traits for their impact on plant phenology (Chuine & Beaubien, 2001), those looking at the mechanistic traits of fruiting dynamics (Isagi *et al.*, 1997; Abe *et al.*, 2016; this work) – for example, the evolution of traits affecting resource allocation in reproduction – and those dedicated to simulating 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 associated ecosystem services (Cleland *et al.*, 2007).

Author contributions

ES, SV and M-C V conceived and led the study and wrote the paper. ES and GO assembled the pollen dataset. ES, IC, Sylvain Delzon and VB assembled the dataset of budburst dates in temperate oak trees. ES and SV analyzed the field data and performed the modeling. Stéphane Dray analyzed autocorrelation within simulated fruiting dynamics. IC, Sylvain Delzon, J-MG, VB and ILR gave fruitful comments during the research process. All authors revised the manuscript.

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References

Abe T, Tachiki Y, Kon H, Nagasaka A, Onodera K, Minamino K, Han Q, Satake A. 2016. Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. *Ecology letters* **19**: 1129–1139.

Andersson B. 1992. Autumn frost hardiness of *Pinus sylvestris* offspring from seed orchard grafts of different ages. *Scandinavian Journal of Forest Research* **7**: 367–375.

Augspurger CK. 2009. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Functional Ecology* **23**: 1031–1039.

Badeau V, Bonhomme M, Bonne F, Carré J, Cecchini S, Chuine I, Ducatillion C, Jean F, Lebourgeois F. 2017. *Les plantes au rythmes des saisons*, 336 pages. Biotope, Mèze, France.

Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G, Green P. 2015. *Package 'lme4'. Convergence 12.* [WWW document] URL https://cran.r-project.org/web/packages/lme4/index.html.

Barringer BC, Koenig WD, Knops JMH. 2013. Interrelationships among life-history traits in three California oaks. *Oecologia* **171**: 129–139.

Bogdziewicz M, Fernández-Martínez M, Bonal R, Belmonte J, Espelta JM. 2017b. The Moran effect and environmental vetoes: phenological synchrony and drought drive seed production in a Mediterranean oak. *Proceedings of the Royal Society B-Biological Sciences* **284**: 20171784.

Bogdziewicz M, Marino S, Bonal R, Zwolak R, Steele MA. 2018b. Rapid aggregative and reproductive responses of weevils to masting of North American oaks counteract predator satiation. *Ecology* **99**: 2575–2582.

Bogdziewicz M, Steele MA, Marino S, Crone EE. 2018a. Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytologist* **219**: 98–108.

Bogdziewicz M, Szymkowiak J. 2016. Oak acorn crop and Google search volume predict Lyme disease risk in temperate Europe. *Basic and Applied Ecology* **17**: 300–307.

Bogdziewicz M, Szymkowiak J, Kasprzyk I, Grewling Ł, Borowski Z, Borycka K, Kantorowicz W, Myszkowska D, Piotrowicz K, Ziemianin M *et al.* 2017a. Masting in wind-pollinated trees: system specific roles of weather and pollination dynamics in driving seed production. *Ecology* **98**: 2615–2625.

Bogdziewicz M, Zwolak R, Crone EE. 2016. How do vertebrates respond to mast seeding? *Oikos* **125**: 300–307.

Bogdziewicz M, Żywiec M, Espelta JM, Fernández-Martinez M, Calama R, Ledwoń M, McIntire E, Crone EE. 2019. Environmental veto synchronizes mast seeding in four constrasting tree species. *American Naturalist* **194**: 246–259.

Buechling A, Martin PH, Canham CD, Shepperd WD, Battaglia MA. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology* **104**: 1051–1062.

Buonaccorsi JP, Elkinton J, Koenig W, Duncan RP, Kelly D, Sork V. 2003. Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony. *Journal of Theoretical Biology* **224**: 107–114.

Caignard T, Kremer A, Firmat C, Nicolas M, Venner S, Delzon S. 2017. Increasing spring temperatures favor oak seed production in temperate areas. *Scientific Reports* **7**: 8555.

Cecich RA, Sullivan NH. 1999. Influence of weather at time of pollination on acorn production of *Quercus alba* and *Quercus velutina*. *Canadian Journal of Forest Research* **29**: 1817–1823.

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Phytologist

Chang-Yang C-H, Sun I-F, Tsai C-H, Lu C-L, Hsieh C-F. 2016. ENSO and frost codetermine decade long temporal variation in flower and seed production in a subtropical rain forest. *Journal of Ecology* 104: 44–54.

Chuine I, Beaubien EG. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* 4: 500–510.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22: 357–365.

Crawley MJ. 2000. Seeds: the ecology of regeneration in plant communities. In: Fenner M, ed. *Seed predators and plant population dynamics, vol. 2.* Wallingford, UK: CABI, 167–182.

Crone EE, Miller E, Sala A. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters* 12: 1119–1126.

Crone EE, Rapp JM. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences* 1322: 21–34.

Dray S, Dufour A-B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1–20.

Dray S, Royer-Carenzi M, Calenge C. 2010. The exploratory analysis of autocorrelation in animal-movement studies. *Ecological Research* 25: 673–681.

Durand Y, Brun E, Merindol L, Guyomarc'h G, Lesaffre B, Martin E. 1993. A meteorological estimation of relevant parameters for snow models. *Annals of Glaciology* 18: 65–71.

Feret PP, Kreh RE, Merkle SA, Oderwald RG. 1982. Flower abundance, premature acorn abscission, and acorn production in *Quercus alba* L. *Botanical Gazette* 143: 216–218.

Fernández-Martínez M, Belmonte J, Espelta JM. 2012. Masting in oaks: disentangling the effect of flowering phenology, airborne pollen load and drought. *Acta Oecologica* 43: 51–59.

Franjić J, Sever K, Bogdan S, Škvorc Ž, Krstonošić D, Alešković I. 2011. Phenological asynchronization as a restrictive factor of efficient pollination in clonal seed orchads of pedunculate oak (*Quercus robur L.*). *Croatian Journal of Forest Engineering: Journal for Theory and Application of Forestry Engineering* 32: 154–156.

Frey BR, Ashton MS, McKenna JJ, Ellum D, Finkral A. 2007. Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. *Forest Ecology and Management* 245: 54–63.

Gamelon M, Douhard M, Baubet E, Gimenez O, Brandt S, Gaillard J-M. 2013. Fluctuating food resources influence developmental plasticity in wild boar. *Biology Letters* 9: 20130419.

Gamelon M, Focardi S, Baubet E, Brandt S, Franzetti B, Ronchi F, Venner S, Sæther B-E, Gaillard J-M. 2017. Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. *Oecologia* 183: 1065–1076.

García-Mozo H, Pablo JH, Carmen G, Gómez-Casero MT, Domínguez E. 2001. Catkin frost damage in Mediterranean cork-oak *Quercus suber* L. *Israel Journal of Plant Sciences* 49: 42–47.

García-Mozo H, Gómez-Casero MT, Domínguez E, Galán C. 2007. Influence of pollen emission and weather-related factors on variations in holm-oak (*Quercus ilex subsp. ballota*) acorn production. *Environmental and Experimental Botany* 61: 35–40.

Gotelli NJ, McCabe DJ. 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology* 83: 2091–2096.

Herrera CM. 1998. Population-level estimates of interannual variability in seed production: what do they actually tell us? *Oikos* 82: 612–616.

Herrera CM, Jordano P, Guitián J, Traveset A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist* 152: 576–594.

Hirst JM. 1952. An automatic volumetric spore trap. *Annals of Applied Biology* 39: 257–265.

Huber PJ. 1964. Robust estimation of a location parameter. *Annals of Mathematical Statistics* 35: 73–101.

Isagi Y, Sugimura K, Sumida A, Ito H. 1997. How does masting happen and synchronize? *Journal of Theoretical Biology* 187: 231–239.

Janzen DH. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7: 347–391.

Kelly D, Sork VL. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33: 427–447.

Kelly D, Geldenhuis A, James A, Holland EP, Planck MJ, Brockie RE, Cowan PE, Harper GA, Lee WG, Maitland MJ et al. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* 16: 90–98.

Koenig WD, Knops JMH. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist* 155: 59–69.

Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* 102: 581–591.

Koenig WD, Knops JMH, Carmen WJ.2008. Timing of flowering and seed production in three California oaks. In: Merenlender A, McCreary D, Purcell KL, eds. *Proceedings of the Sixth Symposium on Oak Woodlands: Today's Challenges, Tomorrow's Opportunities.* Pacific Southwest Forest and Range Experiment Station General Technical Report PSW-GTR-217, 371–380.

Koenig WD, Funk KA, Kraft TS, Carmen WJ, Barringer BC, Knops JMH. 2012. Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. *Journal of Ecology* 100: 758–763.

Koenig WD, Knops JMH, Carmen WJ, Pearse IS. 2015. What drives masting? The phenological synchrony hypothesis. *Ecology* 96: 184–192.

Koenig WD, Alejano R, Carbonero MD, Fernández-Rebollo P, Knops JM, Marañón T, Padilla-Diaz CM, Pearse IS, Pérez-Ramos IM, Vâzquez-Piqué J, Pesendorfer MB. 2016. Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny? *Ecology* 97: 2603–2615.

Lebourgeois F, Pierrat J-C, Perez V, Piedallu C, Cecchini S, Ulrich E. 2008. Déterminisme de la phénologie des forêts tempérées françaises: étude sur les peuplements du réseau RENECOFOR. *Revue Forestière Française* 3: 323–343.

Leiva MJ, Pérez-Romero JA, Mateos-Naranjo E. 2018. The effect of simulated damage by weevils on *Quercus ilex subsp Ballota* acorns germination, seedling growth and tolerance to experimentally induced drought. *Forest Ecology and Management* 409: 740–748.

McShea WJ. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81: 228–238.

Meier U, Bleiholder H, Buhr L, Feller C, Hack H, Heß M, Lancashire PD, Schnock U, Stauß R, Van den Boom T, et al. 2009. The BBCH system to coding the phenological growth stages of plants–history and publications. *Journal für Kulturpflanzen* 61: 41–52.

Misson L, Degueldre D, Collin C, Rodriguez R, Rocheteau A, Ourcival JM, Rambal S. 2011. Phenological responses to extreme droughts in a Mediterranean forest. *Global Change Biology* 17: 1036–1048.

Monks A, Kelly D. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Austral Ecology* 31: 366–375.

Muñoz A, Bonal R, Espelta JM. 2014. Acorn – weevil interactions in a mixed-oak forest: outcomes for larval growth and plant recruitment. *Forest Ecology and Management* 322: 98–105.

Nussbaumer A, Waldner P, Apuhtin V, Aytar F, Benham S, Bussotti F, Eichhorn J, Eickenscheidt N, Fabianek P, Falkenried L et al. 2018. Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe. *Forest Ecology and Management* 429: 336–350.

Ogaya R, Peñuelas J. 2004. Phenological patterns of *Quercus ilex, Phillyrea latifolia,* and *Arbutus unedo* growing under a field experimental drought. *Écoscience* 11: 263–270.

Ostfeld RS, Keesing F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution* 15: 232–237.

Pearse IS, Koenig WD, Funk KA, Pesendorfer MB. 2015. Pollen limitation and flower abortion in a wind-pollinated, masting tree. *Ecology* 96: 587–593.

Pearse IS, Koenig WD, Kelly D. 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist* 212: 546–562.

Pearse IS, Koenig WD, Knops JMH. 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos* 123: 179–184.

Pélisson P-F, Bel-Venner M-C, Rey B, Burgevin L, Martineau F, Fourel F, Lecuyer C, Menu F, Venner S. 2012. Contrasted breeding strategies in four sympatric sibling insect species: when a prooviegnic and capital breeder copes with a stochastic environment. *Functional Ecology* 26: 198–206.

Pélisson P-F, Bernstein C, François D, Menu F, Venner S. 2013. Dispersal and dormancy strategies among insect species competing for a pulsed resource. *Ecological Entomology* 38: 470–477.

Pérez-Ramos IM, Padilla-Díaz CM, Koenig WD, Marañón T. 2015. Environmental drivers of mast-seeding in Mediterranean oak species: does leaf habit matter? *Journal of Ecology* 103: 691–700.

Pesson P, Louveaux J. 1984. *Pollinisation et productions végétales.* Paris, France: INRA, Quae.

Rees M, Kelly D, Bjørnstad ON. 2002. Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist* 160: 44–59.

Rey B, Pélisson P-F, Bel-Venner M-C, Voituron Y, Venner S. 2015. Revisiting the link between breeding effort and oxidative balance through field evaluation of two sympatric sibling insect species. *Evolution* 69: 815–822.

Richardson SJ, Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH. 2005. Climate and net carbon availability determine temporal patterns of seed production by *Nothofagus. Ecology* 86: 972–981.

Sabit M, Ramos JD, Alejandro GJ, Galan C. 2016. Seasonal distribution of airborne pollen in Manila, Philippines, and the effect of meteorological factors to its daily concentrations. *Aerobiologia* 32: 375–383.

Satake A, Iwasa YOH. 2000. Pollen coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology* 203: 63–84.

Satake A, Iwasa Y. 2002. The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *Journal of Ecology* 90: 830–838.

Schermer É, Bel-Venner M-C, Fouchet D, Siberchicot A, Boulanger V, Caignard T, Thibaudon M, Oliver G, Manuel N, Gaillard J-M, *et al.* 2019. Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecology Letters* 22: 98–107.

Smaill SJ, Clinton PW, Allen RB, Davis MR. 2011. Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology* 99: 870–877.

Sork VL, Bramble J, Sexton O. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74: 528–541.

Tachiki Y, Iwasa Y. 2013. Coevolution of mast seeding in trees and extended diapause of seed predators. *Journal of Theoretical Biology* 339: 129–139.

Ulrich E. 1995. Le réseau RENECOFOR: objectifs et réalisation. *Revue Forestière Française* 2: 107–124.

Vacchiano G, Ascoli D, Berzaghi F, Lucas-Borja ME, Caignard T, Collalti A, Mairota P, Palaghianu C, Reyer CPO, Sanders TGM, *et al.* 2018. Reproducing reproduction: How to simulate mast seeding in forest models. *Ecological Modelling* 376: 40–53.

Venner S, Pélisson P-F, Bel-Venner M-C, Débias F, Rajon E, Menu F. 2011. Coexistence of insect species competing for a pulsed resource: toward a unified theory of biodiversity in fluctuating environments. *PLoS ONE* 6: e18039.

Venner S, Siberchicot A, Pélisson P-F, Schermer E, Bel-Venner M-C, Nicolas M, Débias F, Miele V, Sauzet S, Boulanger V, *et al.* 2016. Fruiting strategies of perennial plants: a resource budget model to couple mast seeding to pollination efficiency and resource allocation strategies. *American Naturalist* 188: 66–75.

Vitasse Y, Delzon S, Dufrêne E, Pontailler J-Y, Louvet J-M, Kremer A, Michalet R. 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agricultural and Forest Meteorology* 149: 735–744.

Wald A, Wolfowitz J. 1943. An exact test for randomness in the non-parametric case based on serial correlation. *Annals of Mathematics and Statistics* 14: 378–388.

Wolff JO. 1996. Coexistence of white-footed mice and deer mice may be mediated by fluctuating environmental conditions. *Oecologia* 108: 529–533.

Yang LH, Edwards KF, Byrnes JE, Bastow JL, Wright AN, Spence KO. 2010. A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs* 80: 125–151.

Yi X, Bartlow AW, Curtis R, Agosta SJ, Steele MA. 2019. Responses of seedling growth and survival to post-germination cotyledon removal: An investigation among seven oak species. *Journal of Ecology* 107: 1817–1827.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

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

Fig. S2 Relationship between budburst 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 at > 30 d after budburst date in the temperate region.

Fig. S7 Analysis of the relative contribution of the late frost and the mean temperature impacting pollen aerial diffusion in the fruiting dynamics under four 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 at > 30 d after budburst date in the temperate region.

Method 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 budburst 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 budburst date.

Table S7 Testing the sensitivity of fruiting intensity to weather conditions around the budburst 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.

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