

1 The Moran effect and environmental vetoes: phenological synchrony and drought drive seed
2 production in a Mediterranean oak

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4 Michał Bogdziewicz^{1,2*}, Marcos Fernández-Martínez^{2,3}, Raul Bonal^{4,5}, Jordina Belmonte^{6,7},
5 and Josep Maria Espelta²

6

7 ¹ Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University,
8 Poznań, Poland

9 ² CREAM, Cerdanyola del Valles, Catalonia, 08193 Spain

10 ³ CSIC, Global Ecology Unit, CREAM-CSIC-UAB, Bellaterra, 08193 Barcelona, Catalonia,
11 Spain

12 ⁴ Forest Research Group, INDEHESA, University of Extremadura, Plasencia, Spain

13 ⁵ DITEG Research Group, University of Castilla-La Mancha, Toledo, Spain

14 ⁶ ICTA-UAB, Universitat Autònoma de Barcelona 08193, Bellaterra, Catalonia, Spain

15 ⁷ Unitat de Botànica, Departament de biologia Animal, Biologia Vegetal i Ecologia,
16 Universitat Autònoma de Barcelona 08193, Bellaterra, Catalonia, Spain

17

18 *corresponding author, michalbogdziewicz@gmail.com, Umultowska 89, 61-064 Poznań,

19 Poland

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20 **Abstract**

21 Masting is the highly variable production of synchronized seed crops, and is a common
22 reproductive strategy in plants. Weather has been long recognized as centrally involved in
23 driving seed production in masting plants. However, the theory behind mechanisms
24 connecting weather and seeding variation has only recently been developed, and still lacks
25 empirical evaluation. We used 12-years long seed production data for 255 holm oaks
26 (*Quercus ilex*), as well as airborne pollen and meteorological data, and tested whether masting
27 is driven by environmental constraints: phenological synchrony and associated pollination
28 efficiency, and drought-related acorn abscission. We found that warm springs resulted in short
29 pollen seasons, and length of the pollen seasons was negatively related to acorn production,
30 supporting the phenological synchrony hypothesis. Furthermore, the relationship between
31 phenological synchrony and acorn production was modulated by spring drought, and effects
32 of environmental vetoes on seed production were dependent on the last year environmental
33 constraint, implying passive resource storage. Both vetoes affected among-trees synchrony in
34 seed production. Finally, precipitation preceding acorn maturation was positively related to
35 seed production, mitigating apparent resource depletion following high crop production in the
36 previous year. These results provide new insights into mechanisms beyond widely reported
37 weather and seed production correlations.

38

39 Key words: environmental constraint, mast seeding, Moran effect, seed production,
40 phenological synchrony hypothesis, seed abscission,

41

42 **Introduction**

43 Masting, or mast seeding, is a common reproductive strategy in perennial plants,
44 characterized by high inter-annual variability in seed production synchronized over large

45 areas [1]. It results in severe fluctuations in food availability for seed-feeding animals
46 producing cascade effects through trophic levels [2, 3]. Despite its clear importance, our
47 understanding of the proximate mechanisms driving masting across different taxa remains
48 incomplete [4]. It has been long recognized that resources and weather are centrally involved
49 in driving seed production patterns in masting plants [1, 5, 6, 7, 8], but it is only recently that
50 attention has turned to the mechanisms linking seed production and weather variability [4, 7-
51 13].

52 Despite masting being a phenomenon that takes place at the population level, it
53 originates at the individual level by combining two processes: inter-annual variability in seed
54 production, and synchronization among individuals. The inter-annual variation in seed
55 production is driven in part by plant resources through preventing individuals from producing
56 sequential large crops [4, 14]. Therefore, weather may affect seed production by affecting
57 plant resource state, e.g. by providing good conditions for photosynthate accumulation [13-
58 16] or by influencing resource remobilization [17, 18]. Among-individual synchronization in
59 reproduction is believed to be driven by environmental variation and associated pollination
60 efficiency [4, 14]. Plants can similarly respond to a weather signature, such as temperature or
61 rainfall, resulting in synchronized flowering [8, 11, 19, 20]. Synchronized flowering might be
62 also the result of plants reaching a resource threshold as predicted by the resource budget
63 model [16, 21]. In such systems, plant populations should show high inter-annual variation in
64 flowering intensity, and seed production should be determined by high flower density and
65 associated high pollination success, i.e. pollen coupling [16, 19, 22-25]. Alternatively,
66 weather might drive population-wide pollination success and seed maturation rates creating
67 the Moran effect [12, 26]. In this case, annual variability in flowering intensity is less
68 important, and flower to fruit transition drives seed production [4, 5, 19, 27, 28]. However,

69 the theory behind these mechanisms has only recently been developed, and it largely lacks
70 empirical evaluation [4, 14].

71 Two main hypotheses have been proposed for how the weather conditions may affect
72 effectiveness of pollen transfer among plants (i.e. the pollination Moran effect). Rainfall
73 during flowering may wash pollen out of the atmosphere and limit pollination success [29].
74 Alternatively, annual differences in the synchrony of flowering within the population, driven
75 by variation in the spring temperature, may determine pollen availability along with flowering
76 synchrony and thus fertilization success, i.e. *the phenological synchrony hypothesis* [30].
77 Irrespective of weather effects on pollination success, weather can affect seed crop size by
78 affecting seed maturation rates [5, 28, 31], e.g. water stress may lead to high fruit abscission
79 [27, 28, 32]. Furthermore, environmental veto processes are expected to interact with resource
80 dynamics [4, 14]. For example, if reproduction was vetoed in one year (e.g. pollination failure
81 caused by desynchronized flowering), more resources should be available for reproduction
82 during the following year [4, 30]. Finally, because environmental vetoes are expected to occur
83 over large spatial scales, they can be considered possible mechanisms behind large-scale
84 synchrony of seed production observed in masting plants [33, 34]. However, we currently
85 know little about how these mechanisms interact to create masting dynamics.

86 The main aim of this study is to explore whether seed production in a Mediterranean
87 oak is a consequence of two interacting constraints: namely, pollination efficiency driven by
88 phenological synchrony and drought. To reach this aim, we use acorn production data from
89 255 trees spanning 12 years for *Quercus ilex* (holm oak), as well as corresponding airborne
90 pollen and meteorological data. We explore how seeding dynamics are related to the number
91 of pollen grains in the air (proxy for flowering intensity), pollen seasons length (proxy for
92 phenological synchrony), spring water deficit, and summed rainfall in the six months
93 preceding seed maturation. Oaks are thought to be ‘fruit maturation masting species’, i.e. fruit

94 density is largely driven by variable ripening of a much more constant flower crop [4, 19, 27].
95 Thus, we hypothesize that phenological synchrony affects pollination success and thus flower
96 to fruit transition [19, 30], and similarly water deficit limit seed production [28, 35].
97 Flowering phenology of oaks should be determined by weather, i.e. cold and wet weather
98 create heterogeneous microclimatic conditions and desynchronize plants, leading to long
99 pollen seasons and reproduction failure. In contrast, warm and dry conditions during pollen
100 seasons lead to synchronous pollen release [30]. Summed precipitation preceding seed fall
101 should positively affect seed production through allowing higher accumulation of resources
102 through higher N mineralization or higher photosynthesis [15, 17]. Furthermore, if the last
103 year crop size depletes plant resources and negatively affects current reproduction, we expect
104 the effect of precipitation to mitigate it, through allowing more efficient resource rebuilding.
105 Similarly, if reproduction in the last year was vetoed by pollination failure or drought (as
106 opposed to low resource state), we expect higher reproductive allocation in the next year due
107 to saved resources [4, 13]. Finally, we test whether environmental forcing mechanisms, i.e.
108 phenological synchrony and spring water deficit, are related to among-trees variability in seed
109 production dynamics.

110

111 **Methods**

112 Study site, species, and seed production data

113 This study was carried out in the Collserola Massif (41° 260' N, 2° 060' E), northeast Iberian
114 Peninsula. The climate is Mediterranean, characterized by mild winters and dry summers.
115 Mean annual temperature is 15.7 ± 1.4 °C and mean annual precipitation is 613.8 ± 34.0 mm.
116 The holm oak (*Q. ilex*) is the most widespread tree species of the Iberian Peninsula. It flowers
117 in spring and acorns grow and ripen in the same year, being dropped in autumn-winter. Crop
118 sizes show strong inter-annual fluctuations [27, 36].

119 We monitored acorn production from 1998 to 2009 in 17 sampling sites (255 trees, 15
120 per plot) in holm-oak dominated forests (mean distance 4.7 ± 2.4 km, Fig. 1S). The other oak
121 present at the site is deciduous *Q. humilis*. Trees were tagged and the number of branches per
122 tree was estimated using a regression model between crown projection and number of
123 branches previously constructed for a sub-sample of trees [27]. We counted acorn production
124 on four branches per tree at the peak of the acorn crop (i.e. September). Then we estimated
125 the total number of acorns produced per tree by multiplying the mean acorn production per
126 branch and the number of branches per tree [see 27 for details].

127

128 Pollen and weather data

129 We used the pollen data on *Quercus* evergreen type from the Catalan Aerobiological Network
130 from two sampling stations close to our study area, and representative of the southeastern and
131 northwestern slopes, respectively: Barcelona ($41^{\circ} 23' N$, $2^{\circ} 9' E$) and Bellaterra ($41^{\circ} 30'$
132 N , $2^{\circ} 6' E$). The pollen grains of evergreen oaks are easily distinguished from deciduous
133 species, thus the presence of *Q. humilis* in our study area [27] does not interfere with our
134 analyses. We matched acorn collection plots with the nearest pollen monitoring station, i.e.
135 near Barcelona (located in Collserola southeastern slope) and near Bellaterra (northwestern
136 slope). This classification resulted in 5 plots being classified as nearest Barcelona and 12
137 nearest Bellaterra [37]. Pollen grains were collected by Hirst traps which are designed to
138 record the concentration of atmospheric particles as a function of time [38]. For each year, we
139 derived two parameters from the pollen data, pollen season length, a measure of flowering
140 synchrony, and total pollen, a measure of overall pollen abundance (following protocols of
141 [19]). The total pollen represents the sum of all daily pollen counts during the pollen season.
142 We determined the duration of the pollen seasons using the 80% method that assumes the
143 season starts when 10% of the total yearly pollen catch is achieved and ends when 90% is

144 reached [39]. We used total pollen as an index of flower production, assuming that more
145 flowers produce more pollen grains [37, 40]. The pollen data collected with pollen traps
146 corresponds well with flowering phenology of trees in the field [29, 37].

147 Data on weather was obtained from two weather stations located within 5 km distance
148 from study sites. Based on the raw data we calculated the spring (April-June) water deficit for
149 each study year (potential evapotranspiration - real evapotranspiration in mm [41]).

150

151 Statistical analysis

152 We calculated masting metrics including individual (CV_i) and population-level (CV_p)
153 coefficients of variation, synchrony within (r_w) and among (r_a) sites, and lag-1 population-
154 level temporal autocorrelation (ACF1) of total pollen, length of pollen season, and seed crop
155 size [42, 43]. We calculated within-site synchrony using Pearson's correlation of all possible
156 pairs of trees in the stand and then calculating the mean of those correlation coefficients.
157 Among-site synchrony was calculated based on all possible pairs of trees.

158 First, we tested for the relationships between selected weather variables and seed
159 production. We build a generalized linear mixed model (GLMM) that included the log-
160 transformed, site-level average of acorn production per tree as response, study site as random
161 effect, and mean maximum temperature during pollen season, average rainfall per day during
162 pollen season, and summed rainfall preceding acorn maturation (January 1 – June 30,
163 hereafter $\text{precip}_{\text{Jan-Jul}}$) as fixed effects. The rainfall window follows the previous studies that
164 found it best explains the increase in oaks leaves area [15]. We also included acorn crop in the
165 previous year to control for the potential effect of resource depletion [42, 44], and its
166 interaction term with $\text{precip}_{\text{Jan-Jul}}$ to test for the potential faster resource rebuild in wet years.
167 Moreover, we included all possible combinations of two-way interaction terms between the
168 previous year and current year's mean maximum temperature during pollen season (potential

169 driver of phenological synchrony), and the rainfall during previous and current pollen season
170 (i.e. driver of spring water deficit), i.e. four interaction terms in total. This was done to test for
171 the potential interacting effects of the previous and current year vetoes on seed production [4,
172 30]. We arrived at the final model structure by removing non-significant interaction terms.
173 We also built a very simple competing model that included difference in temperature between
174 two springs (mean maximum temperature in May) preceding seed fall as fixed effect (i.e. the
175 ΔT model, cf. [11]). We used temperature in May following past studies conducted on
176 Mediterranean oaks [9, 45]. These two models (reduced weather model and ΔT) were
177 compared with each other using the AICc [46]. The veto model outperformed May ΔT model
178 according to the AICc ($\Delta AICc = 118.2$, d.f. equals 4 in the ΔT , while 12 in veto model).

179 Next, we tested for the mechanistic underpinnings between weather variables and seed
180 production by asking the following questions: (1) what is the relationship between weather
181 during pollen season and the duration of the pollen season (i.e., phenological synchrony)? (2)
182 What is the relationship between weather and total pollen? (3) How are the pollen parameters,
183 spring water deficit, and conditions during photosynthate accumulation related to seed
184 production? To test questions one (1) and two (2) we used linear regression with the log-
185 transformed length of pollen season (1) or log-transformed total pollen (2) as response
186 variable, and temperature during pollen season, average rain per day during pollen season,
187 and the interaction term as independent variables. In each of these models we included site of
188 pollen collection (Barcelona and Bellaterra) to account for the nested data structure. We
189 addressed the third (3) question by building a GLMM using a Gaussian family and the
190 identity link. We used log-transformed, average site-level crop size per tree as response
191 variable and site as random effect. Fixed effect included length of the pollen season, total
192 pollen, water deficit index, summed rainfall preceding acorn maturation (January 1 – June
193 30), and acorn crop of the previous year. We also included the following interactions:

194 previous year crop size \times precip_{Jan-Jul}, pollen season length \times total pollen, and all possible two-
195 way interactions between previous year and current pollen season length, and previous and
196 current year spring water deficit, to test for the interacting effects of current- and previous-
197 year vetoes, i.e. six interaction terms in total. We arrived at the final model structure by
198 removing non-significant interaction terms.

199 We tested whether flowering behavior and water deficit synchronizes among and
200 within-site seed production. First, we calculated two types of within-year coefficients of
201 variation. Among-site CV was calculated based on site-level means, thus represented among-
202 sites variability in seed production. Within-site CV was calculated based on tree-level seed
203 production data for each site and year separately. Thus, it represents the within year, within-
204 site variability in seed production. First, we tested whether phenological synchrony and water
205 deficit are related to among-site variability in seed production. Here, we used a regression
206 with the length of pollen season, spring water deficit, and their interaction as independent
207 variables, and among-site CV as response. In the next analysis, we tested whether
208 phenological synchrony and water deficit synchronize trees within study site. Here, we used a
209 Gaussian family, identity link GLMM with site as random effect, and within-site CV as
210 response. Fixed effect included length of the pollen season, total pollen, water deficit, and the
211 interaction term between length of the pollen season and water deficit.

212 We run all analyses in R, and implemented GLMMs via lme4 package [47]. Before
213 running mixed models, we standardized and centered variables to facilitate the interpretation
214 of the results: this allows direct comparisons of effect sizes of different predictors [48]. We
215 checked for collinearity between variables using variance inflation factor from “AED”
216 package [49]. We calculated the R^2 for linear models, and marginal (i.e. the proportion of
217 variance explained by fixed effects) and conditional (i.e. the proportion of variance explained
218 by fixed and random effects) R^2 for GLMMs [50, 51]. We also tested for potential spatial

219 autocorrelation in mean acorn production among plots with Mantel tests, and detected none (r
220 = 0.13; $p = 0.16$).

221

222 **Results**

223 Seed production dynamics of holm oaks in the study site were typical of masting trees, i.e.
224 high inter-annual variation in seed production, both at the population- and the individual-
225 level, and high synchronization (Fig. 1, Table 1). The CV_p of pollen production was one thirds
226 as large as CV_p of seed production (Table 1) indicating that flower production is relatively
227 constant across years, and it is the flower to fruit transition that generates variation among
228 years in fruit crops (Table 2).

229 The final model for seed production vs. weather included six predictors (mean max
230 temp during pollen season in year T and year T-1, the mean daily rain during pollen season in
231 year T and T-1, the summed rainfall Jan-June, and last year crop size) and three interaction
232 terms (between temperature during pollen seasons in year T and T-1, between crop size in
233 year T-1 and rainfall in Jan-June in year T, and between temperature during pollen seasons in
234 year T and daily rain during pollen season in year T-1; Table S1 (a) in Online Appendix). The
235 negative effect of last year crop size on current year seed production was modified by
236 summed rainfall preceding acorn maturation (interaction term: $\beta = 0.55 \pm 0.17$, $p = 0.001$),
237 indicating that the negative effect of the last year crop was canceled if the current year's
238 seasons were wet enough (Fig 2a). The model also included the effect of temperature during
239 pollen season, although it was modified by the last year temperature during pollen season
240 (interaction term: $\beta = 0.57 \pm 0.13$, $p < 0.001$), i.e. the effect of current year spring temperature
241 was positive unless the last year spring was cold, when the slope of the relationship scaled
242 down to 0 (Fig. 2b). Similarly, the effect of the current year temperature during pollen season
243 was modified by the last year average rain during pollen season (interaction term: $\beta = 0.77 \pm$

244 0.14, $p < 0.001$), i.e. the effect of current year spring temperature was positive unless the last
245 year spring was dry, when the slope scaled down to 0. The interaction term between current
246 and previous year average rainfall during pollen season was not significant and was removed
247 from the final model ($p = 0.27$). The variance explained by fixed effects of the model equaled
248 0.54, while the variance explained by both fixed and random effects was 0.61.

249 In agreement with the phenological synchrony hypothesis, the duration of pollen
250 season was negatively related to the average maximum temperature during pollen season,
251 modified by average rainfall during that time (interaction term: $\beta = 0.09 \pm 0.04$, $p = 0.03$),
252 indicating that the positive relationship between temperature and pollen season length
253 leveled-off once the seasons were wet ($R^2 = 0.29$, Fig. 2c). None of the explored weather
254 variables affected total pollen (temperature and rain during pollen season, spring water deficit,
255 all $p > 0.10$).

256 The final model for seed production vs. environmental vetoes included seven
257 predictors (length of pollen season in year T and T-1, pollen abundance, last year crop size,
258 spring water deficit in year T and T-1, and rainfall Jan-June) and three interaction terms
259 (between length of the pollen season in year T and spring water deficit in year T, between
260 length of pollen season in year T and in year T-1, and between spring water deficit in year T
261 and in year T-1; Table S1 (b) in Appendix). In line with the phenological synchrony
262 hypothesis, acorn production was negatively related to pollen season duration, although the
263 effect was strongly dependent on spring water deficit (interaction term: $\beta = -0.97 \pm 0.15$, $p <$
264 0.001 , Fig 2d), i.e. the crop was lowest when high spring water deficit and long pollen
265 seasons were concurrent. In contrast, the effect of total pollen was not significant ($p = 0.10$).
266 The effect of current year pollen season length was modulated by the last year season length
267 (interaction term: $\beta = 0.58 \pm 0.18$, $p < 0.001$), i.e. the effect of the current year synchrony was
268 only apparent if the last year pollination was allowed (i.e. pollen season was short, Fig. 2e).

269 Similarly, the effect of current year spring water deficit was modulated by the last water
270 deficit (interaction term: $\beta = 0.54 \pm 0.24$, $p = 0.03$, graph not shown), i.e. the effect of current
271 year deficit was only negative if the last year water deficit was small (i.e. reproduction
272 allowed). Furthermore, summed rain from January to July was positively related to acorn
273 production ($\beta = 0.79 \pm 0.20$, $p < 0.001$). In this model, the effect of the crop size of the
274 previous year on crop size was not significant ($p = 0.12$, $R^2(m) = 0.64$, $R^2(c) = 0.68$). Other
275 interaction terms were insignificant ($p > 0.30$).

276 Concerning spatial variation in seed production, among-site CV of seed production
277 was not related to the length of the pollen seasons ($p = 0.27$), but increased with spring water
278 deficit ($\beta = 0.26 \pm 0.10$, $p = 0.03$, $R^2 = 0.45$, Fig. 3a). Within-site CV of seed production was
279 positively related to both spring water deficit ($\beta = 0.54 \pm 0.05$, $p < 0.001$, Fig. 3b) and length
280 of pollen seasons ($\beta = 0.16 \pm 0.06$, $p = 0.005$, $R^2(m) = 0.35$, $R^2(c) = 0.44$, Fig. 3c). In both
281 among- and within-site CV models, the interaction terms were insignificant.

282

283 **Discussion**

284 A summary of our findings (Table 2) shows that the Moran effect, in the form of
285 environmental vetoes, i.e. phenological synchrony and associated pollination efficiency
286 together with drought-related fruit abortion, drive mast seeding in Mediterranean oaks. Acorn
287 production was also positively related to summed rainfall preceding acorn maturation, to the
288 extent that it could mitigate the apparent resource depletion following high seed production of
289 the previous year. The likely mechanism is increased N mineralization in wet years [17], and
290 rapid current-year increase in tree photosynthetic capacity (leaf area) driven by favorable
291 weather conditions [15]. Furthermore, crop size was negatively correlated with the length of
292 pollen seasons, our proxy of phenological synchrony [19], suggesting that pollination
293 efficiency is enhanced in warm years [30]. Moreover, the effect of phenological synchrony

294 was attenuated by the last year veto, suggesting that environmental constraints interact with
295 plant resource state in driving seeding dynamics [4, 13].

296 Weather affects seed production in our system through an interplay of two veto
297 processes, i.e. phenological synchrony and spring drought, with the latter having a stronger
298 effect. Across different oak species, seed production correlates with either rain or temperature
299 in spring [5, 9, 52-55]. Based on the patterns we observed, we hypothesize that both
300 phenological synchrony and acorn abortion owing to water-shortage occur in oaks, but
301 depending on the local conditions one of them has a stronger effect on seeding dynamics. In
302 water-limited areas, as in our system, drought-driven acorn abscission has a stronger effect on
303 acorn production than phenological synchrony. Therefore, rainfall overrides the temperature-
304 driven phenological synchrony in correlative studies [9, 45, 52]. In contrast, in mesic forests,
305 pollination efficiency is more important, and thus spring temperature (through
306 synchronization of pollen release) has stronger effect on seeding dynamics than the rainfall
307 [19]. We expect similar gradients across systems that are similarly water-limited but differ in
308 plant densities. For example, the valley oak (*Q. lobata*) in California grows in a
309 Mediterranean, savannah-like landscape, making pollen transfer among individuals
310 constrained [56], and thus highly dependent on the phenological synchrony [10, 30]. In
311 contrast, trees at our study site grow in crowded forests (e.g. 1357 ± 219 stems ha^{-1} in [37].
312 This makes outcross pollen more accessible [57], but induces more severe stress in case of
313 water limitation due to high competition [27, 35]. Generally, mechanistic understanding of the
314 influence of weather variables on seeding dynamics will improve our understanding of the
315 key drivers, especially in enigmatic genera like *Quercus* where consistent links to simple
316 weather signals have not been found.

317 We also found that the Moran effect in the form of environmental veto (i.e. drought or
318 synchrony-related pollination failure) decreases variability in seed production among trees

319 both within- and among-sites (Fig. 3). Recently, environmental veto was incorporated into
320 resource budget models, showing that it might be a driver of observed variability and
321 synchrony of seed production [7, 10, 58]. Our results provide further empirical support for
322 these models, showing that environmental veto is a likely driver of the large-scale synchrony
323 of seed production observed in masting plants [33, 34, 59, 60]. To the extent to which it is
324 true, the spatial synchrony of seeding dynamics should match the spatial synchrony of the
325 veto, a pattern already found in some systems [12, 61]. Past theoretical work concluded that
326 environmental noise alone could not drive large-scale spatial synchronization of trees
327 reproduction [62-64]. However, more recent theoretical models showed that if correlated
328 environmental noise is replaced with reproduction failure caused by environmental veto, then
329 large-scale synchronization may apply [58], a result supported by our study.

330 A previous work relating airborne pollen dynamics to seed production in *Q. ilex* found
331 that the onset of the flowering season had strong effect on acorn production, while total pollen
332 did not [37]. Advancement of theoretical understanding of masting dynamics in last years
333 sheds new light on these findings. Lack of the direct relationship between total pollen and
334 acorn production is expected in species in which the flower to fruit transition drives seeding
335 dynamics, because flower density *per se* should have a smaller effect [4, 19]. Therefore, the
336 importance of pollination efficiency is not ruled out, but it is rather driven by different
337 processes, e.g. phenological synchrony [30]. Furthermore, in systems in which the onset of
338 flowering varies strongly (e.g. by 37 days in our study), pollen seasons that start later in the
339 year are likely to be short, because air temperature tends to be higher as summer approaches
340 (see Fig. 2S in the Online Appendix). With a correlative analysis, it is not possible to
341 distinguish causation, but models including phenological synchrony perform statistically
342 better than those including flowering onset in our data (see Table 2S in Online Appendix).
343 Experimental tests of the pollen limitation across individuals differing in flowering synchrony

344 are crucial to resolve this issue.

345

346 **Conclusions**

347 We found support for a number of theoretical processes proposed to drive the reported
348 correlations between weather and seed production (Table 2). The interactive effects of spring-
349 vetoes on acorn production outperformed spring weather as a cue models (ΔT model, cf.
350 [11]), supporting the notion that weather affects seed production through direct mechanisms
351 rather than through cues [19, 65], at least in oaks [9, 19]. This makes masting dynamics
352 susceptible to global climate changes. Recent models for American oaks showed that inter-
353 annual variability in seed production will likely decrease as a consequence of anticipated
354 warmer springs, associated with more frequent synchronous flowering, and more regular
355 production of smaller seed crops [30]. In the Mediterranean basin, temperatures are predicted
356 to rise while rainfall to decrease, which will increase pollination efficiency, but also increase
357 the occurrence of drought. Therefore, reproduction will likely be vetoed more often,
358 producing a reverse pattern, i.e. less regular production of higher crops. Our results stress the
359 importance of understanding particular mechanisms driving seed production among systems,
360 as different predictions will apply depending on whether the species is a flowering masting
361 one [11, 19], or which veto is most relevant.

362

363 **Data**

364 All data used in the study is archived at Dryad doi:10.5061/dryad.843d1

365

366 **Competing interests**

367 We have no competing interests.

368

369 **Authors' contributions**

370 MB conceived of the study, designed it, carried out the data analysis, and drafted the
371 manuscript; MFM designed the study, collected the field data, and helped draft the
372 manuscript; JB collected the field data; RB collected the field data and help draft the
373 manuscript, JME designed the study, collected the field data, and helped draft the manuscript.
374 All authors interpreted the results and gave final approval for publication.

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553

554 Table 1. Masting metrics for holm oak (*Q. ilex*) at our study sites. Standard deviations are
 555 given in brackets. All variables are unitless except mean acorn production (Mean), which is in
 556 acorns tree⁻¹ year⁻¹.

Species	CVp	CVi	Within- site <i>r</i>	Among- site <i>r</i>	ACF1	Mean
Seed production	1.46 (0.35)	1.41 (0.36)	0.49 (0.15)	0.41 (0.35)	-0.34 (0.11)	306.13* (217.56)
Total pollen	0.40	-	-	0.61 [#]	-0.19	3086.66 (1257.98)
Length of pollen season	0.27	-	-	0.84 [#]	0.43	43.91 (12.13)

557 *mean of site-level means

558 [#]calculated as Pearson correlation between Barcelona and Bellaterra aerobiological stations

559

Table 2. Summary of predicted relationships, variables tested, apparent mechanisms, and the study results.

Predicted pattern	Response variable	Mechanism	Prediction supported?
Inter-annual flowering variability lower than seed variability¹	Total pollen	Flower production is relatively constant across years, and it is the flower to fruit transition that generates variation among years in fruit crops	Yes
Seed production <u>not</u> related to flowering intensity¹	Site-level average acorn production	As above	Yes
Flowering synchrony related to air temperature and rainfall during flowering	Pollen season duration	Homogeneous conditions during warm and dry pollen seasons enhance flowering synchrony among trees	Yes
Seed production related to flowering synchrony (veto 1)	Site-level average acorn production	Higher flowering synchrony among trees enhances pollination efficiency	Yes
Seed production related to spring water deficit (veto 2)	Site-level average acorn production	High water stress induces acorn abscission	Yes
Accumulated rainfall from January until June enhances seed production	Site-level average acorn production	High summed precipitation increase N mineralization and enhances trees photosynthetic capacity allowing higher crop production ²	Yes
Previous year veto interacts with current year veto in driving seed production	Site-level average acorn production	Passive resource storage: environmental veto prevents resource spending, increasing the resource pool for the next year reproductive allocation	Yes
Environmental veto drives among-site synchrony in seed production	CV of seed production among sites	Low water stress allows seed production decreasing the among-site variation in reproductive output	Yes: Water stress
Environmental veto drives within-site synchrony in seed production	CV of seed production among trees, within sites	Low water stress and short pollen seasons allow seed production decreasing the among-tree variation in reproductive output	Yes: Water stress and phenological synchrony

¹We predicted that oaks will show fruit maturation masting, i.e. seed production will be not related to flower production, but rather will be determined by flower to fruit transition driven by phenological synchrony and drought. Therefore, variability of flower production is expected to be lower than variability of seed production (see also [19]).

² N mineralization is enhanced in wet years [17], and high rainfall in from January to July increases tree crown area and associated photosynthetic capacity of trees [13].

Figure 1. (a) Length of the pollen seasons and spring water deficit during the study duration, (b) site-level average acorn production (acorns per tree) of holm oaks.

Figure 2. Interaction plots for the fitted models. Plots show shows the changes in the [coefficient response](#) of one variable in a two-way interaction term conditional on the value of the other included variable, along with their 95% confidence intervals. (a) Relationship between the current and the previous year crop size conditional on the summed rainfall from January till June (b) Relationship between the seed crop size and the current [mean maximum](#) year temperature during pollen season conditional on the previous year [mean maximum](#) temperature during pollen season. (c) Relationship between the length of the pollen season and the temperature during pollen season conditional on the average [daily](#) rain during pollen season. (d) Relationship between the seed crop size and the spring water deficit conditional on the length of the pollen season. (e) Relationship between the seed crop size and the length of the pollen season conditional on the length of the previous year pollen season. See text for the model details. In cases when interaction plots are based on GLMM (a, b, d, e), the predictor [and conditional](#) variables were standardized and axes show standard deviations ([SD](#)). Response variables (y-axis) are given on the scale of partial residuals.

Fig. 3. The relationship between within-year seed production variability (CV) of holm oaks and the spring water deficit (a, b), and phenological synchrony (c). Trend lines are based on the linear regression (a) and GLMM (b, c), shaded regions represent associated standard errors. Points represent measures of CV among sites (a) and among trees within sites (b, c), all within years. Note that the apparent poor fit of the line in (c) is because plots show the raw data, while the model accounts for the spring water deficit and the random effect of study site.