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Does masting scale with plant size? High reproductive variability and low synchrony in small and unproductive individuals

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• **Background and Aims** In a range of plant species, the distribution of individual mean fecundity is skewed and dominated by a few highly fecund individuals. Larger plants produce greater seed crops, but the exact nature of the relationship between size and reproductive patterns is poorly understood. This is especially clear in plants that reproduce by exhibiting synchronized quasi-periodic variation in fruit production, a process called masting.
• **Methods** We investigated covariation of plant size and fecundity with individual-plant-level masting patterns and seed predation in 12 mast-seeding species: *Pinus pinea*, *Astragalus scaphoides*, *Sorbus aucuparia*, *Quercus ilex*, *Q. humilis*, *Q. rubra*, *Q. alba*, *Q. montana*, *Chionochloa pallens*, *C. macra*, *Celmisia lyallii* and *Phormium tenax*.
• **Key Results** Fecundity was non-linearly related to masting patterns. Small and unproductive plants frequently failed to produce any seeds, which elevated their annual variation and decreased synchrony. Above a low fecundity threshold, plants had similar variability and synchrony, regardless of their size and productivity.
• **Conclusions** Our study shows that within-species variation in masting patterns is correlated with variation in fecundity, which in turn is related to plant size. Low synchrony of low-fertility plants shows that the failure years were idiosyncratic to each small plant, which in turn implies that the small plants fail to reproduce because of plant-specific factors (e.g. internal resource limits). Thus, the behaviour of these sub-producers is apparently the result of trade-offs in resource allocation and environmental limits with which the small plants cannot cope. Plant size and especially fecundity and propensity for mast failure years play a major role in determining the variability and synchrony of reproduction in plants.

Key words: Fecundity, mast seeding, plant reproduction, predator satiation, seed predation, super-producers.

INTRODUCTION

Recruitment of the majority of plant species is limited by the availability of seeds (Clark *et al.*, 2007). Thus, individual variation in fecundity within plant populations is a life-history parameter of high evolutionary and ecological significance (Herrera and Jovani, 2010; Moran and Clark, 2012). In a range of plant species, variation among individuals in fecundity tends to be high, with seed production dominated by a few highly fecund individuals (Greenberg, 2000; Herrera and Jovani, 2010; Pesendorfer *et al.*, 2016). Older and larger plants generally produce greater seed crops, but the exact nature of this relationship between plant size and reproduction is poorly understood (Thomas, 2011; Hossain *et al.*, 2017; Pesendorfer *et al.*, 2020). This knowledge gap is especially clear in perennial plants that reproduce through masting cycles, characterized by large, synchronized annual variation in fruit production (Kelly, 1994; Vacchiano *et al.*, 2018).

Recent studies imply that large within-species differences in the extent of the inter-annual variability and synchrony may be driven by the age or size of individual plants, yet they report contrasting relationships (Minor and Kobe, 2017; Pesendorfer *et al.*, 2020). On one hand, older (and presumably larger) European temperate forest trees are more fecund and more variable (Pesendorfer *et al.*, 2020). On the other hand, larger (and presumably older) North American temperate trees produced more seeds, and the top 10 % of the most fecund individuals (called 'super-producers)' had lower annual

variation of seed production (Minor and Kobe, 2017). The size-dependent differences in masting can amplify or reduce the fitness differences among individuals varying in fecundity, as fitness of masting plants depends on the functional benefits that the inter-annual variability and synchrony provide.

The two functional benefits of masting with the most frequent empirical evidence are predator satiation and increased pollination efficiency; here, we focus on the first (Pearse *et al.*, 2016). During conditions of predator satiation, large variation in crop size causes seed predators to starve in low-seed years and to experience satiation in mast years (Satake and Bjørnstad, 2004; Linhart *et al.*, 2014). Even though predator satiation depends on population-level patterns of reproduction, individual plants gain fitness benefits according to their individual degree of annual variability and synchronization of reproduction (Ims, 1990; Koenig *et al.*, 2003; Satake and Bjørnstad, 2004; Żywiec *et al.*, 2013). Seed predation by specialist insect granivores could be especially susceptible to plant-level changes in annual variability or synchrony because of their relatively low mobility (Koenig *et al.*, 2003; Bogdziewicz *et al.*, 2020). Consequently, if large and fecund plants produce seeds more regularly, they could experience increased seed losses if this stable seed supply results in higher local average survival of insect cohorts and a localized build-up of insect populations (Maeto and Ozaki, 2003; Higaki, 2016; Bogdziewicz *et al.*, 2017).

Here, we investigate the covariation of fecundity with respect to plant size, masting patterns and pre-dispersal seed predation using long-term (12–30 years) data for a diverse set of 12 species. We define fecundity as the mean seed production of an individual plant. (1) First, we tested whether fecundity correlates with plant size (Greenberg, 2000; Minor and Kobe, 2017). Next, we tested the relationships among overall fecundity, variability and synchrony. Our hypothesis was that inter-annual reproductive variation and synchrony are linked (correlated) primarily to fecundity by the frequency of non-reproductive years (failure years). Specifically, we predicted that (2) small plants with low fecundity would experience reproductive failure more frequently than larger ones, (3) individual plant variability would be elevated by the proportion of failure years in time series, and (4) synchrony would be reduced by the proportion of size-driven failure years. Consequently, if all our predictions held, (5) reproductive variation across years would be higher and (6) synchrony would be lower in small and unproductive individuals. As we predicted that high-fecundity plants will produce seeds more regularly in comparison with low-fecundity individuals, we predicted that (7) seed predation correlates positively with fecundity. In addition to analysing correlations between size, fecundity and masting patterns as continuous variables, we also characterized seed production patterns for super-producers (10 % most fecund plants) versus the remainder in each species, following Minor and Kobe (2017). This categorical analysis was done to contrast the results of a dichotomous versus continuous approach.

MATERIALS AND METHODS

Study species

Annual variation in reproductive effort was monitored for individual plants by collection of all the cones on the whole plant (*Pinus pinea*), counting all inflorescences and seed pods (*Astragalus scaphoides*), counting all fruits (*Sorbus aucuparia*), counting fruits on selected branches (*Quercus ilex*, *Q. humilis*), using seed traps (*Q. rubra*, *Q. alba*, *Q. montana*) or counting all flowers (*Chionochloa pallens*, *C. macra*, *Celmisia lyallii* and *Phormium tenax*). For ten species (*S. aucuparia*, *P. pinea*, *Q. ilex*, *Q. humilis*, *Q. rubra*, *Q. alba*, *Q. montana*, *C. pallens*, *C. macra*, *C. lyallii*) we also collected plant size data, while for another subset of seven species we collected pre-dispersal seed predation data by insects (*S. aucuparia*, *P. pinea*, *Q. ilex*, *Q. humilis*, *Q. rubra*, *Q. alba* and *Q. montana*). All 12 species show clear masting behaviour (Kelly *et al.*, 2000, 2013; Espelta *et al.*, 2008; Crone *et al.*, 2009; Calama *et al.*, 2017; Bogdziewicz *et al.*, 2018a, 2019). Furthermore, in ten of the 12 focal species, our past investigations indicated that masting decreases the proportion of seeds attacked by pre-dispersal seed predators in high-seed years (Kelly and Sullivan, 1997; Kelly *et al.*, 2000; Crone and Lesica, 2004; Espelta *et al.*, 2008; Żywiec *et al.*, 2013; Calama *et al.*, 2017). The exceptions are two North American oaks, *Q. alba* and *Q. montana* (Bogdziewicz *et al.*, 2018). A description of the ecology of the study species, sites and field procedures is given in the Supplementary Data Appendix S1 and is summarized in Table 1.

Data analysis

Reproductive traits. For each plant, we described masting behaviour using two metrics commonly used in studies of mast seeding: coefficient of variation (CVi, calculated as the ratio between the standard deviation and the mean) and among-individual synchrony (S) (Koenig *et al.*, 2003; Crone *et al.*, 2011). The synchrony of seed production (technically diaspores, or of fruits/flowers/cones, referred to as 'seeds' throughout the text for convenience) of each individual was measured by the average Pearson pairwise correlation of seed production of an individual plant with all other individuals observed at the site (Koenig *et al.*, 2003). We also estimated the proportion of failure years, calculated as the ratio of years for which no seeds were recorded for an individual plant versus the number of years that plant was monitored. To avoid bias due to limited sampling, we used only individuals that were monitored for at least 10 years.

In addition, to contrast the results of the dichotomous versus continuous approaches, we also defined 'super-producers' as the subset of each population that was above the 90th percentile of individual-plant fecundity (Minor and Kobe, 2017). Fecundity was calculated as the annual mean reproductive effort by each plant (total number of seeds produced by an individual plant divided by the number of years a plant was monitored), to adjust for the differences in the number of sampling years among individuals. We then characterized seed production patterns for each sub-population (super-producers versus the other individuals) in each species, using the masting metrics (CVi and S).

Fecundity versus other reproductive traits. To explore whether variation in fecundity was related to focal plant size (prediction 1), we used zero-inflated negative binomial (ZINB) mixed models with plant size (diameter at breast height or basal area index, depending on the species; see Supplementary Data Appendix S1) included as the predictor in both the negative

TABLE 1. *Summary the ecology of study species, sites and field procedures. Details are given in Supplementary Data Appendix S1*

Species	Location	Number of sites	Individuals monitored	Life form	Reproductive trait measured	Collecting method	Plant size measurement
P. pinea	Spain	52	187	Tree	Cones	Census	DBH
A. scaphoides	USA	4	507	Herb	Inflorescences	Census	NA
S. aucuparia	Poland	1	299	Tree	Fruits	Census	DBH
Q. ilex	Spain	17	225	Tree	Acorns	Count on selected branches	DBH
Q. humilis	Spain	17	172	Tree	Acorns	Count on selected branches	DBH
Q. rubra	USA	3	44	Tree	Acorns	Seed trap	DBH
Q. alba	USA	3	51	Tree	Acorns	Seed trap	DBH
Q. montana	USA	2	33	Tree	Acorns	Seed trap	DBH
C. pallens	New Zealand	5	217	Grass	Inflorescences	Census	BA
C. macra	New Zealand	5	125	Grass	Inflorescences	Census	BA
C. lyallii	New Zealand	3	94	Herb	Inflorescences	Census	Rosettes
P. tenax	New Zealand	1	37	Herb	Inflorescences	Census	NA

DBH, diameter at breast height; BA, basal area; NA, data not available.

binomial and binomial part of the model. We used annual seed counts as the response. For each species, we fitted four candidate models, including plant size as a linear or quadratic term in all possible combinations in both logistic and negative parts of the model. Study site (with the exception of those for *S. aucuparia* and *P. tenax*, which were monitored on only one site) and tree ID were included as random terms. To account for differences in sampling effort at the plant level, each model included the log-transformed number of sampling years as an offset. The best model was chosen based on the standard Akaike information criterion and only that one is reported. In the case of *P. pinea* and *Q. montana*, due to ZINB model convergence issues, we first modelled annual seed production as a function of size using negative binomial mixed models and then, using binomial mixed models, regressed probability of failure (no reproduction in a particular year) with plant size.

Next, to explore the putative link between fecundity and masting patterns (predictions 2–4), we built generalized linear mixed models (GLMMs) that included (1) the proportion of failure years as a response and tree-level mean fecundity as a predictor (prediction 2), (2) CVi as the response and proportion of failure years as a predictor (prediction 3), and (3) synchrony as the response and proportion of failure years as the predictor (prediction 4). The first model used a binomial family error term and logit link (prediction 2), and the second one (prediction 3) used a Gaussian error term and identity link. To analyse associations between synchrony and proportion of failure years (prediction 4), we used GLMMs with Tweedie distribution and logit link, with the response normalized as $y\_i = (y\_i + 1)/2$. In the next step, we correlated reproductive variation (prediction 5) and synchrony (prediction 6) with tree-level mean fecundity using GLMMs with Gaussian error term and identity link or Tweedie distribution and logit link, respectively. Finally, we used a GLMM with a binomial family error term and logit link to test whether the annual proportion of damaged seeds correlates with tree-level mean fecundity (prediction 7). In all analyses, we built separate models for each species and considered both linear and quadratic effects of an explanatory term. In addition, when testing predictions 2 and 5 we fitted the relationship between the response and predictor as a self-starting asymptotic function. In all models, we used site ID as a random effect (with the exception of *S. aucuparia* and *P. tenax*, which were monitored on only one site). In the GLMMs testing prediction 7 (predation versus tree-level mean fecundity) we used also tree ID as a random effect and included temporal autocorrelation (lag1). We calculated marginal effects (i.e. the proportion of variance explained by fixed effects) and conditional effects (i.e. the proportion of variance explained by fixed and random effects) with R^2 for our models (Nakagawa and Schielzeth, 2013). All statistics were run in R version 3.4.1 (R Core Team, 2018). We used the glmmTMB package (Brooks *et al.*, 2017) to fit all the models and the DHARMa (Hartig, 2017) package to validate them based on visual inspection of residual patterns.

RESULTS

In nine of ten species for which we had plant size data (all except *Q. montana*), fecundity was significantly related to plant size (Supplementary Data Table S1, Fig. 1). Moreover, in seven out of ten species (exceptions were *C. lyallii*, *Q. montana* and *Q. alba*), larger plants experienced fewer failure years (Supplementary Data Table S1). The variation explained by these models ranged from 5 to 59 % across all species. Similarly, in all species, more fecund plants experienced fewer failure years, and fecundity explained 6–80 % (mean = 22 %) of variance in reproductive failures (Supplementary Data Table S2).

Reproductive variability as measured by CVi was strongly related to the proportion of failure years in the time series of all species, and failures explained most of the variance (mean = 75 %) (Supplementary Data Table S3, Fig. 2). Similarly, reproductive synchrony was strongly related to the proportion of failure years, and failures explained large portions of the variance (mean = 44 %) (Supplementary Data Table S4, Fig. 2). This relationship was significant in 11 out of 12 species tested (all but *Q. humilis*). Consequently, variability (CVi) was negatively, non-linearly related to fecundity in all species (Supplementary Data Table S5), and fecundity explained, on average across species, 41 % of the variance in CVi. Importantly, inter-annual variability was stable across most of the fecundity range and increased sharply for the lowest-fecundity individuals (Fig. 3).

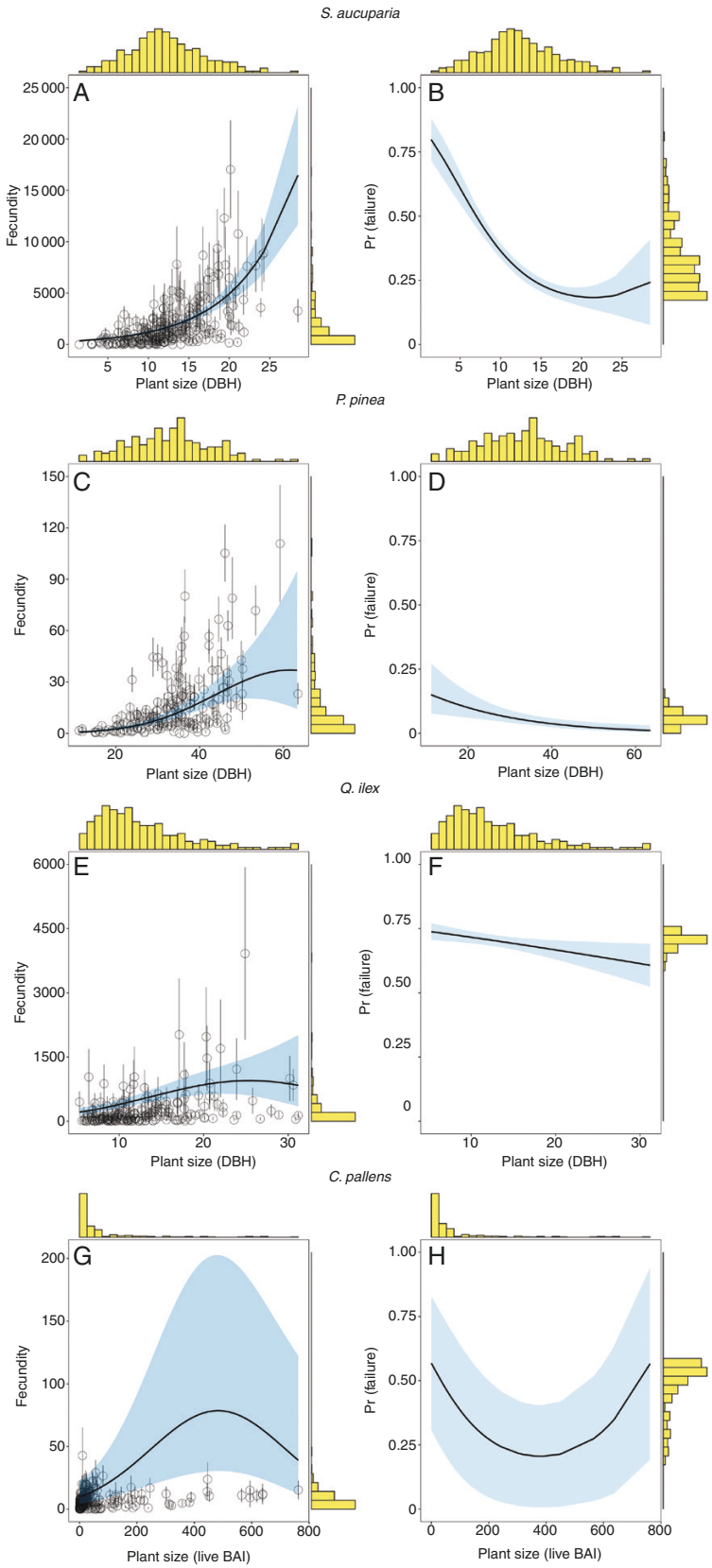

FIG. 1. Relationships between fecundity (modelled as annual seed counts; A, C, E, G) or probability of failure [Pr(failure)] (B, D, F, H) and plant size. Solid lines show statistically significant ZINB model predictions and associated 95 % confidence bands. Points in panels (A), (C), (E) and (G) show long-term mean fecundity (± s.e.) of individual plants. This figure presents a subset of the studied species (see Supplementary Data Table S1 for results for all species). The models included tree ID and site as random effects (see Materials and methods for details). DBH, diameter at breast height; BAI, basal area index.

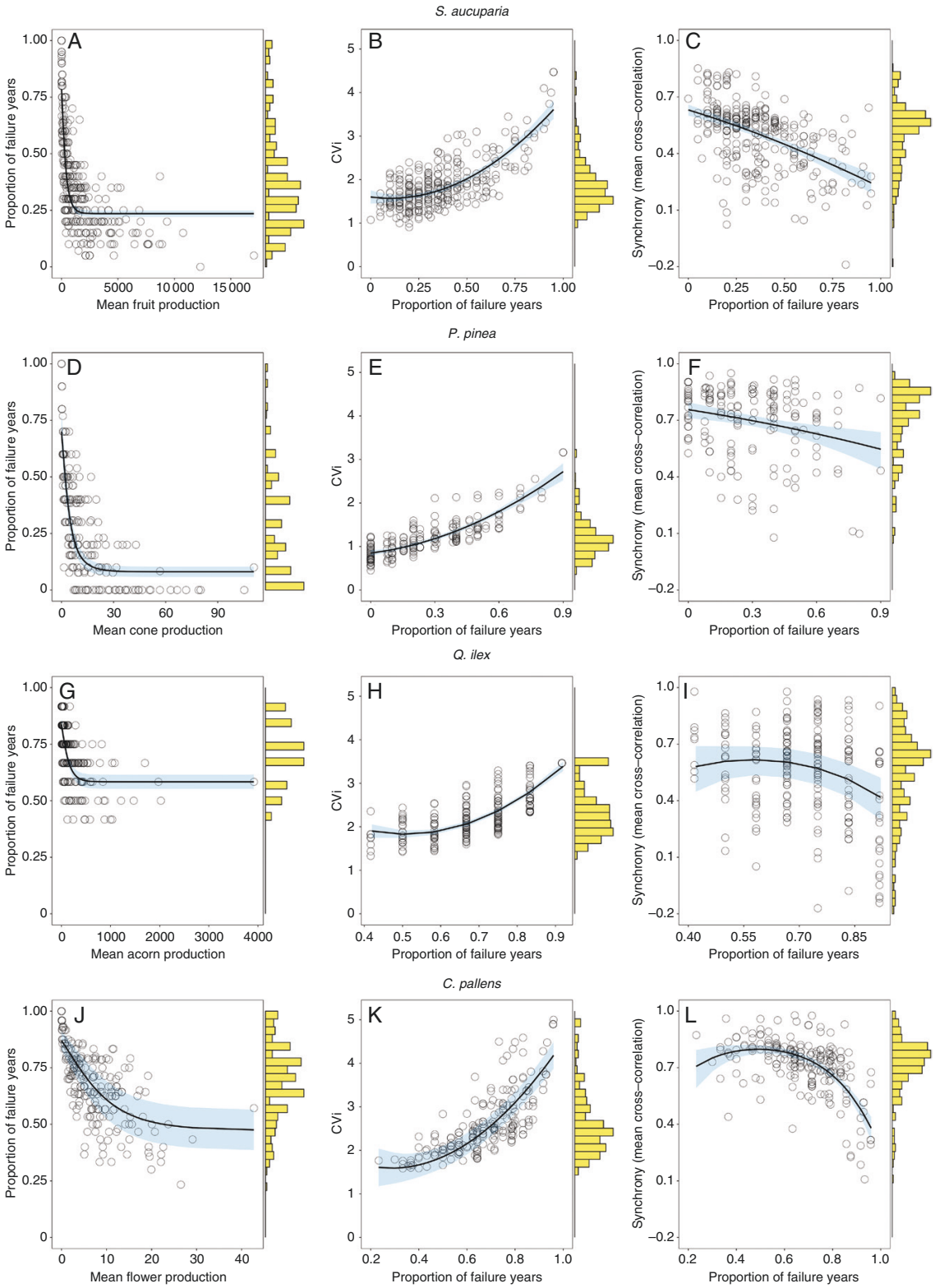

FIG. 2. Relationships between proportion of years with reproductive failure (no reproduction observed) of a plant, plant-level CVi in annual reproduction, synchrony and long-term mean plant fecundity (overall number of fruits produced/number of years a plant was monitored). Solid lines show statistically significant GLMM predictions and shaded areas show associated 95 % confidence bands. This figure presents a subset of the studied species (see Supplementary Data Tables S2–4 for results for all species). The models included site as a random effect (see Materials and methods for details).

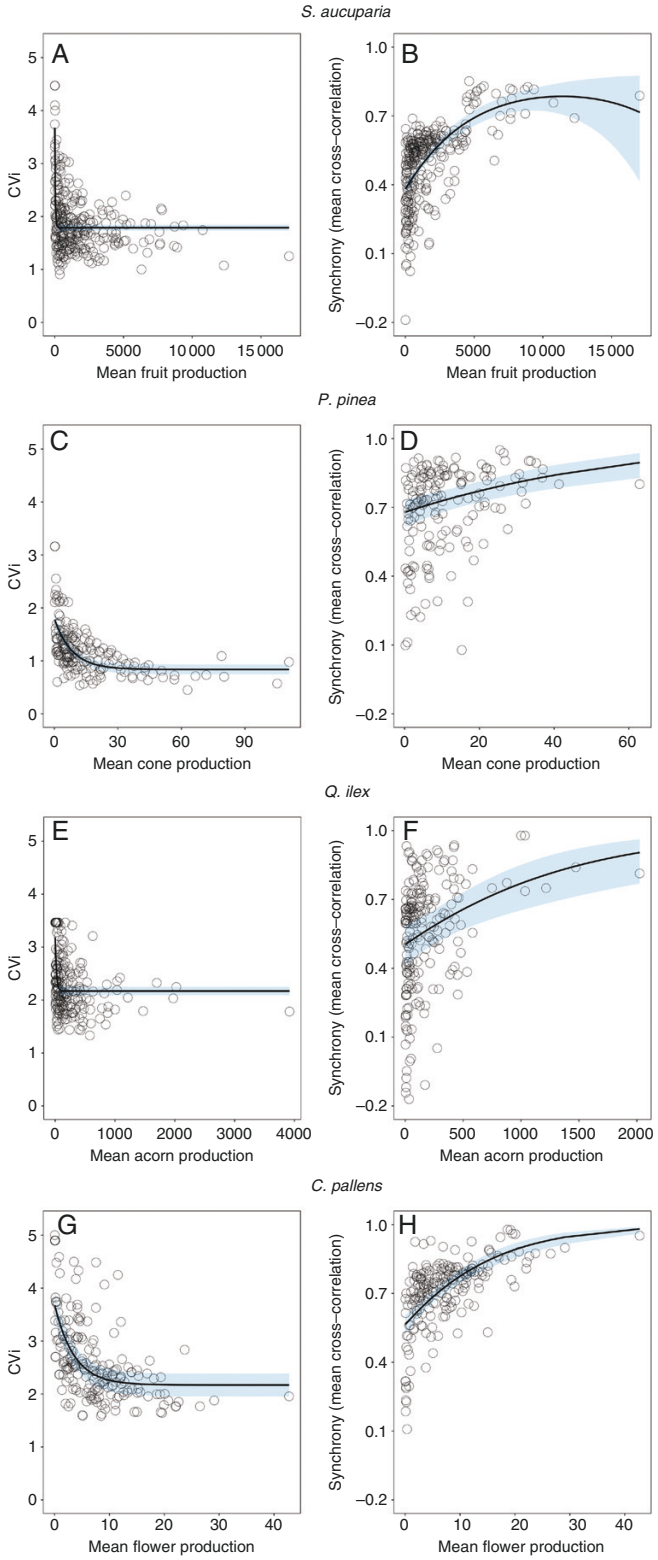

FIG. 3. Scatterplots of plant-level measures of CVi in annual reproduction, synchrony and long-term mean fecundity (overall number of fruits produced/number of years a plant was monitored). Solid lines show statistically significant GLMM predictions and associated 95 % confidence bands. This figure presents a subset of the studied species (see Supplementary Data Tables S5–6 for results for all species). The models included site as a random effect (see Materials and methods for details).

In addition, fecundity was significantly positively correlated to synchrony in ten out of 12 species (all but *Q. montana* and *Q. humilis*), and explained a significant portion of the variance (mean = 49 %, Supplementary Data Table S6, Fig. 3). Seed predation was positively related to fecundity in only two species: *Q. ilex* and *Q. humilis* (Supplementary Data Table S7, Fig. 4).

In the dichotomous comparisons of the super-producers (10 % most fecund plants) versus the remainder of individuals in each species, these highly fecund plants had lower CVi and higher synchrony (S). Depending on the species, super-producers produced 14–53 % of the total seed count in the population (Supplementary Data Table S8).

DISCUSSION

The sources of within-species variation in masting behaviour are largely unknown, but our study shows that significant portions of this variation are driven by differences in mean fecundity, which in turn is correlated with plant size. Small plants produce few seeds, and fail to produce seeds frequently, which elevates their reproductive variation across years and sharply decreases synchrony with other individuals in the population. This result partially agrees with the past observation that larger trees produce more seeds with lower inter-annual variability (Minor and Kobe, 2017). Specifically, a dichotomous comparison of the top 10 % most fecund plants with the remaining 90 % implies that super-producers tend to have lower annual variability of seeding and greater synchrony (Supplementary Data Table S8). Greater synchrony was hypothesized to give super-producers the ability to reap the benefits of masting while also governing regular seed production over time (Minor and Kobe, 2017). Our comparison of this categorical approach with a continuous one indicates that the notion that super-producers behave differently is driven by the smallest and least fertile plants in the population. These plants drive the mean up (in the case of inter-annual variability) or down (in the case of synchrony) for all non-super-producers. In other words, in terms of masting patterns, there are no super-producers, but rather normal plants and sub-producers. This distinction is important biologically, as it shows that rather than the most fecund plants behaving differently from other plants in the population, the least fertile individuals are the outliers.

As well as the importance of continuous rather than dichotomous analyses, our analyses suggest a few other important methodological lessons in the study of individual plant variation. High CV values occur in individuals and populations that have many years with zero reproduction. This is not surprising given that CV is directly mathematically linked to occurrence of zeros in the time series (Crone *et al.*, 2011). In time series with many years with failure, the CV is much less influenced by the amount of reproduction in non-zero years (Crone *et al.*, 2011). Similarly, as in the case of CV, among-plant variation in synchrony was also large and linked to the occurrence of zero years. Shared failure years (e.g. those in response to environmental disturbances like drought, cf. Rees *et al.*, 2002; Bogdziewicz *et al.*, 2018b) would give small and infertile plants greater synchrony, but in fact small plants have lower synchrony. Thus, the failure years were idiosyncratic to each

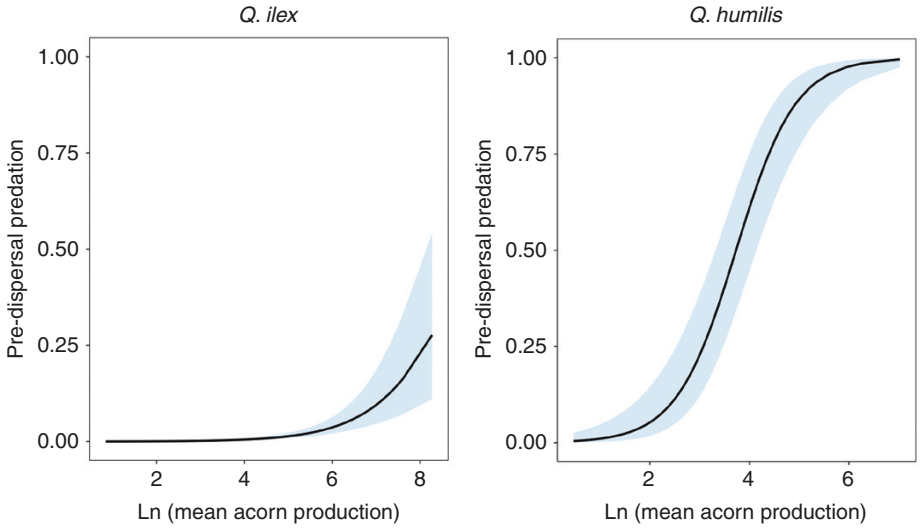

FIG. 4. Plant-level pre-dispersal predation rate versus fecundity (overall number of fruits produced/number of years a plant was monitored). Solid lines show statistically significant GLMM model predictions and associated 95 % confidence bands. This figure presents a subset of the studied species in which the relationship was significant (see Supplementary Data Table S7 for results for all species). The models included tree ID and site as random effects (see Materials and methods for details).

small plant, which implies that these plants fail to reproduce because of plant-specific factors (e.g. internal resource limits), combined with selection for small plants to allocate fewer resources to reproduction and more to growth until they are larger or taller (Miller *et al.*, 2008; Thomas, 2011). Therefore, the failures of the least fertile plants could be a result of resource allocation trade-offs and environmental limits with which the small plants cannot yet cope. In addition, many plants shift resource allocation from growth to reproduction with increasing plant maturity (Thomas, 2011). Understanding the relationship between size and age is not possible in this study because we did not have estimates of plant age for all individuals, noting especially that our multispecies data include many herbaceous plants. Evaluating effects of age *per se*, as well as other differences among individual plants within size classes, could be an interesting area for future research.

In five out of seven species for which we had seed predation data, higher seed predation was not associated with higher fecundity, even though more fecund plants reproduced more regularly. This pattern suggests that failure years do not have a decisive influence on the insect seed predators' populations in these species, possibly because predators are able to move between plants. In support of this idea, recent studies show greater insect immigration into asynchronous trees when the population-level seed production is low (Bogdziewicz *et al.*, 2018a). In two Mediterranean oaks in which we detected a positive correlation between seed predation and fecundity, infrequent failures likely lead to lower insect emigration or higher survival, which over the long term leads to a build-up of the insect populations (Bogdziewicz *et al.*, 2017; Pérez-Ramos *et al.*, 2017). We hypothesize that the species-specific relationship between regular seeding and pre-dispersal seed predation we detected is caused by interactive effects of plant and predator population traits, including predators' costs of migration in low-seed years, insect mobility, and the density of the plant population (Moreira *et al.*, 2017; Bogdziewicz *et al.*, 2018*c*). This warrants further investigation, but will require even larger datasets.

In closing, our analysis shows that, presumably because they are under constant selection to gain economies of scale, within a species plants over a wide size range have remarkably similar masting strategies. The only departures from this are the least fecund plants (sub-producers), which might differ because of fundamental constraints on the smallest feasible reproductive output. Small and low-fertility plants often fail to produce seeds, which elevates their inter-annual variability and decreases reproductive synchrony. This pattern was consistent among all studied species, which included both angiosperms and gymnosperms, evergreen and winter-deciduous species, trees and herbs. A careful generalization based on the sample of 12 species studied here implies that the individual-level differences in annual reproductive variation can be associated with plant size and the propensity of small plants to shift resource allocation away from reproduction in favour of growth. Plant size and fecundity play a major role in determining the variability and synchrony of reproduction in plants. Understanding the mechanisms of the size–fecundity–synchrony relationship could be an important next step in predicting how mast seeding will change in changing environments.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Appendix S1: study species and data collection. Table S1: summary of ZINB mixed models regressing variation in fecundity with plant size. Table S2: summary of generalized mixed models regressing the variation in the proportion of failure years a plant experienced during the study period versus that plant's mean fecundity. Table S3: summary of linear mixed models regressing the variation in annual variability of reproduction of a focal plant with the proportion of failure years in the time series. Table S4:

summary of generalized mixed models regressing the variation in synchrony of reproduction of a focal plant with the proportion of failure years in the time series. Table S5: summary of linear mixed models regressing the variation in plant CVi versus the plant's fecundity. Table S6: summary of generalized mixed models regressing the variation in plant reproductive synchrony versus the plant's fecundity. Table S7: summary of generalized mixed models regressing the variation in pre-dispersal seed predation versus log-transformed mean plant fecundity. Table S8: annual variability and synchrony of seed production in the studied species.

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