

LETTER

Pollen limitation as a main driver of fruiting dynamics in oak populations

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Abstract

In many perennial wind-pollinated plants, the dynamics of seed production is commonly known to be highly fluctuating from year to year and synchronised among individuals within populations. The proximate causes of such seeding dynamics, called masting, are still poorly understood in oak species that are widespread in the northern hemisphere, and whose fruiting dynamics dramatically impacts forest regeneration and biodiversity. Combining long-term surveys of oak airborne pollen amount and acorn production over large-scale field networks in temperate areas, and a mechanistic modelling approach, we found that the pollen dynamics is the key driver of oak masting. Mechanisms at play involved both internal resource allocation to pollen production synchronised among trees and spring weather conditions affecting the amount of airborne pollen available for reproduction. The sensitivity of airborne pollen to weather conditions might make oak masting and its ecological consequences highly sensitive to climate change.

Keywords

Masting, pollen limitation, *Quercus* spp., resource budget model, spring weather conditions.

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INTRODUCTION

Reproduction in many perennial and wind-pollinated plant species is still poorly understood, in particular the phenomenon known as masting, characterised by synchronised and highly variable levels of seed production over the years within a population (Janzen 1976; Kelly & Sork 2002; Crone & Rapp 2014; Pearse *et al.* 2016). Masting may evolve whenever flowering and fruiting effort, being synchronised among trees within populations, maximises individual fruit set and/or offspring survival (Norton & Kelly 1988; Kelly 1994). One well-accepted selective advantage of masting is to lower the risk of seed consuming: seed consumer populations are maintained at low densities in the years with no or low fruiting, resulting in only marginal consumption when rare and unpredictable massive fruiting occurs (Janzen 1971; Silvertown 1980; Kelly *et al.* 2000, 2008; Pearse *et al.* 2016). For allogamous species, another non-exclusive evolutionary cause of masting, the pollination efficiency hypothesis states that occasional high reproductive effort synchronised at the population scale being concomitant with large and synchronous pollen production, would increase the pollination success of individual plants (Kelly *et al.* 2001). Whatever its evolutionary cause, masting leads to increased plant recruitment and thereby drives plant demography and the diversity of plant species in forest ecosystems. By impacting the seed consumer dynamics and evolution (Yang *et al.* 2010; Venner *et al.* 2011; Gamelon

et al. 2013; Pélisson *et al.* 2013; Rey *et al.* 2015; Zwolak *et al.* 2016) and through cascade effects, masting may even affect the whole forest community and all its forest ecosystem services (Crawley 2000; Ostfeld & Keesing 2000; Frey *et al.* 2007; Żywiec *et al.* 2013; Moreira *et al.* 2016; Nussbaumer *et al.* 2016). However, despite masting's substantial evolutionary, ecological and societal effects, the proximate causes of masting are still poorly understood.

A first set of hypotheses aimed at explaining masting assumes that plants within populations seed synchronously because they all respond to similar weather cues in the same way, resulting in high interannual variability in flowering and seeding, as well as tight synchrony among individuals (Kelly *et al.* 2000, 2013). Furthermore, the weather effect on resource acquisition and allocation to reproduction, on pollination or on fecundation success can be viewed as environmental constraints, acting as 'veto' on seeding in extreme cases (Kon *et al.* 2005; Bogdziewicz *et al.* 2017a, 2018). For some masting species, statistically significant relationships have been observed between weather conditions and flowering or fruiting dynamics (Inouye *et al.* 2002; Kelly & Sork 2002; Schaubert *et al.* 2002; Kelly *et al.* 2013). However, for oak species, the weather drivers of masting are more difficult to establish (Sork *et al.* 1993; Herrera *et al.* 1998; Kelly & Sork 2002; Koenig *et al.* 2003; Barringer *et al.* 2013; Kasprzyk *et al.* 2014; Bogdziewicz *et al.* 2017b).

Complementary to exploring the relationships between fruiting dynamics and weather cues, the development of mechanistic

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models (e.g. resource budget models, RBMs) has largely contributed to understand masting over the past two decades (Crone & Rapp 2014). A first set of RBMs raised the novel hypothesis that masting may emerge without any weather fluctuation (Isagi *et al.* 1997; Satake & Iwasa 2002a). These models proposed that masting would result from two interplaying processes: (i) tree internal resource dynamics considering that trees producing large seed crops should experience severe resource depletion and thereby be prevented from flowering (including pollen) and fruiting the following breeding season (i.e. internal resource depletion hypothesis) and (ii) cross-pollination combined with density-dependent pollen limitation expected to synchronise fruiting among trees: any tree breeding asynchronously and allocating heavily to flowering while outcross pollen is rare – due to resource depleted neighbouring trees – would likely have very few flowers pollinated. The resource saved subsequently to fruiting failure would then be allocated to flowering the following year, potentially in synchrony with the other trees in the population. Large interannual variations in fruiting would thus be promoted by alternate years with high and low amounts of airborne pollen resulting from pollen produced synchronously at the population level. Other RBMs allowed substantial advances in understanding masting by introducing the effect of weather on several processes of plant reproduction such as resource acquisition and/or allocation to flowering (Crone *et al.* 2005; Monks *et al.* 2016), floral initiation (Rees *et al.* 2002; Abe *et al.* 2016; Bogdziewicz *et al.* 2018) and pollination (Pesendorfer *et al.* 2016), or by implementing environmental ‘veto’ that might occur at different steps of the reproductive cycle and favour fruiting synchrony (Bogdziewicz *et al.* 2018). RBMs are then a powerful tool to disentangle the underlying mechanisms of masting (Crone & Rapp 2014), which is notably required in fruit-masting species (vs. flower-masting species, *sensu* Pearse *et al.* 2016) as it is expected to be the case for oaks.

Resource budget models raise the central question of the key role of pollen limitation. Such limitation could be driven either by the resource allocation into pollen production (related to the resource depletion hypothesis), and/or by the sensitivity of the pollination process to weather conditions (Pearse *et al.* 2016). In line with the last hypothesis, several empirical studies have shown that daily airborne pollen amounts strongly depends on weather conditions during pollen release and aerial diffusion for many plant species (García-Mozo *et al.* 2012; Grewling *et al.* 2014; Kasprzyk *et al.* 2014; Fuhrmann *et al.* 2016; Sabit *et al.* 2016). Likewise, spring weather are related to fruiting intensity in some masting species (García-Mozo *et al.* 2012; Pearse *et al.* 2014; Fernández-Martínez *et al.* 2015; Koenig *et al.* 2015; Bogdziewicz *et al.* 2017a; Caignard *et al.* 2017; Nussbaumer *et al.* 2018), which suggests that unfavourable weather conditions for pollen release, aerial diffusion or synchronised flowering may cause pollen limitation (Koenig *et al.* 2012, 2015; Bogdziewicz *et al.* 2017b).

However, this so-called ‘pollen limitation hypothesis’ is still being widely debated mainly because (i) substantial amounts of airborne pollen can be detected almost every year for masting species (Clot 2003; Spieksma *et al.* 2003; Geburek *et al.* 2012), (ii) pollination may be effective even at low pollen densities in

wind-pollinated species (Kelly *et al.* 2001; Friedman & Barrett 2009), and (iii) hand-pollen supplementation experiments lead to contradictory outcomes (Tamura & Hiura 1998; Crone & Lesica 2006; Friedman & Barrett 2009; Pearse *et al.* 2015).

The paucity of analyses encompassing large climatic gradients and based on long time series for both airborne pollen amounts available for reproduction and fruiting intensity likely accounts for our current poor understanding of the implication of pollen limitation on masting. Here, we aim to fill this knowledge gap and test the role of pollen dynamics (both interannual fluctuation of airborne pollen amounts and pollen synchrony, i.e. the seasonal spreading of airborne pollen) and pollen limitation on oak masting by analysing long-term and large-scale field data of oak airborne pollen and acorn production dynamics collected in temperate oak populations, and by combining these analyses with the development of a new RBM. This original approach allowed us to elucidate how airborne pollen amount mediates acorn production through both internal resource allocation dynamics (related to resource depletion) and spring weather. Both oak airborne pollen amount and acorn production were found to increase along with warmer and drier spring weather following a logistic function. Furthermore, we found that pollen limitation, driven by weather conditions at time of pollen release and aerial diffusion combined with the resource allocation strategy, strongly influences oak masting. Our findings could be crucial for understanding the impact of climate change on oak tree reproduction, and, by domino effect, on the dynamics of oak forest biodiversity as a whole.

MATERIAL AND METHODS

We focused on two white oak species (*Quercus petraea* and *Q. robur*) that are widespread and abundant in Northern hemisphere forests and well known for their interannual fruiting dynamics that are extremely fluctuating and with noticeable consequences on the whole forest ecosystem (Crawley & Long 1995; Frey *et al.* 2007; Venner *et al.* 2011; Gamelon *et al.* 2013; Pélisson *et al.* 2013).

Field data

We analysed pollen and acorn datasets acquired independently through long-term and large-scale field observations in temperate French oak populations (44 pollen-sampling sites surveyed for 22 years from 1994 to 2015, and 30 acorn-sampling sites surveyed for 14 years from 1994 to 2007), and weather data available for each pollen- and acorn-sampling sites (see Appendix S1, Tables S1, S2 and Figs S1, S2 in the Supporting Information for a detailed description of the datasets). From oak pollen data, we computed two variables: (i) the yearly amount of airborne pollen recorded at each site and, (ii) the duration of the seasonal spreading of airborne pollen (i.e. the number of days corresponding to the interquartile range of daily amounts of airborne pollen), which is a proxy of the synchrony level of pollen release among trees (called hereafter ‘pollen synchrony’).

Statistical analyses

Data concerning these two oak species were pooled for statistical analysis, then modelling, because pollen morphology does not allow discriminating them and no significant species effect was observed in acorn production (see Appendix S1, Table S3 and Fig. S3 for a complete justification). The intensity of interannual fluctuations of both airborne pollen amount and acorn production were estimated by computing for each site the temporal population Coefficient of Variation (CVp) of these two variables (Herrera 1998; Koenig *et al.* 2003). To test whether interannual pollen dynamics is in line with the resource depletion hypothesis (i.e. negative lag-1 year autocorrelation), we calculated the autocorrelation coefficient for each of the 44 pollen-sampling sites, and tested with Student's *t*-tests if the averaged coefficient (calculated from all 44 lag-1 year autocorrelation coefficients) differed from zero.

Contrary to the work of Lebourgeois *et al.* (2018) that was based on the same pollen and acorn datasets as in our study, we considered that the two datasets cannot be directly crossed. Indeed, based on their method we found that annual oak airborne pollen amount as well as pollen synchrony were poorly estimated at the acorn sites (Appendix S2 and Table S4). We then developed an indirect, yet robust, method by first identifying the weather conditions impacting pollen dynamics, then testing their impact on fruiting dynamics.

To test the sensitivity of pollen dynamics to weather at different time periods, we crossed annual airborne pollen amount, and then pollen synchrony, with meteorological data. For each calendar month, we computed mean values for temperature and rainfall and perform a principal component analysis (PCA) on these two weather variables. We then used the first Principal Component (called hereafter 'Weather Index' (WI) that captured between 52% and 73% of both temperature and rainfall variability) to reflect the observed weather variation (Appendix S3 and Table S5). We split the whole pollen dataset in two mirror sub-datasets, each of these comprising full time series of 22 pollen-sampling sites evenly distributed over similar altitude, longitude and latitude gradients, and we used them separately to run two independent statistical analyses (Fig. S1). Using a first sub-dataset (called hereafter 'calibration dataset'), we performed an exploratory analysis to detect without any a priori the candidate periods when weather variables influence airborne pollen amount and/or pollen synchrony. We then fitted generalised linear mixed models (GLMMs with Gaussian family and identity link) with log-transformed airborne pollen amount as the dependent variable, the lag-1 autocorrelation of airborne pollen amount and different WI as covariates, and the factors 'site' and 'year' as random effects to increase the probability of identifying candidate periods and key weather conditions (Table S6). On the second sub-dataset (called hereafter 'validation dataset'), we tested whether the WI effects previously identified were detected again by fitting generalised linear models (GLMs with Gaussian family and identity link) with the factors 'site' and 'year' as fixed effects (Table S7). Then, we calculated the proportion of the 'site' and 'year' effects that was accounted for by WI using an analysis of deviance (ANODEV, Skalski *et al.* 1993; Grosbois *et al.* 2008; Lebreton *et al.* 2012) (Table S8).

Considering that pollen limitation might depend on weather conditions impacting the amount of airborne pollen and/or pollen synchrony, we tested the prediction that the WI (identified then validated with pollen dataset) would also be correlated to the fruiting intensity at the acorn-sampling sites. We fitted a negative binomial GLM using a log link, with the acorn number as the dependent variable, the lag-1 year acorn number and WI as covariates, and the factors 'site' and 'year' as fixed effects, which analysis was followed by an ANODEV, as for pollen data analysis (Appendix S3, Tables S3 and S9).

All statistical analyses were performed with the R free software environment (v.3.4.3, <http://cran.r-project.org>). We performed the PCA and performed temporal autocorrelation analysis using the `dudi.pca` and `acf` functions from the *ade4* package (Dray & Dufour 2007). The best-fitted family distribution used in the linear model was determined using the *fitdistrplus* package (Delignette-Muller & Dutang 2015). Several GLMMs including various additive effects were fitted using the `lmer` function from *lme4* packages (Bates *et al.* 2015).

The model

We built a RBM (detailed in Appendix S4) to explore to what extent pollen limitation could be involved in masting. We showed from empirical analyses that 'April Weather Index' (AWI), which is negatively related to rainfall and positively with temperature in April, was the weather variable the most highly correlated to both the amount of airborne pollen and acorn production (Tables S3, S6 and S7). We then included the effect of AWI on the amount of pollen available for reproduction. Since the results obtained with AWI or April mean temperature (AT) were very similar (Fig. S4), and to allow easier comparison with other studies on masting, we replaced AWI with AT in a second model. In the following methods and results sections, we only present the case of AT.

In our model, we considered that pollen limitation possibly results from internal resource depletion of trees determining the amount of resource that the trees may allocate to pollen production a given year, and/or from the spring weather impacting the amount of airborne pollen available for reproduction. Our RBM was inspired from a former one (see Venner *et al.* 2016 and Appendix S4 for details), though with two major changes. First, based on our empirical results, we fitted a logistic relationship between spring weather (i.e. AT), and a coefficient weighting the pollen availability for reproduction by reducing the total amount of pollen produced a given year by a set of neighbouring trees (Appendix S4 and Table S10). Second, following Monks *et al.* (2016), we replaced the unrealistic threshold model with a continuous, smoothing logistic function linking the amount of resources allocated to flowering to the level of tree reserves. In our study, an average depletion coefficient (DC) of 5 has been empirically estimated (see Appendix S4 for details), and considering balanced resource allocation into male and female flowering (Norton & Kelly 1988). We also looked for average DC of 2 and 8 considering male- and female-biased allocation to flowering respectively (Figs S5 and S6).

We compared the observed pollen and fruiting patterns (using both CVp and the mean relationships $\text{Pollen} \sim \text{AT}$,

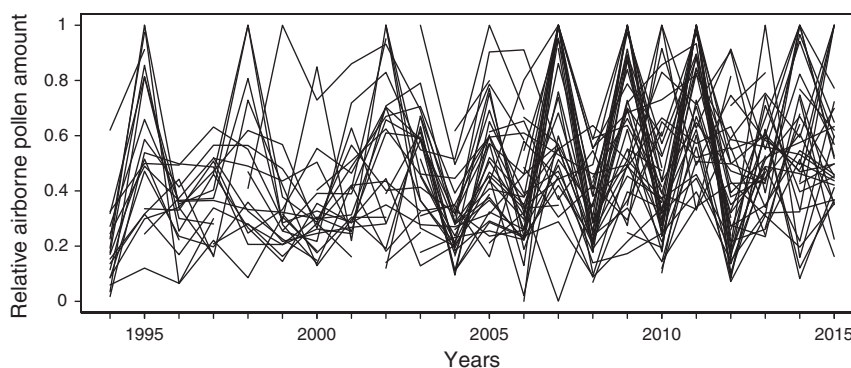


Figure 1 Interannual dynamics of oak airborne pollen amounts. Annual airborne pollen amounts from *Quercus* spp. were measured from 1994 to 2015 at each of the 44 pollen-sampling sites surveyed (see Fig. S1 for a map of the pollen sites and Table S1 for their GPS coordinates). The relative airborne pollen amount is computed for any given locality as the ratio of the absolute airborne pollen amount (i.e. estimate of the annual number of pollen items per cubic metre of air) measured at a given year to the maximum value ever found at that site.

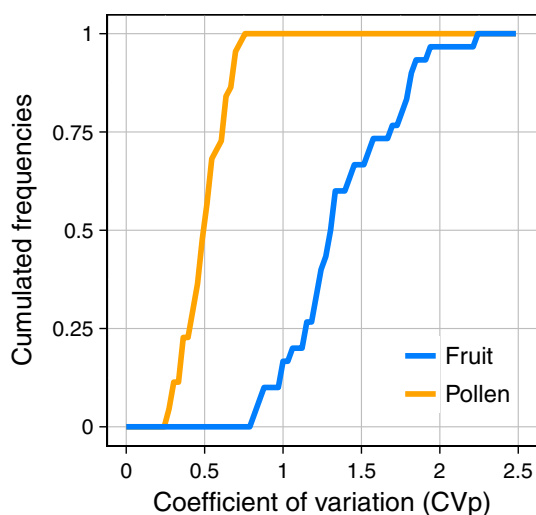


Figure 2 Interannual fluctuations in oak pollen amount and acorn production in the field. The amplitude of interannual fluctuations were described from the distribution of the population Coefficient Variation (CVp). The cumulative frequency distribution of the CVps was calculated from (i) the oak acorn crop collected in each of the 30 acorn-sampling sites surveyed each year from 1994 to 2007 (blue line) (see Fig. S2 for a map of the acorn-sampling sites and Table S2 for their characteristics) and (ii) from the annual airborne pollen amount for each of the 44 pollen-sampling sites surveyed each year from 1994 to 2015 (orange line) (see Fig. S1 for a map of the pollen-sampling sites and Table S1 for their GPS coordinates).

Fruit \sim AT) to the data simulated considering or not pollen limitation. In the pollen limitation context, the pollination success depended on the airborne pollen amount following a logistic function (see Venner *et al.* 2016 for detailed justification). Under no pollen limitation, we considered that there was always enough pollen to ensure constant and maximum pollination success. We further examined the case when pollen limitation would be due to the resource allocation strategy alone ('resource-driven pollen limitation') or to spring weather alone ('weather-driven pollen limitation').

RESULTS

Resource depletion and spring weather as main drivers of pollen dynamics

We tested whether the interannual pollen dynamics in oak trees supports the hypothesis of the synchronised resource depletion and allocation into pollen production within tree populations. Because the amount of airborne pollen depends on the amount of resources trees allocated to male flower production, we predict that airborne pollen amounts would greatly fluctuate over years, notably with years of low pollen production following years during which large amounts of pollen were produced. Accordingly, the oak pollen dynamics analysed from a 22-year annual survey over 44 sites clearly followed a biennial rhythm with alternating years of high and low airborne pollen amounts (Fig. 1). Using the validation dataset, we showed that the negative temporal autocorrelation (1-year lag coefficient averaging -0.28 , Student's t -test: $t = -6.68$; d.f. = 43; $P < 0.001$; 95% CI $[-0.36; -0.19]$) accounted for 17.7% of the variation observed in annual airborne pollen amount within pollen-sampling sites (Table S8). Airborne pollen amounts fluctuated over the years, yet to a lesser extent than did oak acorn production (median CVp for pollen equals 0.5 vs. 1.3 for acorns; Fig. 2).

Under the pollen limitation hypothesis, the weather conditions influencing the amount of airborne pollen and/or pollen synchrony would also influence the acorn crop. Of the numerous months tested using the calibration dataset, we showed that the amount of airborne pollen solely depended on April weather (i.e. weather at time of pollen release and aerial diffusion at our study sites; see Appendix S3, Fig. S7 and Table S6). The amount of annual airborne pollen increased according to a logistic function with AWI (Fig. 3a, and Tables S6, S7) that is, with increasing temperature and decreasing rainfall (Appendix S3 and Fig. S8). Using the validation dataset, we showed that the AWI overall accounted for 12.8% of the variation observed in airborne pollen amounts and also accounted for 50% of the 'year' effect (see ANODEV; Table S8). In complement, we showed that the amount of airborne pollen and acorn production both increased, according to a logistic

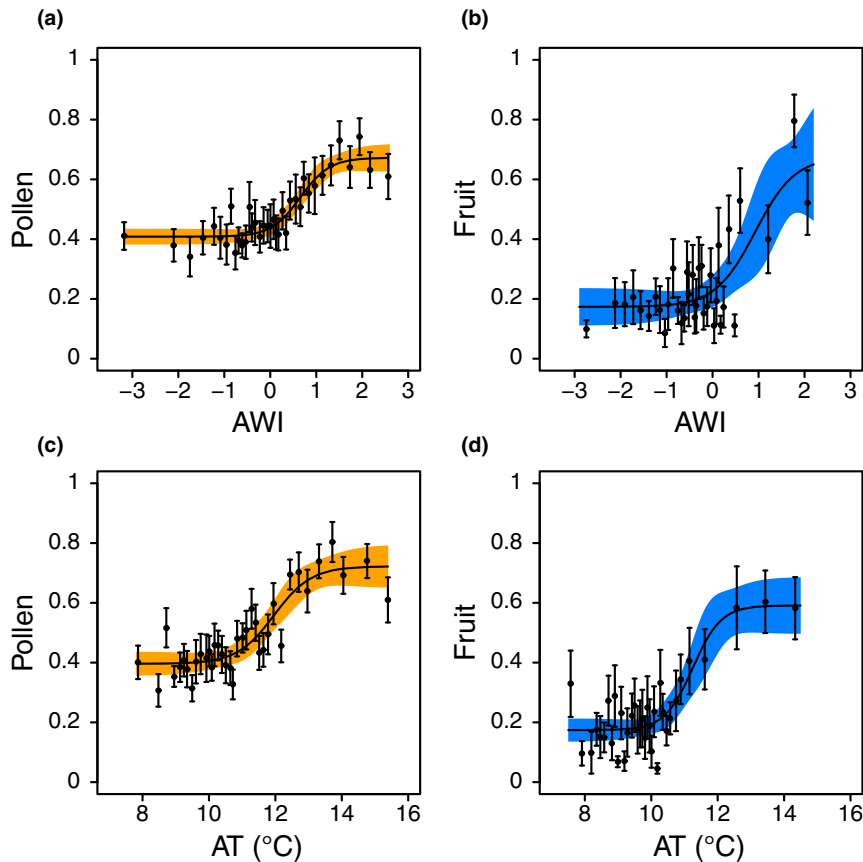


Figure 3 Impact of spring weather on oak airborne pollen amount and acorn production. Airborne pollen amount (a,c) and acorn production (b,d) both increased following a logistic function with the April Weather Index (AWI) (a,b) (which is positively correlated to ambient temperature and negatively correlated to rainfall (Appendix S3 and Fig. S8 for further details)), and with the April mean temperature (AT) alone (c,d). The fitted pollen and acorn data were computed as relative (i.e. the ratio between the value at a given year of one site to the maximum value ever found at that site). For pollen, data collected yearly for 22 years at each of the 44 sites were ranked according to their corresponding AWI (or AT) values, then sets of 14 consecutive values were made to compute means and SD (black dots and their interval segments) of airborne pollen amount (in all 518 *site year* combinations available). The same was done for acorn data (in all 420 *site year* combinations available), except that means and SD were computed on sets of 12 consecutive values. Shaded areas show the 95% confidence interval of the model estimates.

function, with the AWI (Fig. 3a,b; Tables S3, S6, S7 and S10). Similar results were obtained when April mean temperature (i.e. AT) was used instead of AWI (Fig. 3c,d).

The airborne pollen amount was not correlated to pollen synchrony (Table S11 and Fig. S9). Using the calibration dataset, we showed that pollen synchrony was not correlated with AWI (nor with AT) but correlated with weather in September and October of the previous year, and in March of the current year, that is, a few weeks before pollen release and aerial diffusion take place (Table S6). These relationships between pollen synchrony and weather were not robust, however, since no effect of any weather variable was detected when tested on the validation dataset (Table S7), and furthermore, they had no detectable effect on fruiting intensity (Table S12).

Pollen dynamics as a key driver of fruiting dynamics in oak trees

To disentangle the respective role of the ‘resource-driven pollen limitation’ (resulting from internal resource depletion) and that of the ‘weather-driven pollen limitation’ (operating on pollen aerial diffusion) on oak masting, we developed a RBM

simulating pollen and fruiting dynamics under various conditions of pollen limitation. Because robust results are generated by only accounting for the effect of the weather conditions in April (AT, or AWI) on both airborne pollen amount and acorn production, only these weather effects have been included in our model.

Without any pollen limitation, that is, considering the fertilisation rate to be high and independent of the true airborne pollen availability, tree reproduction should theoretically be desynchronised (Satake & Iwasa 2002a,b), which would homogenise the amount of pollen and fruit produced each year at the population level. Accordingly, our simulations show weak interannual variation in airborne pollen amounts as well as in acorn crops (Fig. 4a). The simulated airborne pollen amounts were sensitive to AT (Fig. 4e), similarly to the observed data, contrary to the acorn abundance that remained consistently high (Fig. 4i).

In the subsequent simulations, pollen limitation is included in the RBM through a pollination function that describes the positive logistic response of the pollination success to the pollen availability (see Venner *et al.* 2016 and Appendix S4 for

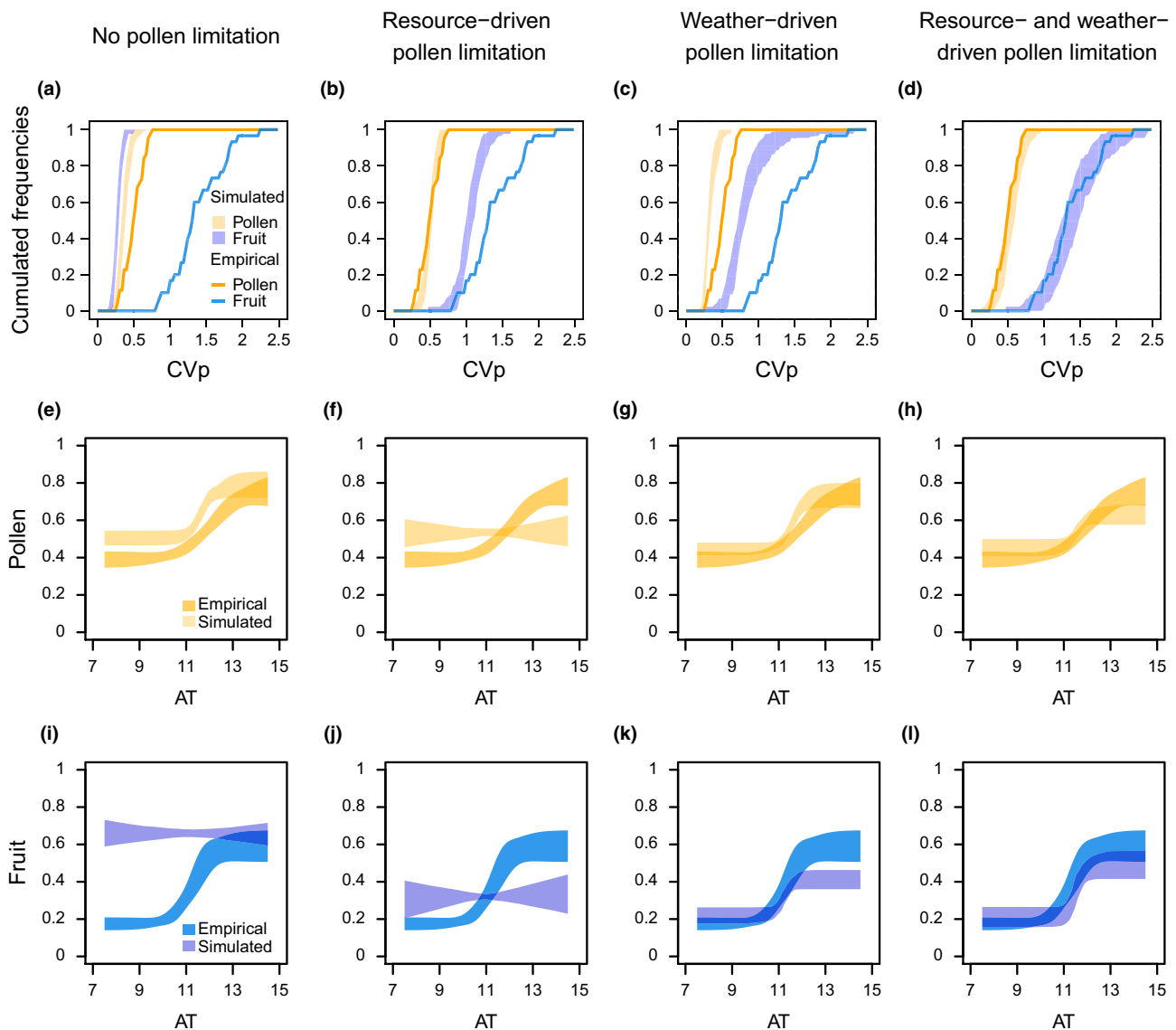


Figure 4 Model outputs compared to empirical datasets for oak airborne pollen and acorn production. Simulated data (light-shaded areas) correspond to different cases of pollen limitation: ‘no pollen limitation’ (a,e,i), ‘resource-driven pollen limitation’ (b,f,j), ‘weather-driven pollen limitation’ (c,g,k), or ‘resource- and weather-driven pollen limitation’ (d,h,l). (a–d) Cumulative frequency distribution of the population Coefficient of Variation (CVp) calculated from empirical oak pollen and acorn data (lines) and simulated data (light-shaded areas). (e–l) Mean relationships between the relative airborne pollen amount (e–h) or relative fruiting abundance (i–l) along with spring weather (AT, April mean Temperature). The simulated relationships display the 95% credible interval for pollen and acorns respectively (i.e. the interval including 95% of the simulations; see Materials and Methods and Appendix S4 for more details and Figs S5 and S6 for a sensitivity analysis to the depletion coefficient). In (e)–(l), the observed relationships (dark-shaded areas) correspond to the 95% confidence interval (see Fig. 3).

further details). This amount of pollen may depend on (i) the resource allocation of trees in pollen production, (ii) the spring weather (i.e. AT) during pollen release and aerial diffusion (iii) or both. When pollen dynamics and limitation are considered to depend either on the dynamics of internal resource alone (Fig. 4b,f,j) or on spring weather alone (Fig. 4c,g,k), the simulations failed to match field data. Considering the ‘resource-driven pollen limitation’ alone, the simulated pollen fluctuations were similar to the observed ones but the simulated acorn production fluctuated much less than the observed ones (Fig. 4b), while the simulated airborne pollen amounts as well as fruit production were logically

independent of spring weather (Fig. 4f,j). Considering the ‘weather-driven pollen limitation’ alone, pollen and acorn varied according to logistic functions with AT (Fig. 4g,k), but we found lower simulated pollen and acorn fluctuations compared to the observed ones (Fig. 4c).

Assuming that pollen limitation is mediated both by the dynamics of internal resources and spring weather, our model predicts that airborne pollen amounts should fluctuate over the years, though to a lesser extent than fruiting. These findings satisfactorily match our empirical data, for both pollen and acorns (Fig. 4d). We found greater variation in acorn crops compared to airborne pollen amounts, which would be

due to the logistic shape of the function that links fruit set (or pollination success) to the amount of airborne pollen (Fig. S10). In complement, the simulated airborne pollen amount and acorn production were also highly sensitive to spring weather, similarly to what was observed from empirical data (Fig. 4h,l). We obtained qualitatively the same results with the three values of DC tested (Figs S5 and S6). When we considered either empirical or simulated data individually collected at each site and each year we found positive yet loose relationship between pollen (or fruiting) and AWI (Fig. S11). Further simulations were made to compare logistic *vs.* linear relationships between the coefficient weighting pollen availability and spring weather for their effect on pollen and acorn dynamics. Unlike logistic function, the linear function largely and consistently underestimated the influence of weather conditions on masting pattern, leading to strong discrepancy between simulated and observed patterns (Fig. S12).

DISCUSSION

Whether pollen dynamics and limitation are key drivers of masting is a challenging question to understand the dynamics of forest biodiversity and predict its future in the context of climate change. We provided here evidence of such decisive role of pollen in oak masting. Mechanisms at play involved two major components: (i) the synchronised internal resource dynamics and depletion among trees that generates alternating years with high and low pollen production at the population scale and (ii) the high sensitivity of the amount of airborne pollen to spring weather.

The oak pollen dynamics shows negative temporal autocorrelation with alternating years of high and low airborne pollen amounts (Fig. 1). This biennial rhythm may unlikely be governed by weather conditions but rather results from the synchronised internal resource depletion and allocation in pollen production among trees within populations. Over the last decade, many theoretical investigations have proposed that switching between low and high pollen availability at the population level may be one of the key mechanisms of masting (Isagi *et al.* 1997; Satake & Iwasa 2002a; Pesendorfer *et al.* 2016; Venner *et al.* 2016). On the basis of the extended field network and survey of airborne pollen, we provide original and robust results supporting this ‘resource-driven pollen limitation’ hypothesis. Our results are in line with previous studies that pointed out the role of resource limitation in masting species, including oaks (Rapp *et al.* 2013; Pesendorfer *et al.* 2016), which suggest that flower and pollen production depend on the level of nitrogen reserve that fluctuates before and after a massive fruiting event (Sala *et al.* 2012; Han *et al.* 2014; Miyazaki *et al.* 2014; Abe *et al.* 2016), even if the limiting resource for pollen and fruit production remain controversial (Ichie *et al.* 2013; Pearse *et al.* 2016; Han & Kabeya 2017).

We also showed that the weather conditions driving oak pollen dynamics impacted acorn crops. Consistently with many studies showing that weather during pollen release and aerial diffusion may impede airborne pollen amounts (Fernández-Martínez *et al.* 2012; Grewling *et al.* 2014; Kasprzyk *et al.* 2014; Fuhrmann *et al.* 2016; Sabit *et al.* 2016), we found that the oak airborne pollen amounts was positively correlated

with warm and dry April weather (Fig. 3a,b). Interestingly, oak airborne pollen amounts and acorn crops similarly increased with AWI, even though acorn and oak pollen datasets had been collected in separate sites and years. Similar results were also obtained when replacing AWI by April mean temperature (i.e. AT) (Fig. 3c,d). Such similar logistic responses of pollen amount and acorn crops to spring weather provide one of the most relevant empirical support for a ‘weather-driven pollen limitation’ that would reduce acorn crop by impeding pollen availability for reproduction.

Previous studies have suggested that pollen synchrony (i.e. the duration of the seasonal spreading of airborne pollen) could be one of the main drivers of oak masting (Koenig *et al.* 2015; Pesendorfer *et al.* 2016; Bogdziewicz *et al.* 2017b) because high spring temperatures are known for their synchronising effect on leaf budburst – leaf phenology providing a proxy of pollen phenology (Koenig *et al.* 2012) – and are also favourable to high fruiting (Pearse *et al.* 2014; Caignard *et al.* 2017; Nussbaumer *et al.* 2018). Our results show that pollen synchrony is not correlated to the annual airborne pollen amount (Fig. S9), which suggests that their effects can be unravelled. Here, we found that pollen synchrony does not correlate with the weather conditions at time of pollen release and aerial diffusion (i.e. April), but does with those occurring ahead to this period. Yet, these weather variables seem to have only a weak or no effect on pollen synchrony. They indeed vanished when tested using the validation dataset, and furthermore, they had no detectable effect on fruiting intensity. These results therefore suggest that the annual pollen amount, rather than pollen synchrony, determines pollination success and by extent fruiting success. Our results thus conflict with a recent work based on the same datasets than in our study (Lebourgeois *et al.* 2018), in which the authors found no effect of annual airborne pollen amount on acorn production and concluded that their results supported the pollen synchrony hypothesis. However, their results and interpretation are questionable since they are drawn from poor estimates of pollen amount and synchrony at the fruiting sites (Appendix S2, and Table S4) and they did not directly test the effect of pollen synchrony on fruiting. Disentangling the effects of the amount of airborne pollen and of pollen synchrony requires further robust and rigorous empirical cross-analyses with fruiting success (fruit set).

Our RBM revealed that pollen limitation in oak population must be mediated both by the dynamics of internal resource synchronised among trees (resource-driven pollen limitation) and by spring weather impacting the amount of pollen available for reproduction (weather-driven pollen limitation). When these two conditions were met, and provided that the coefficient weighting pollen availability was logistically related to the weather variable, our model predicts that the amount of airborne pollen would fluctuate over the years, though to a lesser extent than fruiting, and that pollen and acorn amounts would be highly sensitive to spring weather, similarly to the observed data (Fig. 4d,h,l). In contrast, whenever any of these two conditions was lacking (Fig. 4, first 3 panel columns), or when linear relationship was assumed between the coefficient weighting pollen availability and spring weather (Fig. S13), the simulated results departed from those observed in the

field. Moreover, empirical studies of masting have often considered linear relationships between weather variables and fruit production (but see Kelly *et al.* 2008, 2013). Our RBM, combined with another recent theoretical work (Fernández-Martínez *et al.* 2017a), stresses the need to address nonlinear 'weather-fruit' relationships to more accurately assess the weather drivers of masting.

Although our work provides new information supporting the pollen limitation hypothesis, this may not be the only mechanism governing masting in oaks or other plant species (see Pearse *et al.* 2016). In some cases, and independently of pollination, weather conditions may strongly influence flowering or fruiting allocation processes. Weather conditions can act either as cues to which plants respond synchronously (Ashton *et al.* 1988; Kelly & Sullivan 1997; Kelly *et al.* 2000, 2013; Koenig 2002; Koenig & Knops 2013; Kon & Saito 2015; Fernández-Martínez *et al.* 2017b) or as environmental constraints (Sarvas 1962; Kon *et al.* 2005; Bogdziewicz *et al.* 2017a, 2018). Weather may impede or even prevent reproduction (environmental veto) in rare years, particularly when late spring frost cause fertilised flowers to abort massively (Chang-Yang *et al.* 2016), leading to amplify fruiting synchrony (Crone & Rapp 2014; Pearse *et al.* 2016; Bogdziewicz *et al.* 2017a,b, 2018). RBMs applied to masting in oak tree populations suggest that both environmental veto (Bogdziewicz *et al.* 2018) and pollen limitation (Pesendorfer *et al.* 2016, our study) play a key role in masting. Interestingly, these two processes could be closely linked: oak pollen is released quite early in the season (i.e. April) at a time when weather conditions are commonly unfavourable to pollen release and aerial diffusion (Fig. 3c) making weather-driven pollen limitation a key driver. In addition, flowers maturing in early spring may be most sensitive to frost, which is likely to favour the occurrence of environmental vetoes. The way these two mechanisms jointly operate deserves further work combining modelling and accurate field observations.

To conclude, our work examining the pollen limitation hypothesis suggests that any subtle change in weather conditions during pollen release and aerial diffusion is likely to cause significant changes in pollen limitation and oak tree reproduction, which effect may be emphasised because of the logistic shape of the 'pollen-weather' relationship (Fig. 3). In consequence, by affecting the degree of pollen limitation, our study highlights that climate change might strongly impact oak masting and its ecological cascade effects. Our findings provide better understanding of the mechanisms underlying oak masting and a robust, credible model for oak forest reproduction and the associated biodiversity dynamics in the context of climate change.

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AUTHORSHIP

ES, SV and M-C V conceived and led the study. ES, MT, GO, MN and TC assembled the dataset; ES and DF analysed field data; ES, SV and AS performed modelling. ES and SV wrote the paper. SD, J-M G, VB and TC gave fruitful comments during the research process. All authors revised the manuscript.

DATA ACCESSIBILITY STATEMENT

Authors confirm that the data supporting the results will be available online if the manuscript is accepted for publication in Ecology Letters. Data are available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.dv3vg56>

PUBLICATION ETHICS AND CONFLICT OF INTEREST

Authors declare no competing interest and confirm that the manuscript has not been submitted elsewhere for publication.

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SUPPORTING INFORMATION

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

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