Seed predation selects for reproductive variability and synchrony in perennial plants

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Summary

- Annually variable and synchronous seed production by plant populations, or masting, is a widespread reproductive strategy in long-lived plants. Masting is thought to be selectively beneficial because interannual variability and synchrony increase the fitness of plants through economies of scale that decrease the cost of reproduction per surviving offspring. Predator satiation is believed to be a key economy of scale, but whether it can drive phenotypic evolution for masting in plants has been rarely explored.

- We used data from seven plant species (*Quercus humilis*, *Quercus ilex*, *Quercus rubra*, *Quercus alba*, *Quercus montana*, *Sorbus aucuparia* and *Pinus pinea*) to determine whether predispersal seed predation selects for plant phenotypes that mast.

- Predation selected for interannual variability in Mediterranean oaks (*Q. humilis* and *Q. ilex*), for synchrony in *Q. rubra*, and for both interannual variability and reproductive synchrony in *S. aucuparia* and *P. pinea*. Predation never selected for negative temporal autocorrelation of seed production.

- Predation by invertebrates appears to select for only some aspects of masting, most importantly high coefficient of variation, supporting individual-level benefits of the population-level phenomenon of mast seeding. Determining the selective benefits of masting is complex because of interactions with other seed predators, which may impose contradictory selective pressures.

Introduction

Understanding patterns of selection in wild populations is a major goal in evolutionary biology (Quinn *et al.*, 2009; Kingsolver & Diamond, 2011; Siepielski *et al.*, 2017). Annually variable and synchronous seed production by plant populations, or masting, is a widespread reproductive strategy in long-lived plants (Tanentzap & Monks, 2018; Fernández-Martínez *et al.*, 2019) that has dramatic effects on food webs, macronutrient cycling, carbon storage and disease risk in humans (Bogdziewicz *et al.*, 2016; Clark *et al.*, 2019). This reproductive behavior is thought to be favored by selection because interannual variability and synchrony increase the fitness of plants through economies of scale that decrease the cost of reproduction per surviving offspring (Kelly, 1994; Bogdziewicz *et al.*, 2020a). Predator satiation and wind pollination are believed to be the main economies of scale (Kelly & Sork, 2002; Pearse *et al.*, 2016), but whether they can drive phenotypic evolution for masting has rarely been explored. Here, we used long-term monitoring data from seven plant species (*Quercus* spp., *Sorbus* spp. and *Pinus* spp.) and asked whether seed predation selects for phenotypes that mast.

The predator satiation hypothesis states that masting reduces losses of seed to predators (Kelly *et al.*, 2000; Espelta *et al.*, 2008; Fletcher *et al.*, 2010). Years of high seed production should satiate predators (i.e. functional response), whereas predators should be starved in low-seed years and have lower density and thus lower rates of predation (i.e. numerical response) (Fletcher *et al.*, 2010; Bogdziewicz *et al.*, 2020b). Predator satiation and starvation will be most effective if plants seed in phase with other individuals within populations, that is, high reproductive synchrony (Bogdziewicz *et al.*, 2018b, 2020a). However, selection for these responses will strongly depend on factors like the mobility, life history and diet of individual seed predators (Moreira *et al.*, 2017). Mobile predators may favor synchrony at scales comparable to their movements (e.g. a few km in vertebrates; Curran & Webb, 2000), whereas relatively immobile predators like micromoths can be satiated locally by single large trees (Nilsson & Wastljung, 1987), resulting in little to no selective benefit of

population synchrony (Satake *et al.*, 2004). Some highly mobile predators may even be attracted to large seed crops and consume relatively more seeds than they would otherwise, thereby selecting against interannual variability and/or synchrony in reproduction (Kelly *et al.*, 2001; Koenig *et al.*, 2003). Similarly, there is little evidence of predator satiation for diapausing insects that delay emergence to high-seed years. For example, *Curculio* spp. weevils damage similar proportions of *Quercus crispula* acorns regardless of seed production because they pupate in high-seed years and then emerge mostly 2 yr later, when trees have recouped the resources to produce another large seed crop (Maeto & Ozaki, 2003). Predator satiation may also be less effective for animals with long generations and life span (i.e. slower reproduction) that move more freely among habitats and change their diets (Ostfeld & Keesing, 2000; Bogdziewicz *et al.*, 2016). Generalist species can also sustain themselves on alternate food sources during low-seed years, avoiding starvation and numerical reduction, and return to seeds of interest as they become increasingly available (Fletcher *et al.*, 2010).

Many plant species host several different predispersal seed predator species (Gripenberg *et al.*, 2019; Xi *et al.*, 2020), and so can experience different and potentially contradictory selection pressures depending on the traits of their predators. For example, yellow birch (*Betula alleghaniensis*) fitness should benefit from greater interannual variability to satiate relatively immobile invertebrate seed predators (Kelly *et al.*, 2001; Koenig *et al.*, 2003). Concurrently, there may be selection to minimize synchrony among trees to avoid attracting birds (Koenig *et al.*, 2003), thereby eliminating one of the characteristic features of masting. The selective responses may be more contradictory in other cases. For example, plants predated by insects with and without diapause may face little and strong selection for seed production in consecutive years, respectively, and so masting may also be beneficial for reducing some seed predators (Kelly *et al.*, 2000). For these reasons, masting dynamics, characterized by interannual variability and synchrony, will be a balance among competing selection pressures from different seed predator species with different numerical and functional responses.

Here, we explore associations between seed predation and plant phenotypes representing different interannual variabilities and reproductive synchronies. We used seed production data for over 1000 trees belonging to seven species (*Quercus humilis*, *Quercus ilex*, *Quercus rubra*, *Quercus alba*, *Quercus montana*, *Sorbus aucuparia* and *Pinus pinea*) which were followed for 12–20 yr. We also used data on a subset of predispersal seed predators: invertebrates with and without diapause, which together should behave differently from birds and rodents that are important predators for some of the study species (Paulsen & Högstedt, 2002; Muñoz & Bonal, 2011; Lichti *et al.*, 2014). In studied populations of *Q. humilis* and *Q. ilex*, decreased seed predation by *Curculio* spp. weevils in mast years has been observed (Espelta *et al.*, 2008). Similarly, the proportion of predated fruits by *Argyresthia conjugella* and cones by *Dioryctria mendacella* decreases in masting years in *S. aucuparia* (Żywiec *et al.*, 2013) and *P. pinea* (Calama *et al.*, 2017), respectively. In the three eastern North American oaks, satiation of *Curculio* weevils in mast

years was detected only in *Q. rubra*, and only in well-synchronized years (Bogdziewicz *et al.*, 2018b). In *Q. alba* and *Q. montana*, masting does not decrease predispersal seed predation (Bogdziewicz *et al.*, 2018b). Based on these patterns, we predicted that predispersal insect predation should select for the following reproductive patterns in all species except *Q. alba* and *Q. montana*:

- *High interannual variability*, as a stable seed supply can result in higher local average survival of predator cohorts and a localized build-up of their populations (Kelly *et al.*, 2000; Maeto & Ozaki, 2003; Bogdziewicz *et al.*, 2017). Variability may also depend on selection for synchrony, if predators are attracted over large areas to groups of trees with large seed crops or are relatively immobile (Koenig *et al.*, 2003).
- *High synchrony* in species in which satiation requires population-level masting, such as *Q. rubra* (Bogdziewicz *et al.*, 2018b).
- *Negative temporal autocorrelation* because the specific sequence of low-seed and high-seed years should help escape predation (Kelly & Sork, 2002; Koenig *et al.*, 2003). However, this prediction will have the weakest support as plants only require predation to be proportionally smaller in high-seed years to receive an economy of scale rather than starving predators *per se* (Kelly & Sork, 2002). Temporal autocorrelation can also arise simply as a by-product of selection for interannual variability (Pearse *et al.*, 2016; Bogdziewicz *et al.*, 2020a).

Materials and Methods

Data collection

We monitored reproductive effort and predispersal seed predation for individual plants by collection of all the cones through the whole plant (*P. pinea*), counting all fruits (*S. aucuparia*), counting seeds on selected branches (*Q. ilex* and *Q. humilis*) or using seed traps (*Q. rubra*, *Q. alba*, *Q. montana*). Description of the ecology of the study species, sites and field procedures is given in the Supporting Information.

Seed predators

Our populations of *Q. humilis* and *Q. ilex* are mainly attacked by two *Curculio* weevils: *C. glandium* and *C. elephas* (Espelta *et al.*, 2009). *Curculio glandium* dominates the community, but there are species-specific differences in the infestation: c. 88% of acorns of *Q. ilex* are infested by *C. glandium*, while this estimate is c. 65% in *Q. humilis* (Espelta *et al.*, 2009). Both weevil species undergo prolonged diapause. However, the timing of *C. glandium* adults emergence is fixed and happens 2 yr after larval development, whereas *C. elephas* spreads the emergence over 3 yr (Pélisson *et al.*, 2013). *Pinus pinea* cones are infested by moth *Dioryctria mendacella*. That species has a complex and poorly studied life cycle, with a minimum of two overlapping generations per year (Calama *et al.*, 2017). *Sorbus aucuparia* fruits are infested mainly by apple fruit moth *Argyresthia conjugella* which has limited prolonged diapause abilities, with c. 97% of individuals emerging after the first overwintering season (Kobro *et al.*,

2003). Seeds of the three species of the North American oaks are mainly infested by three weevil groups (i.e. *Curculio*, *Conotrachelus* and *Cyrtepistomus*; M. A. Steele, unpublished).

Analysis

Seed production and masting behavior We calculated individual-tree level masting metrics widely used to characterize plant reproductive patterns (Herrera *et al.*, 1998; Koenig *et al.*, 2003; Crone *et al.*, 2011): interannual variability of seed production of individuals (coefficient of variation, CV_i), 1 (AR1) and 2 yr lag (AR2) autocorrelation coefficients of seed production at the individual level, wherein negative numbers indicate populations that alternate between years of high and low seed production, and synchrony of seed production by plants, as measured by the average pairwise Pearson's correlation of seed production of individual plants in a site through time. We also calculated a population-level coefficient of variation (CV_p) for each species.

Population-level predator satiation We started by testing whether population-level predator satiation operates in our populations. We tested for functional and numerical responses of seed predators to seed production with binomial generalized linear mixed models (GLMMs). For each species, we constructed two models. Each model had the proportion of predated seeds as a response, site and individual plant ID as random intercepts, and either population-level seed production in the current year (functional response) or a change in population-level seed production between consecutive years (current year/previous year) as fixed effects. All models included an observation-level random intercept to account for overdispersion and an autoregressive order-1 temporal autocorrelation structure.

Phenotypic selection We estimated phenotypic selection in the studied populations using regression-based techniques developed by Lande & Arnold (1983). The method estimates the strength of natural selection from effect sizes when regressing fitness on the phenotype (Conner & Hartl, 2004). For each selection analysis described in the following, we built two types of models. We constructed univariate models for each masting metric to estimate selection differentials (S) for each reproductive trait (indirect selection). We also estimated selection gradients (β), which measure direct selection on each trait after removing indirect selection from all other traits in the analysis by using multiple regressions.

We tested whether predation selected for masting in our model species using separate GLMMs with a binomial error term for each species. Using the tree ID and site as the random intercepts and an autoregressive order-1 temporal autocorrelation structure, we modeled the proportion of predated seeds in a given plant i of a given plot j in the year k as a function of tree-level masting metrics: interannual variation (CV_i), among-plant synchrony (mean Pearson pairwise cross-correlation), and lag1 (AR1) or lag2 (AR2) temporal autocorrelation in seed production. Directional and nonlinear selection differentials were estimated by including linear and quadratic effects of independent variables, respectively. We also tested for all possible two-way interactions between different metrics. The interactions and quadratic terms were removed from final models if not statistically significant. We ran all statistics in R v.3.6.1 and mixed models using the package GLMMTMB v.0.2.3 (Brooks *et al.*, 2017).

Results

Time series of all seven species were typical of mast-seeding trees. All species had $CV_p > 1$ (Table 1). Individual-level CV_i ranged from 1.20 (*P. pinea*) to 2.52 (*Q. humilis*). Synchrony (the correlation among individual trees in seed production through time) of individuals within populations was consistently positive, ranging from 0.34 in *Q. humilis* to 0.70 in *P. pinea* (Table 1). Confirming previous studies on our populations, we detected functional responses of seed predators to masting in all species except *Q. montana* and *Q. alba* (Supporting Information Fig. S1), and numerical responses in all species except *Q. rubra*, *Q. montana* and *Q. alba* (Fig. S2).

We focus our results and discussion on selection gradients (β), which measure direct selection on each trait after removing indirect selection from all other traits in the analysis. We detected directional selection on reproductive synchrony in three out of seven species studied: *Q. rubra*, *S. aucuparia* and *P. pinea* (Fig. 1;

Table 1 Masting metrics and average predispersal seed predation in the studied species.

Species	CVp	CVi	Synchrony	AR1	Mean predation	N plants	Study length (yr)
Quercus humilis	1.58 (0.53)	2.52 (0.72)	0.34 (0.25)	−0.13 (0.13)	0.14 (0.31)	172	12
Quercus ilex	1.79 (0.31)	2.35 (0.58)	0.56 (0.23)	−0.16 (0.14)	0.07 (0.21)	225	12
Quercus rubra	1.46 (0.24)	1.97 (0.64)	0.50 (0.20)	−0.08 (0.16)	0.23 (0.30)	44	16
Quercus alba	1.56 (0.17)	2.32 (0.80)	0.38 (0.17)	−0.11 (0.20)	0.19 (0.27)	51	16
Quercus montana	1.38 (0.08)	2.17 (0.75)	0.41 (0.14)	−0.10 (0.17)	0.12 (0.26)	33	16
Sorbus aucuparia	1.39 (na)*	1.88 (0.57)	0.49 (0.15)	−0.18 (0.17)	0.71 (0.30)	299 (50)**	20
Pinus pinea	1.00 (0.26)	1.20 (0.45)	0.70 (0.17)	0.06 (0.23)	0.15 (0.27)	187	13

We used plants that were observed at least for 10 yr. Values show means and SDs. CVp, population-level coefficient of variation; CVi, individual-level coefficient of variation; AR1, lag1 temporal autocorrelation of seed production. Synchrony was measured as average pairwise Pearson's correlation of seed production of individual plants in a site through time.
Sorbus aucuparia was observed in one large (27 ha) site, and thus SD could be not calculated (na).
**Value in parentheses is the subset of plants for which seed predation data were available, while the metrics were calculated based on all monitored trees.

Tables S1, S2). In *S. aucuparia* and *P. pinea*, the selection on synchrony depended on interannual variability (CVi) (Fig. 2). In *S. aucuparia*, plants with higher synchrony experienced less predation, but only if they were seeding relatively regularly (i.e. if they had low values of CVi). This pattern was reversed for highly variable plants, and phenotypes that were both highly variable and synchronized tended to experience high predation rates (Fig. 2). By contrast, in *P. pinea*, predation increased with increasing interannual variability for poorly synchronized plants (Fig. 2). In turn, high variability and high synchrony helped to escape predation (Fig. 2).

We detected directional selection on high interannual variability of seed production (CVi) in four out of seven species: *Q. humilis*, *Q. ilex*, *S. aucuparia* and *P. pinea* (Tables S1, S2; Fig. 3). In *Q. humilis* and *Q. ilex*, individual plants with larger CVi had lower predation rates. Selection gradients for high CVi were twice as large in *Q. humilis* ($\beta = -2.06$, SE = 0.37) than in *Q. ilex* ($\beta = -1.06$, SE = 0.29). In *S. aucuparia* and *P. pinea*, the selection on CVi was dependent on reproductive synchrony, as explained in the previous paragraph (Fig. 2).

Predation did not select for negative temporal autocorrelation in any species. This was true for both the lag-1 and lag-2 temporal autocorrelation of seed production (Table S1).

Discussion

We found that seed predation selected for mast seeding only in species with evidence of population-level predator satiation (i.e all but *Q. montana* and *Q. alba*). Predation selected for interannual variability of reproduction in two Mediterranean oaks (*Q. humilis* and *Q. ilex*), for synchrony in the temperate *Q. rubra*, and, to a limited degree, for both interannual variability and reproductive synchrony in *S. aucuparia* and *P. pinea*. As predicted, predation did not select for negative temporal autocorrelation of seed production in any species. Taken together, our results are consistent with predictions for the selective effects of invertebrate seed predators on masting (Koenig *et al.*, 2003). Predation by invertebrates, some of which display diapause, appears to select only for some aspects of masting, most importantly high CVi. Determining the selective benefits of masting is complex because of interactions with other seed predators, which may impose contrary selective pressures (Curran & Webb, 2000; Koenig *et al.*, 2003; Żywiec *et al.*, 2018). However, it is reassuring that in all cases where population-level benefit is present we found clear individual-level benefits of mast seeding.

Theory predicts that predation pressure should select for interannual variation and frequent failure years to enhance starvation
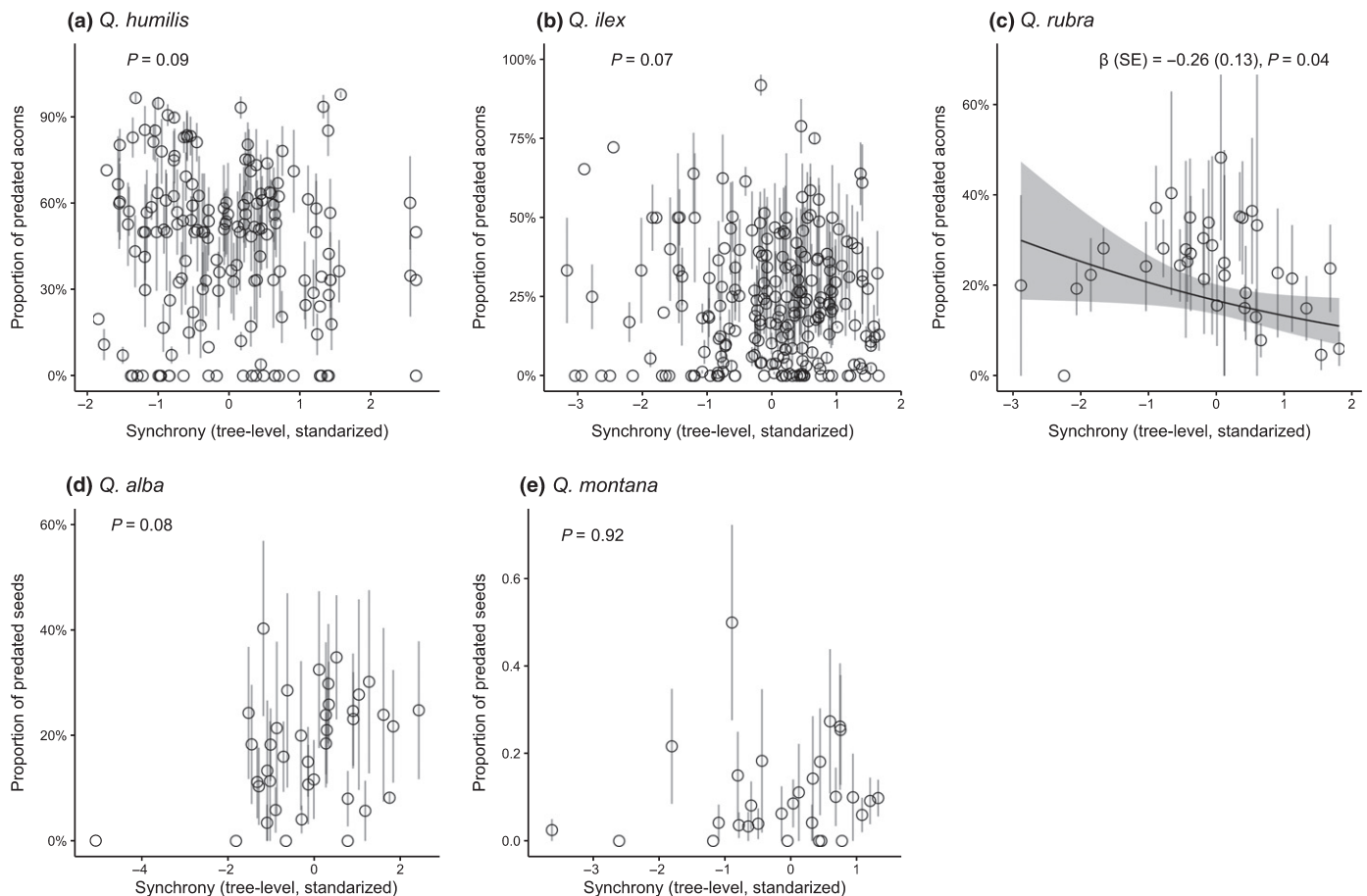

Fig. 1 Selection gradients on spatiotemporal synchrony of reproduction. Fitness measure is the proportion of predated seeds. Results are from generalized linear mixed models for five oak species observed over 12–18 yr. Ribbons are 95% confidence intervals for the model estimates. Relationships were only plotted if statistically significant. Points are tree-level observations and associated standard errors. Panels (a–e) present relationships per species.

Fig. 2 Selection on synchrony and interannual variability (CVi) in *Sorbus aucuparia* and *Pinus pinea*. (a, b) The relationship between seed predation of *S. aucuparia* fruits (a) and *P. pinea* cones (b) and interannual variability (CVi) of reproduction was conditional on reproductive synchrony. Points are estimated marginal means of seed predation from generalized linear mixed models and associated 95% confidence intervals (see also Supporting Information Table S1). Both metrics (CVi and synchrony) were standardized. CVi and synchrony were categorized for visualization, but were inputted as continuous variables in the models.
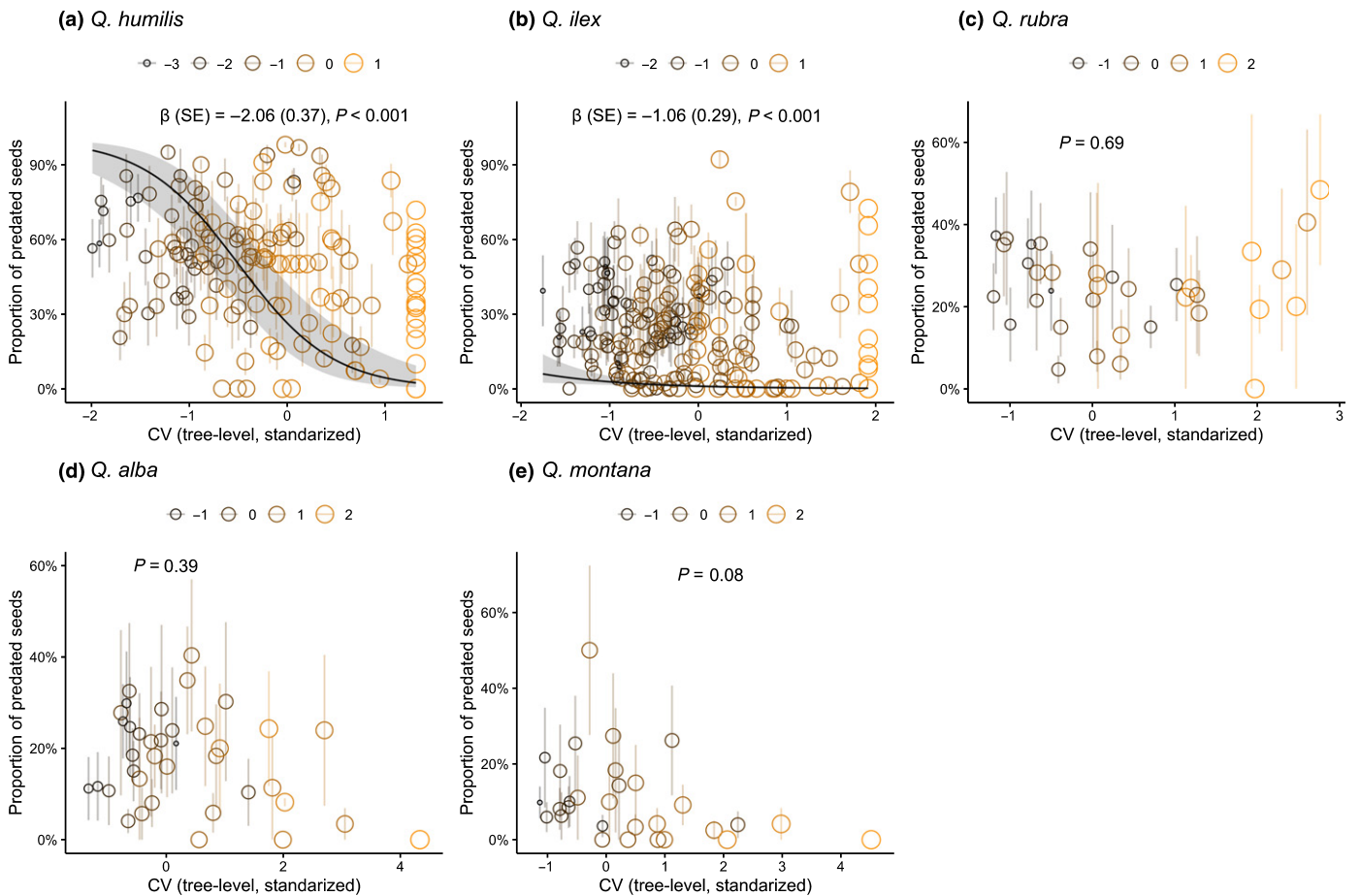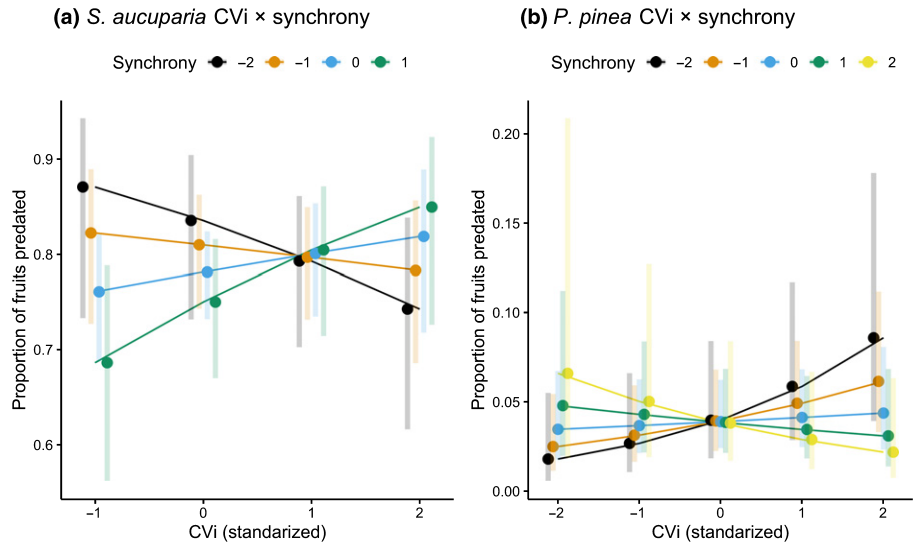

(a) *S. aucuparia* CVi × synchrony

(b) *P. pinea* CVi × synchrony

(a) *Q. humilis*   **(b)** *Q. ilex*   **(c)** *Q. rubra*   **(d)** *Q. alba*   **(e)** *Q. montana*

Fig. 3 Selection gradients on interannual variability (CVi). Fitness measure is the proportion of predated seeds. Results from generalized linear mixed models for five oak species observed over 12–20 yr. Ribbons are 95% confidence intervals for the model estimates. Relationships were only plotted if statistically significant. Points are tree-level observations and associated standard errors. Size and colors of the points are scaled to the standardized proportion of zeros in the time series. Panels (a–e) present relationships per species.

of seed predators (Kelly, 1994; Kelly *et al.*, 2000). This pressure should be especially strong in plant–animal networks that involve seed predators capable of undergoing prolonged diapause, as the

diapause can buffer the insect population against famine years (Kelly *et al.*, 2000; Pélisson *et al.*, 2012). As an illustrative example, a New Zealand masting tussock grass, *Chionochloa*

crassiuscula, that is under strong selection from cecidomyiid flies which can undergo a prolonged diapause reproduced only twice over 26 yr of monitoring (Kelly *et al.*, 2000). In our populations, individuals of *Q. humilis* and *Q. ilex* with high interannual variability of reproduction suffered less seed predation. The two-fold larger selection for interannual variation in *Q. humilis* compared with *Q. ilex* aligns with predation pressure being twice as large in the former (mean seed predation was 14% in *Q. humilis* and 7% in *Q. ilex*). The selection difference is also consistent with the more variable prolonged diapause length of *C. elephas* that infests *Q. humilis*, but not *Q. ilex* acorns at our sites (Espelta *et al.*, 2009). In other species, high interannual variability was not related to seed survival (*Q. rubra*, *Q. alba*, *Q. montana*), or it was dependent on synchrony as in the case of *S. aucuparia* and *P. pinea*. Exploring whether masting helps to escape predation more frequently in systems where the timing of predator diapause is fixed or predictable appears a fruitful avenue for future research.

The opposing selection landscapes in *S. aucuparia* and *P. pinea* can be attributed to different mobility of their seed predators (Satake *et al.*, 2004; Calama *et al.*, 2017). In *S. aucuparia*, predation selected against the most variable and simultaneously the most synchronized phenotypes. Previous theoretical studies implied that selection can act to decrease both individual variability and synchrony if predators are attracted over a wide area to groups of trees with unusually large seed crops (Koenig *et al.*, 2003). In *P. pinea*, well-synchronized and highly variable phenotypes experienced the least predation. This implies relatively limited mobility of the insect that is well satiated by synchronized fluctuation of highly variable pines. The concurrent increasing predation on variable but unsynchronized individuals could be a consequence of between-tree dispersion from trees that had large seed production in the previous year, but had not reproduced in the current season (Bogdziewicz *et al.*, 2018a). In support of this, previous studies indicated that population dynamics of *A. conjugella*, the seed predator of *S. aucuparia*, are synchronized over hundreds of kilometers (Satake *et al.*, 2004). In turn, fluctuations of population dynamics of *D. mendacella*, the seed predator of *P. pinea*, are localized and synchronized only up to 1500 m (Calama *et al.*, 2017). Together, this result provides new empirical support for the notion that adaptive significance of reproductive patterns may change depending on the ecological context.

In oaks, seed predation did not select for reproductive synchrony, with the exception of *Q. rubra*. The phenotypic selection for high synchrony in *Q. rubra* agrees with the observation that high seed production resulted in weevil satiation in that species only if the whole population produced a bumper crop (Bogdziewicz *et al.*, 2018b). In *Q. alba* and *Q. montana*, seed predation did not select for any aspect of masting. This was expected as predator satiation proved to be ineffective in these species owing to the rapid numerical response of insect populations to bumper crops (Bogdziewicz *et al.*, 2018b). The general lack of selection for synchrony in oaks is probably a consequence of poor mobility of their main predispersal seed predator, *Curculio* weevils (Pélisson *et al.*, 2013; Ruiz-Carbayo *et al.*, 2018). This would agree with the theoretical, but so far untested, assumption that

relatively immobile insect seed predators can fail to select for increase individual reproductive synchrony in plants (Koenig *et al.*, 2003). Nonetheless, we note that lack of insect predator satiation in these oaks does not preclude satiation of post-dispersal predators (Greenberg & Zarnoch, 2018). Given that weevils appear able to circumvent many of the effects of mast seeding, satiation of post-dispersal seed predators and enhanced dispersal by scatter hoarders is potentially a more important selection agent for masting in the studied oak species (Lichti *et al.*, 2014).

Our results provide broad support for the concept that seed predators should select for different aspects of mast seeding depending on their life-history traits. More specifically, predispersal seed predation by relatively immobile insects should select for high individual plant-level variability (CVi) (Norton & Kelly, 1988; Koenig *et al.*, 2003; Bogdziewicz *et al.*, 2020a). It is important to highlight that masting can also be selected for by post-dispersal predators (Curran & Webb, 2000; Lichti *et al.*, 2014), pollination efficiency (Kelly *et al.*, 2001; Bogdziewicz *et al.*, 2020a), improved dispersal (Zwolak *et al.*, 2016), or nutrient economy and associated tradeoff between growth and reproduction (Fernández-Martínez *et al.*, 2019). Moreover, as many plant species host several different pre- and post-dispersal seed predators, they will experience different and potentially contradictory selective pressures depending on the traits of their predators. The tension between these forces will result in complex selective pressures on the reproductive schedules of individual plants. For example, in animal-pollinated *S. aucuparia*, strong masting could starve and satiate pollinators in a similar manner to other predator populations (Herrera *et al.*, 1998; Żywiec *et al.*, 2018). Understanding the adaptive significance of plant reproductive patterns now requires integrating ecological context, including predator life-history traits, with the role of selection by other drivers such as pollination and nutrient economy.

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Author contributions

MB conceived the ideas and designed the study. JS, AJT, RC, SM, MAS, BS, ŁP and MŻ collected the data, MB and JS analyzed the data, and MB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval 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.

Fig. S1 Population-level predator satiation shows a functional response to mast seeding.

Fig. S2 Population-level predator satiation shows a numerical response to mast seeding.

Methods S1 Study species and data collection.

Table S1 Selection gradients (β) for interannual variation (CVi), synchrony and temporal autocorrelation of seed production (AR1 or AR2) in model species predicted with mixed-effects models.

Table S2 Selection differentials (S) for interannual variation (CVi), synchrony and temporal autocorrelation of seed production (AR1 or AR2) in model species predicted with mixed-effects models.

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