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Reference:

Bogdziew icz Michal, Zyw iec Magdalena, Espelta Josep M., Fernandez-Martinez Marcos, Calama Rafael, Ledw on Mateusz, McIntire Eliot, Crone Elizabeth E..- Environmental veto synchronizes mast seeding in four contrasting tree species
American naturalist - ISSN 0003-0147 - 194:2(2019), p. 246-259
Full text (Publisher's DOI): https://doi.org/10.1086/704111
To cite this reference: https://hdl.handle.net/10067/1618630151162165141

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Running title: Environmental veto drives masting

Environmental veto synchronizes mast seeding in four contrasting tree species

Michał Bogdziewicz[1,2*], Magdalena Żywiec[3,4], Josep M. Espelta[2], Marcos Fernández- Martinez[5], Rafael Calama[6], Mateusz Ledwoń[7], Eliot McIntire[8], Elizabeth E. Crone[9]

[1] Department of Systematic Zoology, Adam Mickiewicz University, Poznań, Poland

[2] Centre for Ecological Research and Forestry Applications, University Autonoma de Barcelona, Spain

[3] Centro de Ecologia Aplicada "Prof. Baeta Neves" (CEABN-InBIO), Instituto Superior de Agronomia, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal

[4] Władysław Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31 512, Kraków, Poland

[5] Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology, University of Antwerp, 2610 Wilrijk, Belgium.

[6] INIA-CIFOR, Ctra A Coruña km 7.5, 28040 Madrid, Spain

[7] Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

[8] Dépt des Sciences du Bois et de la Forêt, Pavillon Abitibi-Price, Univ. Laval, QC, Canada

[9] Department of Biology, Tufts University, 163 Packard Ave, Medford, MA 02155, USA

Key-words: costs of reproduction; density-dependent pollination success; environmental veto; mast seeding; pollen coupling; resource budget model;

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ABSTRACT

Synchronized and variable reproduction by perennial plants, called mast seeding, is a major reproductive strategy of trees. The need to accumulate sufficient resources after depletion following fruiting (resource budget), the efficiency of mass flowering for outcross pollination (pollen coupling), or the external factors preventing reproduction (environmental veto) could all synchronize masting. We used seed production data for four species (*Quercus ilex*, *Q. humilis*, *Sorbus aucuparia*, *Pinus albicaulis*) to parametrize resource budget models of masting. Based on species life history characteristics, we hypothesized that pollen coupling should synchronize reproduction in *S. aucuparia* and *P. albicaulis*, while in *Q. ilex* and *Q. humilis* environmental veto should be a major factor. Pollen coupling was stronger in *S. aucuparia* and *P. albicaulis* than in oaks, while veto was more frequent in the latter. Yet, in all species, costs of reproduction were too small to impose a replenishment period. A synchronous environmental veto, in the presence of environmental stochasticity, was sufficient to produce observed variability and synchrony in reproduction. In the past, vetoes like frost events that prevent reproduction have been perceived as negative for plants. In fact, they could be selectively favored as a way to create mast seeding.

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Introduction

Masting is characterized by synchronized and highly variable levels of seed production over years within a population (Crone and Rapp 2014; Pearse et al. 2016). It is a major reproductive strategy of plants worldwide that has cascading effects on plant and animal population dynamics, plant growth, carbon stocks, regeneration, nutrient cycling, or future species composition (Herrera et al. 1998; Bogdziewicz et al. 2016; Vacchiano et al. 2018). The consequences of mast-seeding for plant fitness and community dynamics have been studied for decades, but the proximate mechanisms driving it remain poorly understood (Satake 2004; Kelly et al. 2013; Crone and Rapp 2014; Pearse et al. 2014, 2016; Han and Kabeya 2017). Nonetheless, much recent progress in the field was generated through applying resource budget models of masting (Isagi et al. 1997, Satake and Iwasa 2000, Venner et al. 2016) to various plant species (Rees et al. 2002, Crone et al. 2005, Monks et al. 2016, Abe et al. 2016, Pesendorfer et al. 2016, Bogdziewicz et al. 2018, Schermer et al. 2019). In these past studies, models were carefully adapted to include specific natural history of individual species. Here, we build on these advances by evaluating whether and how generalized resource budget models can explain mast-seeding across a diverse group of species.

Mast seeding is the result of two mechanistic processes occurring at the individual and at the population level, respectively: annual variability in seed production by individual trees, and synchronization among individuals. One possible driver of variability within individuals through time is environmental stochasticity (Lyles et al. 2009; Fernández-Martínez et al. 2017*a*; Noble et al. 2018). Plants may vary in reproduction if production of large fruit crops is restricted to years of favorable weather conditions (Kelly and Sork 2002; Espelta et al. 2008). A second widely studied driver of among-year variability in seed production is non-linear allocation of resources

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(Pearse et al. 2016). The idea was formalized by the resource budget (RB) model that assumes that plants choose to accumulate a threshold level of resources to initiate reproduction (Isagi et al. 1997; Pearse et al. 2016). If this threshold cannot be reached in one season, then plants accumulate resources over several years, which leads into intermittent seed production even in a constant environment (Isagi et al. 1997; Satake and Iwasa 2000).

In cases where environmental stochasticity creates annual variability in reproduction, it may simultaneously produce among-plant synchrony, if plants within populations experience similar weather conditions (Koenig and Knops 2013; Bogdziewicz et al. 2017*a*; Fernández-Martínez et al. 2017*b*). Reproductive synchrony can also be created by an environmental veto, in which seeding failure is caused by weather events. Such a veto could emerge in at least two forms: either as the absence of weather cues that trigger flowering or as a catastrophic weather event that prevents flower or fruit maturation (Rees et al. 2002, Abe et al. 2016, Monks et al. 2016, Pesendorfer et al. 2016, Bogdziewicz et al. 2018). Finally, synchrony among individual plants could be also produced via positive density-dependent pollination efficiency ('pollen coupling'; Satake and Iwasa 2000, Crone et al. 2009, Venner et al. 2016).

Generally, because masting has evolved repeatedly in numerous plant lineages (Pearse et al. 2017; Tanentzap and Monks 2018), it can be a product of different proximate mechanisms in different species. In accordance, depending on the species, seed crop size variation can result from either annual variation in flower production or annual variation in fruit maturation (Pearse et al. 2016, Bogdziewicz et al. 2017b). In the first group of species, flowering is highly variable among years, and large flowering effort usually translates into large seed crops (so called 'flowering masting species', e.g. *Celmisia* sp., *Chionochloa* sp. *Fagus sylvatica*, *F. crenata*, *Nothofagus* sp., *Pinus albicaulis*; Kelly et al. 2013, Rapp et al. 2013, Abe et al. 2016,

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Bogdziewicz et al. 2017b). In such species, it appears plausible that variable flowering synchronizes plant reproduction through positive density-dependent pollination efficiency (pollen coupling), although an environmental veto in the form of lack of a needed weather cue could also synchronize reproduction (Rees et al. 2002). In the second group of species, flower production is relatively constant across years. In this case, the flower to fruit transition generates variation among years in fruit crop (so called 'fruit maturation masting', e.g. *Quercus robur*, *Q. alba*, *Q. ilex*; Sork et al. 1993, Espelta et al. 2008, Pérez-Ramos et al. 2010, Pearse et al. 2015; but see Schermer et al. 2019). Thus, density-dependence of pollination efficiency is unlikely to play major synchronizing role, and masting is more likely be driven by an intermittent environmental veto (Bogdziewicz et al. 2018).

According to contrasting life history characteristics as outlined above, species should differ in the mechanisms that allow them to synchronize their reproduction depending whether they are ‘flowering masting’ or ‘fruit maturation masting’. In this study, we selected four tree species that can be broadly categorized into these two groups: two flowering masting species, *Sorbus aucuparia* (204 individuals, 17 years, Poland), and *Pinus albicaulis* (192 individuals, 25 years, USA), and two fruit maturation masting oak species, *Quercus ilex* (255 individuals, 12 years, Spain) and *Q. humilis* (255 individuals, 12 years, Spain). We hypothesized that these species should differ in the mechanisms that allow them to synchronize their reproduction. Specifically, in oaks fruit density is largely driven by variable ripening of a much more constant flower crop (Espelta et al. 2008; Pearse et al. 2016). Therefore, we hypothesized that masting should be a consequence of endogenous resource feedback (as predicted by the RB model) and reproductive failure (veto) synchronized among individuals. In the other two species (*S. aucuparia*, *P. albicaulis*) flowering is highly variable among years (Żywiec et al. 2012; Rapp et

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al. 2013). Therefore, we hypothesized that the endogenous resource feedback together with pollen coupling should drive masting in these species, while vetoes might be less frequent and less important. Of course, as environmental vetoes can affect both flowering and fruiting, independently of flowering, they are likely to occur in both masting groups.

Our study involved the following steps. First, we characterized seed production of each species by calculating the masting metrics that describe the species-specific reproductive patterns (Koenig et al. 2003; Crone et al. 2011). Second, we reconstructed each tree's deviations from equilibrium energy budget using Rees et al.'s (2002) regression technique, and used these to estimate the RB model parameters using zero-inflated negative binomial models to separate environmental veto and lack of stored resources as causes of seed failure (Bogdziewicz et al. 2018). We then parametrized RB models for each species and ran the models to simulate seed production over time and compared the simulated time series to the ones observed in the field.

Methods

Field studies of reproduction

Seed production was monitored for individual trees by either counting seeds on the branches (*Q. ilex* and *Q. humilis*), or on the whole crown (*S. aucuparia*), or reconstructing the cone production from reproductive scars (*P. albicaulis*). We monitored acorn production for 255 trees of each of the *Quercus* species at 17 sites (15 trees per site) from 1998 to 2009. We monitored fruit production for 204 *S. aucuparia* trees at one large site (2000-2016). We reconstructed *P. albicaulis* cone bearing from cone scars for 240 trees across 36 sites, and the length of the reconstructed time series varied from 7 to 42 years (median = 20 years; see Crone et al. 2011). In this analysis we used only the last 25 years of data, as it provided the most complete

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record. We also included only site-years that had at least 5 observations. The data presented is deposited at Dryad Digital Repository (Bogdziewicz 2019, doi:10.5061/dryad.f9s73ms).A detailed description of ecology of reproduction of studied species, sites, and field procedures is given in the Online Appendix. Past studies have indicated that mast seeding provides a fitness advantage (enhanced pollination efficiency, lowered seed predation, or both) for all studied species (see Online Appendix for details).

We described seed production using three metrics of variation and synchrony, widely used in studies of mast seeding: variability of seed production of individuals (coefficient of variation, CVi), population-level variability of seed production (CVp), and synchrony of seed production by plants (S), as measured by the average pairwise correlation of seed production of individual plants in a population through time.

Resource budget model and its empirical parameters

We based our analysis on the RB model (Isagi et al. 1997; Satake and Iwasa 2000; Abe et al. 2016). In short, the model assumes that an individual plant flowers depending on whether it reaches a resource threshold ($D_{i,t} \leq C$ for not flowering, $D_{i,t} > C$ for flowering plants, where C is the minimum resource threshold needed for reproduction, D_t is the amount of the internal resources of plant i in year t, and each plant i gains resources $P_{i,t}$ in year t). Once the threshold is reached, reproduction is initiated and a plant allocates an amount of resources proportional to the excess into flowering, which depletes resources by an amount $A(D_{i,t} - C)$. Here, A is the resource cost of reproduction (the depletion coefficient, i.e. a multiplier that determines how strongly the resources are depleted). If seed production and resource depletion depend on the number of flowering plants, i.e. pollination efficiency is density-dependent (pollen coupling),

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resource depletion becomes $A f_t^{\beta} (D_{i,t} - C)$, where f_t is the proportion of flowering plants in a population in a year t (as a surrogate of pollen availability), and β scales the strength of pollen coupling. This model predicts annual seed production by individual plants for $A < 2$, and supra-annual seed production (even in a constant environment) by individual plants when $A \geq 2$ (Satake and Iwasa 2000).

The RB model can be extended with an environmental veto. A veto prevents reproduction despite available resources; $\theta_{i,t}$ is the probability that environmental conditions in year t will prevent seed production in a plant, and $E_{i,t}$ (a threshold value) is a random number uniformly distributed between 0 and 1 (Abe et al. 2016, Bogdziewicz et al. 2018). We also added b as a coefficient allowing for a small amount of seed production regardless of resource state (cf. Rees et al. 2002), added to increase both statistical feasibility (see Crone et al. 2005, Bogdziewicz et al. 2018), and biological realism (see Pearse et al. 2016). These assumptions lead to the following model, where all parameters are defined above:

$$D_{i,t+1} = \begin{cases} D_{i,t} + P_{i,t} & \text{if } E_{i,t} \leq \theta_{i,t} \\ D_{i,t} + P_{i,t} - A f_t^{\beta} b & \text{if } D_{i,t} \leq C \text{ and } E_{i,t} > \theta_{i,t} \\ D_{i,t} + P_{i,t} - A f_t^{\beta} \left(D_{i,t} - C + b\right) & \text{if } D_{i,t} > C \text{ and } E_{i,t} > \theta_{i,t} \end{cases} \qquad \text{eq. (1)}$$

(The decline of resources above the threshold, C, occurs because of seed production, as described in eq. 2, below)

We first reconstruct each plant's stored resources in each year from seed production data using Rees et al.'s (2002) method that allows internal resource dynamics to be estimated from time series of reproductive effort and resource gain without directly measuring a plant's energy stores. In short, they rearranged the RB model (Isagi et al. 1997; Satake and Iwasa 2000) in terms

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of deviations from an equilibrium energy budget of a plant, and showed that $D_{i,t}$ are residuals from the regression of cumulative reproduction vs. cumulative energy gain (Rees et al. 2002, see also Appendix A in Crone et al. 2005). Following their procedures, we fitted a linear model with cumulative reproduction (summed seed count) as a response and cumulative years (a surrogate of resource acquisition over time) as a predictor (Rees et al. 2002). We fitted linear mixed models (LMMs) implemented via 'lme4' package with a Gaussian family error term (Bates et al. 2014), separately for each species. We used tree ID as a random intercept and year as a random slope. The random intercept is an estimate of stored resources in a plant at the beginning of the study (Rees et al. 2002), which is likely to differ among plants. The random slope allowed heterogeneous resource acquisition of individuals over time, which is likely to differ among individuals due to, e.g. differences in size or age (Crone et al. 2005). Negative residuals of these GLMMs are an estimate of stored resources of each individual plant has in each year, while positive residuals indicate depleted energy stores (Rees et al. 2002, Crone et al. 2005, Bogdziewicz et al. 2018).

Next, to estimate depletion coefficient, β (pollen coupling) and θ_t (veto), we analyzed seed production by each individual tree in each year, as a function of its estimated stored resources and the proportion of plants producing seeds in each study site (Crone et al. 2005, Bogdziewicz et al. 2018). To incorporate the possibility of seed failure (veto), we used zero-inflated negative binomial (ZINB) mixture models implemented via '*glmmTMB*' package (Brooks et al. 2017). Following Bogdziewicz et al. (2018), we rearranged the RB model to predict seed production dynamics, $S_{i,t+1}$, as a function of stored resources, $D_{i,t}$:

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$$S_{i,t+1} = \begin{cases} 0 & \text{if } E_{i,t} \leq \theta_t \\ A f_t^{\beta} b & \text{if } D_{i,t} \leq C \text{ and } E_{i,t} > \theta_t \\ A f_t^{\beta}\left(D_{i,t} - C + b\right) & \text{if } D_{i,t} > C \text{ and } E_{i,t} > \theta_t \end{cases} \qquad \text{eq. (2)}$$

As explained by Bogdziewicz et al (2018), these parameters can be estimated using a ZINB model, where θ_t is the probability of a "true" zero (veto) in year *t* (the subscripts in θ differ between eq. 1 and 2, as in ZINB models we only estimate failure probabilities for each year, but not for each plant and year). The first condition $E_{i,t} \leq \theta_t$ describes the logit part of the ZINB model, where θ_t is the probability that a plant fails to reproduce regardless of whether resources are available. The second and third lines of eq. (2) describe seed production when the veto does not occur, and create a piecewise "hockey stick" relationship between seed production and stored resources (Rees et al. 2002), with an inflection point at $D_{i,t} = C$ and slope and intercept proportional to $A f_t^{\beta}$. To illustrate the relationship between the piecewise linear regression and the log-link count term of a ZINB model, we transform the dynamics to a log scale:

$$\ln[S_t] = \ln[A] + \beta \ln[f_t] + \ln\left[R_{i,t}\right] \qquad \text{eq. (4)}$$

where

$$R_{i,t} = \begin{cases} b & \text{if } D_{i,t} \leq C \\ D_{i,t} - C + b & \text{if } D_{i,t} > C \end{cases} \qquad \text{eq. (5)}$$

From eq. (4), the intercept term for the count part of a ZINB model is an estimate of $\ln[A]$, and the slope with respect to $\ln[f_t]$ (proportion of reproducing plants in the population) is an estimate of β. Direct proportionality between seed set and stored resources is modeled by first, calculating stored resources for each plant in each year from $D_{i,t}$ (following Rees et al. 2002, see above) and, second, including this estimate of resources in the ZINB model as an offset. This relationship makes eq. 2 a generalized case of the regression technique used by Rees

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et al. (2002) for models without environmental veto. Eq. (2) is equivalent to the model used by Rees et al. (2002) if $\theta_t = 0$ (for all t) and $\beta = 0$. In practice, we implemented these models by searching over possible values of C and b using a grid search, finding ML values for other parameters using the *glmmTMB* package (Brooks et al. 2017), and choosing the combination of parameters (including C and b) with the highest overall likelihood. Possible ranges of C and b values were identified by inspecting the scatterplots of seed production vs. estimated resources, and by visually inspecting likelihood surfaces to ensure fitted estimates were not at the minimum or maximum of the range searched.

For each species, we explored five model structures representing different hypotheses about environmental correlation and pollen coupling. These included following models, summarized in Table 1: 1) pollen coupling, 2) pollen coupling and correlated seed failure (veto), 3) pollen coupling and uncorrelated seed failure, 4) veto, and 5) null model. To estimate pollen coupling, we included ln[f_t] (proportion of reproductive individuals) in the count part of the model. To include correlated seed failure (veto), we made the logit part of the ZINB model a function of year (included as a categorical variable to estimate the proportion of plants with seed failure in each year). Uncorrelated seed failure was modeled as a constant average probability that a tree would experience seed failure in any given year. In three out of four species, site was included as random effect in the model (except *S. aucuparia*, where fruit production was monitored on one site). We followed an information-theoretic (based on AIC) approach to identify the most parsimonious models for each species (Burnham and Anderson 2003).

In case of *P. albicaulis* cones take two years to mature (see Online Appendix: *Reproductive ecology of model trees and study sites*). Thus, in this species we also fit models using a modified RB model in which seed production in one year is determined by resource

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status at the end of the previous year. We compared these two types of models with AIC, because it is not clear at which stage of seed development cycle the resource status of a plant determines investment into seeds (Allen et al. 2017; Bogdziewicz et al. 2018). For the lagged model, we aligned estimates of resource status from the GLMM step of the analysis at the start of year *t-1* with cone production at the end of year *t* for use in ZINB models (as opposed to aligning resource status at the start of year *t* with cone production at the end of year *t*).Parameters of RB models were similar to these of unlagged models, so we present only the unlagged ones though the paper (see Table A2 in Online Appendix for the parameters of lagged models).

The ZINB model differs subtly from the Rees et al. (2002) and Crone et al. (2005) approaches in that it uses a log-link function and negative binomial distribution, rather than a normal distribution. For comparison we show parameter estimates fit using the exact models used by Rees et al. (2002) and Crone et al. (2005), along with the analogous variants of our models in the online Appendix (Table A3). Furthermore, including proportion of seeding plants as a surrogate of pollen availability is possibly an underestimation, since some plants that flower may eventually not produce seeds, which is especially plausible in years of low seed production. We compared inference from above-described models to ones where proportion of reproduction plants was rescaled to be larger, especially at low densities (see Online Appendix for the details). Note that this supplemental analysis is highly preliminary, because the true relationship between proportion of flowering plants and seeding plants is unknown.

Simulations of seed production

We used RB parameters estimated for the highest AIC-scoring model to simulate time series of seed/cone production for populations of each species. For all four species, estimated

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depletion coefficients (*A*) were below 2 (see *Results*), which according mathematical analysis (Satake & Iwasa, 2000; Satake & Iwasa, 2002b) suggests that endogenous resource dynamics does not contribute to seeding dynamics in focal populations. Thus, to determine whether endogenous resource dynamics and different synchronizing mechanisms contribute to the observed seeding pattern, we conducted six simulations for each species. This included seed production based on: 1) correlated variation in resource gain, 2) correlated seed failure (veto), 3) correlated variation in resource gain and veto, 4) correlated variation in resource gain and pollen coupling, 5) correlated variation in resource gain, veto, and pollen coupling, 6) all three mechanisms and endogenous resource dynamics (summarized in Table 2B). The scenarios were narrowed down to include the biologically plausible ones, while some were ruled out a priori, e.g., we did not explore pollen coupling only because estimated parameters fell in the non-periodic region of parameter space (see *Results*). We simulated seed production by populations of 20 trees for 500 years. We used the last 15 steps (years) of each simulation to calculate seed production parameters (CVi, CVp, S; see Field studies of reproduction for metrics definitions). We used the last 15 years of simulations to calculate masting metrics because it is typical of the length of the time series we had for each species, although this choice has negligible influence on the results.

To model annual variation in the environmental veto we calculated the logit-scale mean and standard deviation of the probability of seed failure using the annual estimates of the probability of 0's in the ZINB model. Then, in each year, we first sampled the probability of seed failure for that year, then used a binomial distribution to determine whether each individual tree experienced seed failure. In other words, we first sampled whether failure happened in particular year, and then sampled particular individuals experiencing failure. To model environmental

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stochasticity, we used the variance of the count term (seeds per stored resource) in the ZINB model (see Bogdziewicz et al. 2018 for details). Variations in costs of reproduction and annual resource gain are mathematically confounded in the RB model (Satake & Iwasa, 2002a; Satake, 2004), so this term combines both sources of variation (for simplicity, we call it variation in resource gain throughout the text).

Results

Field studies of reproduction

Time series of all species were generally typical of mast seeding trees (Fig. 1). Three out of four populations had CVp and CVi above 1 (with the exception of *P. albicaulis* where CVp equaled 0.88). Synchrony of individuals within populations (mean pairwise correlation coefficient ± SD) was 0.24 ± 0.14 in *Q. humilis*, 0.38 ± 0.21 in *P. albicaulis*, 0.49 ± 0.15 in *Q. ilex*, and 0.62 ± 0.25 in *S. aucuparia*.

Empirical parameters of resource budget model

Residuals from the LMMs of cumulative seed production through time showed the expected pattern of higher seed production in years following high estimated resources (high negative residuals), with a noticeable threshold for reproduction (break-point in piecewise regression) and evidence of environmental veto (zero's in years when plants had resources above the threshold level; Fig. 2). However, none of the study species had estimated values of A (depletion coefficient) > 2 (range: 0.71 – 1.64; Table 2). That is, no species had parameters suggesting that individual-level seed production would fluctuate endogenously, in the absence of environmental variation.

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For all species, the AIC-best ZINB models of seed production included both correlated seed failure (veto) and density-dependent pollen coupling (Table A1). In this model, the pollen coupling coefficient, β, was highest for *S. aucuparia* followed by *P. albicaulis* and was noticeably lower in both oaks (*Q. ilex* and *Q. humilis*) (Table 2). In contrast, the proportion of years with seed failure was higher for oak species than for the other two species (Table 2, Fig. 3).

Empirically-based models: simulations

Simulations indicated that fluctuations in seed production of all four species reflect correlated seed failure (veto) and stochastic environmental variation in resource gain, but endogenous resource dynamics are not a contributing factor (Fig. 4). In all species, simulated time series with among year variation in resource gain and veto (with or without pollen coupling) reproduced time series with CVp and S similar to observed dynamics (SD's of the metrics overlapped; Fig. 4). In other words, environmental stochasticity together with a strong environmental veto was sufficient to recreate seed production dynamics, while adding further mechanisms (pollen coupling, endogenous resource dynamics) was not necessary (Fig. 4). Both sources of environmental variation (veto and variation in resource gain) were necessary to reproduce dynamics in the studied forest trees. If the veto was excluded, simulations failed to produce sufficient variability and overestimated synchrony. This effect was especially strong in oaks (Fig. 4). Simulations with the veto but no variation in resource gain were sufficient to reproduce observed synchrony, but underpredicted variation in seed production (Fig. 4).

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Discussion

In line with our hypothesis, pollen coupling was stronger in the 'flowering masting' tree species (*S. aucuparia*, *P. albicaulis*) than in 'fruit maturation masting' oaks (*Q. ilex* and *Q. humilis*). Further, also in line with hypothesis, seeding failure was more frequent in oaks than in the other trees. Yet, pollen coupling and endogenous resource feedbacks were not required to produce patterns of seed production in any of the studied species. In all of them, the depletion coefficient estimates were smaller than the threshold value for endogenously generated variation in seed production (Satake and Iwasa 2000). Instead, our simulations suggested that variation in seed production was achieved through having a correlated environmental variation acting together with a strong environmental veto. This result provides empirical support for the notion that environmental variation may induce masting if costs of fruit production are small (Satake and Iwasa 2002); however, our case studies show that this synchronization happens when plants are susceptible to weather events that prevent reproduction in some years. More recent models point to the potentially important role of large environmental stochasticity in driving the phenomenon (Lyles et al. 2009, 2015, Fernández-Martínez et al. 2017a, Noble et al. 2018, Bogdziewicz et al. 2018), though many of these models also include an endogenously cyclical component. Our results suggest that for many masting species, environmental variation and weather vetoes could drive masting. In the past, vetoes like frost events that prevent reproduction have been perceived as negative for plants. In fact, they could be selectively favored as a way to create mast seeding (Dave Kelly, pers. comm.).

Although they are few in number, all of the past studies that used similar methods to ours to estimate costs of reproduction in masting plants reported higher depletion coefficients, with A ranging between 2 and 3 for *Chionochloa pallens* (Poaceae), *Quercus rubra, Q. alba, Fagus*

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crenata (all Fagacae), and *Astragalus scaphoides* (Fabaceae) (Rees et al. 2002, Crone et al. 2005, Abe et al. 2016, Bogdziewicz et al. 2018). As a consequence, in these plant species, the endogenous resource feedbacks were involved in driving reproductive dynamics. In contrast, we were unable to detect effects of endogenous dynamics on seed production in any of our species. One possible mechanism for these differences is that, although the set of species evaluated in past studies is diverse, they were all carefully selected by researchers to be likely candidates for resource budget models, e.g., based on patterns of mast-seeding that were highly consistent with this model. Alternatively, it may be that the models used in past studies were more carefully tuned to the biology of each species, which increased the power of these models to detect endogenous resource dynamics. For example, Rees et al. (2002) included specific veto effects due to a specific temperature threshold, and Crone et al. (2005) included precipitation as a driver of resource gain, as opposed to the phenomenological variance terms in the models we applied to four species in this paper. In any case, generic application of RB models without tuning them to species biology did not reveal strong endogenous components of mast-seeding, and, for our four species, a model of correlated environmental drivers (a strong veto which acts to synchronize the population) was sufficient to predict population-level patterns of seed production.

Past studies on two of our study species, *Q. ilex* and *S. aucuparia,* indicated a paramount role of the current and previous year’s weather conditions on plant resource acquisition and seed production (Żywiec et al. 2012; Fernández-Martínez et al. 2015; Bogdziewicz et al. 2017*a*). This result is consistent with our model-based conclusion that stored resource dynamics are not important for mast-seeding. In contrast, resource depletion following a strong mast event in one of our study species, *P. albicaulis*, was found to impose a replenishment period longer than a year before a subsequent mast event (Sala et al. 2012). Superficially, this result seems

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inconsistent with our model-based conclusions. One possible way to reconcile this discrepancy is that resource depletion in *P. albicaulis* was localized to cone-bearing branches, and a whole-tree depletion is delayed to the following year (Sala et al. 2012). Thus, in years of moderate reproduction, resource depletion may be limited to cone-producing branches, in which case subsequent seed production may occur in branches that did not reproduce the year before, reducing annual variation in reproductive output (Sala et al. 2012). This hypothesis is supported by the low CVp of that population (0.88). If true, resource depletion as estimated in this study would be smaller than the branch-level depletion, highlighting complex resource dynamics and the a need for evaluation of reproductive costs at both the modular (branch) and individual level and over multiple years (Sánchez-Humanes et al. 2011; Sala et al. 2012; Funk 2017). Alternatively, it may be that our power to detect effects of resource depletion in the current model-based study was limited by the noise associated with inferring cone production from counts of scars on a sample of branches, as opposed to direct observation of plant reproduction (e.g. a small fraction of branches was sampled per tree, and aborting cones may leave scars on the branch). Ultimately, while these modelling studies are intriguing, experiments are required to rule out or confirm the role of endogenous resource cycles in driving reproduction.

Studies centered on seeding and weather correlates are often successful in finding consistent links between seed production and weather cues (Piovesan and Adams 2001; Schauber et al. 2002; Kon and Noda 2007; Calama et al. 2011; Ascoli et al. 2017; Vacchiano et al. 2017). However, oaks are an enigmatic exception (Crawley and Long 1995; Koenig and Knops 2014; Pérez-Ramos et al. 2015). In this study, and a previous one applying similar techniques to two eastern North American oak species, *Querucs rubra* and *Q. alba* (Bogdziewicz et al. 2018), we found a high frequency of reproductive failure in oak species. The importance of an

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environmental veto across these species hints why oaks are inconsistent in their links between weather and seeding (Koenig and Knops 2014; Pérez-Ramos et al. 2015). We hypothesize that if correlated resource gain is a primary factor driving reproduction, then weather conditions favoring nutrient acquisition would correlate with seeding (Smaill et al. 2011; Tanentzap et al. 2012), and these correlations will be spatially conserved (Vacchiano et al. 2017), a pattern that has been elusive in oaks. In contrast, if a veto is an important part of the seeding dynamics, then weather links should depend on main constraints of the focal population, which in turn will vary with local conditions (Bogdziewicz et al. 2017*a*). This hypothesis could be tested empirically by comparing spatial organization of weather cues within oak species along climatic gradients (see e.g. Bogdziewicz et al. 2019).

Pollen coupling was stronger in the intermittent flowering species (*S. aucuparia* and *P. albicaulis*) than in oaks (Table 1). This is in line with recent theoretical developments that predict pollination efficiency in oaks to be more dependent on phenological synchrony than on flowering density (Koenig et al. 2015; Bogdziewicz et al. 2017*b*). However, in contrast to our hypothesis and current theory, pollen coupling was not necessary to produce masting in either species. Proximate and ultimate factors are often intertwined in studies of plant reproduction, especially in masting plants (Pearse et al. 2016). Based on our results, we hypothesize that positive density-dependence in pollination efficiency provides fitness advantage for the studied trees (Kelly et al. 2001; Rapp et al. 2013; Moreira et al. 2014), but it is not necessarily involved as a proximate factor.

Interestingly, the strongest positive density-dependence of pollination efficiency was found in animal-pollinated *S. aucuparia*. In animal-pollinated species, high inter-annual variation of flower supply has been considered disadvantageous due to possible pollinator satiation (Herrera

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et al. 1998; Kelly and Sork 2002). However, high flower set may trigger both numerical and functional response of pollinators, which increases the visitation rate and possibly pollen transfer (Crone 2013). Such an effect may be important in our *Sorbus* population, given that several social pollinators are present at our study site (*Apis mellifera*, *Bombus* sp., *Evylaeus* sp.). These pollinators are possibly capable of unlagged numerical increase in years of high flowering intensity (Crone 2013), while other insect-pollinated plant species are scarce in subalpine spruce forest (Holeksa 2003). However, the same set of environmental factors makes high variation in reproduction hazardous – if high seed year is preceded by a failure year, pollinator populations may not be able to respond fast enough, leading to high competition for pollinators (Żywiec et al. 2018).

In closing, environmental variability and environmental vetoes appear to be a crucial driver of reproductive patterns in studied trees. Positive density-dependent pollination efficiency is present in all, and relatively strong in some species, but still not necessarily involved as synchronizing mechanisms. Environmental variation has long been a hypothesis for how reproduction is synchronized among plants (Kelly 1994, Crone and Rapp 2014, Pease et al 2016). Yet, it has been surprisingly difficult to detect in some cases (e.g. in oaks). Our results suggest that detecting this relationship requires thinking beyond simple correlative relationships between environmental drivers and seed production. In particular, we were only able to recreate patterns of observed seed production when we included an environmental veto to operate along with the environmental variation. While our study focused on strong vetoes (i.e. cases when reproduction was completely blocked), we would like to note that other types of weather cues include those that suppress (or promote) reproduction gradually, such as cold (or warm) summers (e.g. Kelly et al. 2013; Monks et al. 2016; Vacchiano et al. 2017). In turn, plants' susceptibility

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to weather vetoes is likely subject to selection as variability and synchrony provides fitness advantage through economies of scale (Pearse et al. 2016). Finally, the resource budget model was so far tested in twelve species, including four tested here (species studied in the past: *Q. rubra, Q. robur*, *Q. alba, Q. lobata, Fagus crenata*, *Chionochloa pallens, Astragalus scaphoides*; Rees et al. 2002, Crone et al. 2005, Abe et al. 2016, Pesendorfer et al. 2016, Bogdziewicz et al. 2018; Schermer et al. 2019). Careful generalization based on that limited sample suggests that endogenous resource feedbacks are often but not always involved, and that environmental vetoes are an important driver of synchronous reproduction in plants.

Acknowledgments

We thank Dave Kelly and Anonymous Reviewers for insightful comments that helped us improve the manuscript, and Dave Kelly for raising the idea that plants susceptibility to weather vetoes is likely subject to selection. MB was supported by (Polish) NSF grant Sonatina no. 2017/24/C/NZ8/00151, MFM was supported by a postdoc subsidy at the University of Antwerp. This study was also funded by the Polish State Committee for Scientific Research (grant nos. 6 P04G 045 21 and 3 P04G 111 25), the Polish Ministry of Science and Higher Education (N304 362938), and the statutory fund of the Institute of Botany of the Polish Academy of Sciences. RC contribution was supported by INIA funded project AT-2013-004 and Spanish National project RTA-2013-00011-C2.1.

Authorship statement: MB designed the study, MB and ECC performed analyses, MŻ, JME, MFM, RC, ML, EM, ECC collected data, and analyzed output data. MB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Appendix: Online Supplement

Methods: Reproductive ecology of model trees and study sites

The evergreen *Quercus ilex* and the winter-deciduous *Q. humilis* (both Fagaceae) are two Mediterranean, wind-pollinated, long-lived (up to >1000 years) oaks. The two species differ in their leaf habit but they share other life-history traits, such as fruit development, pollination, and maturation of acorns in one year. Data on their seed production were collected in Collserola Natural Park (Barcelona, NE Iberian Peninsula). Climate is Mediterranean, with 620 mm of mean annual precipitation and mean monthly temperatures with a maximum of 23.3°C in August and a minimum of 7.9°C in January. In this population, masting helps escape seed predation by insects (Espelta et al. 2008, 2017). Pollination efficiency is driven by phenological synchrony (Bogdziewicz et al. 2017*a*). Drought-induced acorn abortion, and the previous year's acorn production appear to be important determinants of crop size (Espelta et al. 2008; Fernández-Martínez et al. 2015).

Sorbus aucuparia (Rosaceae) is a deciduous fleshy-fruited tree that lives 100–150 years. Flowering and fruit maturation occur within one year. The flowers are pollinated by a wide range of insects. Seed production data were collected in a subalpine old-growth spruce forest on Babia Góra massif (1,725 m a.s.l.) in the Western Carpathians (Poland) at an altitude of 1170–1310 m. The climate is cool with 3.3 °C mean annual temperature, 1,470 mm mean annual rainfall, and a snow-free period of 7 months. In this population, masting helps escape pre-dispersal seed predation (Żywiec et al. 2013). Fruit production strongly correlates with current-year precipitation and previous-year temperature (Żywiec et al. 2012).

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Pinus albicaulis (Pinaceae) is a long-lived (~ 500 years), stress-tolerant tree found in relatively cool climates, usually at high elevations with relatively low rainfall. Cones take two years to develop. The study sites were located at the northern Rocky Mountains (US), ca. 2300 m elevation. Mean annual air temperature is 1.1°C, with mean January and July temperatures of −6.7 and 12.2°C, respectively. Mean total annual precipitation was 572 mm. This species shows evidence of resource depletion following high-seed years (Sala et al. 2012), positive density-dependent pollination efficiency (Rapp et al. 2013), and fitness benefits of mast-seeding through enhanced seed dispersal (McKinney et al. 2009).

Methods: Seed data collection

Quercus ilex and *Q. humilis*

We monitored acorn production from 1998 to 2009 in 17 sampling sites (255 trees, 15 per plot) in holm-oak-dominated forests (mean distance 4.7 + 2.4 km). Trees were tagged and the number of branches per tree was estimated using a regression model between crown projection and number of branches previously constructed for a subsample of trees. We counted acorn production on four branches per tree at the peak of the acorn crop (i.e. September). Then we estimated the total number of acorns produced per tree by multiplying the mean acorn production per branch and the number of branches per tree (Espelta *et al.*, 2008).

S. aucuparia

We demarcated a 27-hectare (564 × 480 m) rectangular plot. All rowan trees in the plot with diameter at least 4 cm were mapped. The analysis used a group of 204 trees, i.e., all trees that

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bore fruits at least once in the studied period. The whole plot is situated within one forest type and sandstone is the only bedrock type. Each year, all trees were searched for fruits at the beginning of September before birds began to feed on them. Fruit production was measured by binocular observations, counting the number of infructescences (corymbs with fruits) on individual trees. For each tree, in five infructescences all fruits were counted. The fruit production of a tree was determined as the product of its number of infructescences and the average number of fruits in five infructescences (Zywiec *et al.*, 2012; Żywiec *et al.*, 2013).

P. albicaulis

We sampled *P. albicaulis* at 36 sites across the northern US Rocky Mountains from 2004 to 2006. We sampled the largest climbable tree we encountered at each site and a subsequent sample of 1–12 of the largest climbable trees along a distance gradient from that first individual out to 5 km distant. Some sites had low sample sizes (< 5 individuals) due to a dearth of live individuals. In each tree, we harvested 2–7 cone-bearing branches and estimated cone production over time by counting cone scars in relation to annual growth constrictions. We verified that two independent observers recorded perfect agreement of estimated years, and ~5% error in the number of cones produced in a given year. We estimated total cone production in each year by counting the total number of cone-bearing branches on each tree, identified by their upright growth form. The estimated cone production per tree was then the product of the average cones per branch and the number of cone-bearing branches (Crone *et al.*, 2011; Rapp *et al.*, 2013).

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Results: Model selection tables for the zero-inflated negative binomial models of seed production in focal trees.

Table A1. Model selection tables for the ZINB models. Models are ranked according to the AIC value; logLik – log-likelihood; AIC – Akaike's information criterion adjusted for small sample size; ΔAIC = AIC_i – minAIC. Pollen coupling is represented by the log(proportion of reproducing plants in the population), correlated seed failure was included as a function of year in the logit part of the model.

a) *Q. ilex*

Model	**d.f.**	**logLik**	**AIC**	**ΔAIC**
Pollen coupling + correlated seed failure (veto)	15	-9089.95	18209.92	0
Correlated seed failure (veto)	14	-9131.31	18290.63	80.7
Pollen coupling + uncorrelated seed failure	5	-9540.62	19091.26	881.5
Pollen coupling	4	-9889.54	19787.09	1577.2
Null model	2	-10078.90	20161.80	1951.2

b) Q. humilis

Model	**d.f.**	**logLik**	**AIC**	**ΔAIC**
Pollen coupling + correlated seed failure (veto)	15	-6571.32	13172.64	0
Correlated seed failure (veto)	14	-6590.06	13208.13	35.5
Pollen coupling + uncorrelated seed failure	5	-6754.30	13518.60	346.0
Pollen coupling	4	-7081.23	14170.48	997.8
Null model	2	-7170.75	14345.51	1172.9

c) *S. aucuparia*

Model	**d.f.**	**logLik**	**AIC**	**ΔAIC**
Pollen coupling + correlated seed failure (veto)	18	-19799.22	39634.45	0
Correlated seed failure (veto)	17	-20100.30	40234.69	600.2
Pollen coupling + uncorrelated seed failure	4	-20305.74	40619.48	985.0

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Pollen coupling	3	-20401.13	40808.27	1173.8
Null model	2	-21121.69	42247.37	2612.9

d) *P. albicaulis*

Model	**d.f.**	**logLik**	**AIC**	**ΔAIC**
Pollen coupling + correlated seed failure (veto)	26	-5666.80	11385.61	0
Correlated seed failure (veto)	25	-5766.80	11583.60	198.0
Pollen coupling + uncorrelated seed failure	5	-5812.33	11634.66	249.0
Pollen coupling	4	-5865.52	11739.05	353.4
Null model	2	-6228.90	12461.81	1076.2

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Resource budget model parameters estimated for the lagged model for *P. albicaulis*.

Parameter estimation of the lagged model for pines

Because *P. albicaulis* develops cones one year before fertilization, we also fit models to this species using a modified RB model in which seed production in one year is determined by resource status at the end of the previous year. To build these models, we aligned estimates of resource status from the GLMM step of the analysis at the start of year *t-1* with acorn production at the end of year *t* for use in ZINB models (as opposed to aligning resource status at the start of year *t* with acorn production at the end of year *t*). This change corresponds to the following mechanistic model, where all parameters are as in the main text:

$$\ln[S_{t+1}] = \ln\left[Af_t^{\beta}R_{i,t}\right] = \ln[A] + \beta\ln[f_t] + \ln\left[R_{i,t}\right]$$

$$R_{i,t} = \begin{cases} b & \text{if } D_{i,t} \leq C \\ D_{i,t-1} - C + b & \text{if } D_{i,t} > C \end{cases}$$

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Resource budget parameters for the lagged models for pines

Table A2. Resource budget model parameter estimates based on the highest AIC-ranked **lagged** models of seed production in *P. albicaulis*. The best AIC ranked models were these including pollen coupling and correlated reproductive failure (veto), similarly as un-lagged models (see main text for details on hypothesis testing). ΔAIC of the second-best model was 236.2 (model selection tables not shown).

Model type	**1: Depletion coefficient, A (± 95%CI)**	**2: Pollen coupling, *β* (SE)**	**3: Average proportion of years with no reproduction**	**4: Among-year variation in seed failure (logit-scale)**	**5: Among-year variation in resource gain (1/θ)**	**6: Average seed production (SD)**	**7: reproduction below threshold *b***	**8: resource threshold for reproduction *C***
Unlagged	0.71 (0.65 – 0.75)	0.80 (0.06)	0.21	1.38	0.37 (0.31 – 0.43)	2.84 (1.70)	5.5	0.5
Lagged	0.41 (0.35 – 0.49)	1.02 (0.06)	0.24	1.42	0.40 (0.34 – 0.47)	2.93 (1.78)	11	-1.0

1: Back-transformed (exp()) intercept for count term in ZINB model. 2: slope of ln(seed production) vs. ln(proportion plants flowering) for count term in ZINB model. 3: Average proportion of 0 years in ZINB model. 4: SD of year-specific coefficients for the proportion of 0 years in the ZINB model. 6: Calculated by first averaging within all trees of the focal species, and then taking mean of that average (this parameter was obtained from the data, not from the model). 7: Reproduction below the threshold for count term in the ZINB model (estimated as part of an offset term). 8: Break-point in piecewise regression for count term in the ZINB model.

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Comparison of parameter estimates fit using the exact model used by Rees et al. (2002) and Crone et al. (2005), along with the analogous variants of our model.

Table A3. Comparison of the depletion coefficient (a) and pollen coupling (b) estimated with the ZINB-based method (current paper) and with the piecewise linear regression of seed production vs. estimated resources (Rees et al. 2002, Crone et al. 2005). In the latter method, the depletion coefficient *A* is a slope of regression of seed count vs. estimated resources after the break-point (see Rees et al. 2002, Crone et al. 2005 for details). While pollen coupling *β* is estimated with a piecewise linear regression models, where seed production is both resource and pollen limited, i.e. with seed production above the resource threshold dependent on both stored resources and the proportion of flowering plants at each site in each year.

a) Depletion coefficient

Species	**Piecewise linear regression estimates of *A* (SE)**	**ZINB estimate of *A* (SE)**
Q. ilex	1.83 (0.03)	1.64 (0.12)
Q. humilis	1.47 (0.04)	1.67 (0.12)
S. aucuparia	1.05 (0.04)	1.10 (0.03)
P. albicaulis	0.74 (0.03)	0.71 (0.05)

b) Pollen coupling

Species	**Piecewise linear regression estimates of *β***	**ZINB estimate of *β***
Q. ilex	0.35 (0.02)	0.64 (0.06)
Q. humilis	0.07 (0.03)	0.45 (0.06)
S. aucuparia	0.61 (0.03)	3.35 (0.08)
P. albicaulis	0.27 (0.04)	0.80 (0.06)

* In this method, pollen coupling coefficients are lower than in ZINB estimates, especially in case of flowering masting species (*S. aucuparia* and *P. albicaulis*). It is because in these species far larger proportion of 0 seed (failure) years was caused by lack of resources than by environmental veto (in contrast to oaks, where veto is much more frequent, cf. Table 1). ZINB

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models excluded these 0s in the estimation of β (through including estimated resources as an offset), so β was no longer biased by such observations.

Underestimated proportion of flowering plants.

In the ZINB models we used proportion of seeding plants as a surrogate for proportion of flowering plants f_t to estimate the density-dependence of seed production (pollen coupling). It is possibly an underestimation as some plants that flower may not produce seeds.

To explore this, we first rescaled the proportion of seeding plants using the formula:

$$sf_t = f_t + \left(0.5 - \left(\frac{f_t}{1 + f_t}\right)\right)$$

[Figure A1 goes here]

Next, we refitted ZINB models for each species (cf. Table A1) using the rescaled proportion of reproducing individuals as independent variable in the count part of the models. In all cases, the AIC model selection tables were virtually the same as in the original analysis (cf. Table A1 and A4). We note, however, that the while we explored this one possible alternative scenario, the true relationship between proportion of reproducing individuals and proportion of flowering plants is unknown, and this exercise does not provide ultimate solution to this problem.

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Table A4. Model selection tables for the ZINB models with re-scaled proportion of reproducing individuals. Models are ranked according to the AIC value; logLik – log-likelihood; AIC – Akaike's information criterion adjusted for small sample size; ΔAIC = AIC$_i$ – minAIC.

a) *Q. ilex*

Model	d.f.	logLik	AIC	ΔAIC
Pollen coupling + correlated seed failure (veto)	15	-8999	18030.5	0
Correlated seed failure (veto)	14	-9135	19059.2	267.8
Pollen coupling + uncorrelated seed failure	5	-9524	19815.9	1028.7
Pollen coupling	4	-9903	18298.3	1785.5
Null model	2	-10078	20161.8	2131.3

b) *Q. humilis*

Model	d.f.	logLik	AIC	ΔAIC
Pollen coupling + correlated seed failure (veto)	15	-6571	13172.6	0
Correlated seed failure (veto)	14	-6590	13208.1	35.5
Pollen coupling + uncorrelated seed failure	5	-6754	13518.6	346.0
Pollen coupling	4	-7081	14170.5	997.8
Null model	2	-7170	14345.5	1172.9

c) *S. aucuparia*

Model	d.f.	logLik	AIC	ΔAIC
Pollen coupling + correlated seed failure (veto)	18	-19766	39569.4	0
Correlated seed failure (veto)	17	-20104	40241.8	672.4
Pollen coupling + uncorrelated seed failure	4	-20374	40757.8	1188.3
Pollen coupling	3	-20454	40914.8	1345.3
Null model	2	-21121	42247.4	2677.9

d) *P. albicaulis*

Model	d.f.	logLik	AIC	ΔAIC

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Pollen coupling + correlated seed failure (veto)	26	-5766	11583.6	0
Correlated seed failure (veto)	25	-5795	11601.7	18.1
Pollen coupling + uncorrelated seed failure	5	-5837	11682.5	98.4
Pollen coupling	4	-6228	12461.8	878.2
Null model	2	-7262	14557.8	2974.2

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Tables

Table 1. Models for fitting time series data for seed production by individual trees to different combinations of proximate drivers of masting. Each model included individual seed production as a response and estimated individual plant resource state as an offset. ZINB – zero inflated negative binomial model; f_t - proportion of reproductive individuals

Possible proximate drivers of masting (i.e. RB model parameters estimated)	**Model structure**		
	Model type	Count part	Logit part
Pollen coupling	negative binomial GLMM*	$\ln[f_t]$	no zero-inflation
Pollen coupling + correlated seed failure (veto)	ZINB	$\ln[f_t]$	year as a categorical predictor
Pollen coupling + uncorrelated seed failure	ZINB	$\ln[f_t]$	one constant zero term
Veto	ZINB	intercept only	year as a categorical predictor
Null	negative binomial GLMM*	intercept only	no zero-inflation

*except in *S. aucuparia* where we used GLM as the species was monitored on one large site, for the other three species site was included as random effect

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Table 2. Estimated parameters of the resource budget model for each species (A) and proximate mechanisms included in each simulation (B).

A) Resource budget model parameter estimates based on the highest AIC-ranked (cf. Table A1) models of seed production in studied species.

Species	**1: Depletion coefficient, A (± 95%CI)**	**2: Pollen coupling, *β* (SE)**	**3: Average proportion of years with no reproduction (± 95%CI)**	**4: Among-year variation in seed failure (logit-scale) (± 95%CI)**	**5: Among-year variation in resource gain (1/θ) (± 95%CI)**	**6: Average seed production (± 95%CI)**	**7: reproduction below threshold *b***	**8: resource threshold for reproduction on *C***
Q. ilex	1.64 (1.40 - 1.91)	0.64 (0.06)	0.59 (0.53 – 0.67)	1.68 (1.23 – 2.64)	1.07 (0.99 – 1.16)	376.1 (303.0 – 449.2)	251	100
Q. humilis	1.67 (1.38 - 1.95)	0.45 (0.06)	0.56 (0.51 – 0.65)	1.08 (0.79 – 1.70)	0.89 (0.81 – 0.98)	161.4 (115.0 – 206.9)	101	50
S. aucuparia	1.10 (1.03 - 1.16)	3.35 (0.08)	0.08 (0.06 – 0.42)	4.14 (3.03 – 6.52)	1.85 (1.74 – 1.96)	2424.3 (2055.1 – 2793.6)	1700	601
P. albicaulis	0.71 (0.65 - 0.75)	0.80 (0.06)	0.21 (0.12 – 0.27)	1.38 (1.01 – 2.17)	0.37 (0.31 – 0.43)	2.84 (2.60 – 3.09)	5.5	0.5

1: Back-transformed (exp()) intercept for count term in ZINB model. 2: slope of ln(seed production) vs. ln(proportion plants flowering) for count term in ZINB model. 3: Average proportion of 0 years in ZINB model. 4: SD of year-specific coefficients for the proportion of 0 years in the ZINB model. 6: Calculated by first averaging within all trees of the focal species, and then taking mean of that average (this parameter was obtained from the data, not from the model). 7: Reproduction below the threshold for count term in the ZINB model (estimated as part of an offset term). 8: Break-point in piecewise regression for count term in the ZINB model.

B) Simulations*

Proximate mechanism	**RB parameters included (cf. Table 2A)**
Correlated variation in resource gain	5, 6, 7, 8
Veto	3, 4, 6, 7, 8
Correlated variation in resource gain and veto	3, 4, 5, 6, 7, 8
Correlated variation in resource gain and pollen coupling	2, 5, 6, 7, 8
Correlated variation in resource gain, veto, and pollen coupling	2, 3, 4, 5, 6, 7, 8
Correlated variation in resource gain, veto, pollen coupling, and endogenous resource feedback	1, 2, 3, 4, 5, 7, 8

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*Parameters not included in the simulation were set to 0, with the exception that the depletion coefficient was not included in simulations without resource feedback (baseline seed production was based on the population long-term mean)

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Figure Legends

Figure 1. Field measurements of seed production time series in the studied species. Each line represents one tree. The CVp (coefficient of variation) of the studied population were: *Q. ilex* 1.47, *Q. humilis* 1.12, *S. aucuparia* 1.49, *P. albicaulis* 0.88.

Figure 2. Seed production in studied trees as a function of estimated stored resources. Solid lines indicate estimates obtained from ZINB model with pollen coupling and correlated seed production failure, and dashed lines indicate correlated reproduction failure only. Models with higher slope fit the data better (cf. Table A1), which indicates higher per resource seed production with increasing number of reproducing individuals within population (positive-density dependent pollination efficiency). Size of dots is scaled to the number of trees reproducing at a given site in a given year.

Figure 3. Population-level proportions of reproductive failures in studied species estimated with ZINB models.

Figure 4. Masting metrics for simulated seed production dynamics. All simulations were based on resource budget model parameters (cf. Table 2) derived from best AIC-scoring ZINB model for each species (cf. Table A1). ‘EV’ indicate simulations based only on correlated environmental variation in resource gain. “Veto” indicates simulations with only correlated seed failure included as a dynamic’s driver. ‘EV + Veto’ indicates simulations based on both sources of environmental variation. “EV + PC” indicates simulations based on environmental variation in resource gain and pollen coupling. ‘EV + Veto + PC’ indicated simulation based on all these mechanisms. ‘Full + RsF’ includes the full model (EV + Veto + PC) with endogenous resource dynamics. CVp is the population-level, CVi individual-level coefficient of variation of seed production; S is synchrony (cross-correlation among individual plants across years). Dots represent means, while whiskers standard deviations. Horizontal dashed lines show the metrics means for the field populations, while the shaded areas SDs of that means. Different colors indicate simulations based on different set of drivers.

Figure A1. The relationship between proportion of seed producing plants (data-derived variable) and the rescaled proportion based on the equitation above. Black line is the proportion of seeding plants vs. proportion of seeding plants (original variable), while red line is the rescaled proportion of seeding plants vs. the original variable.

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Figure 1

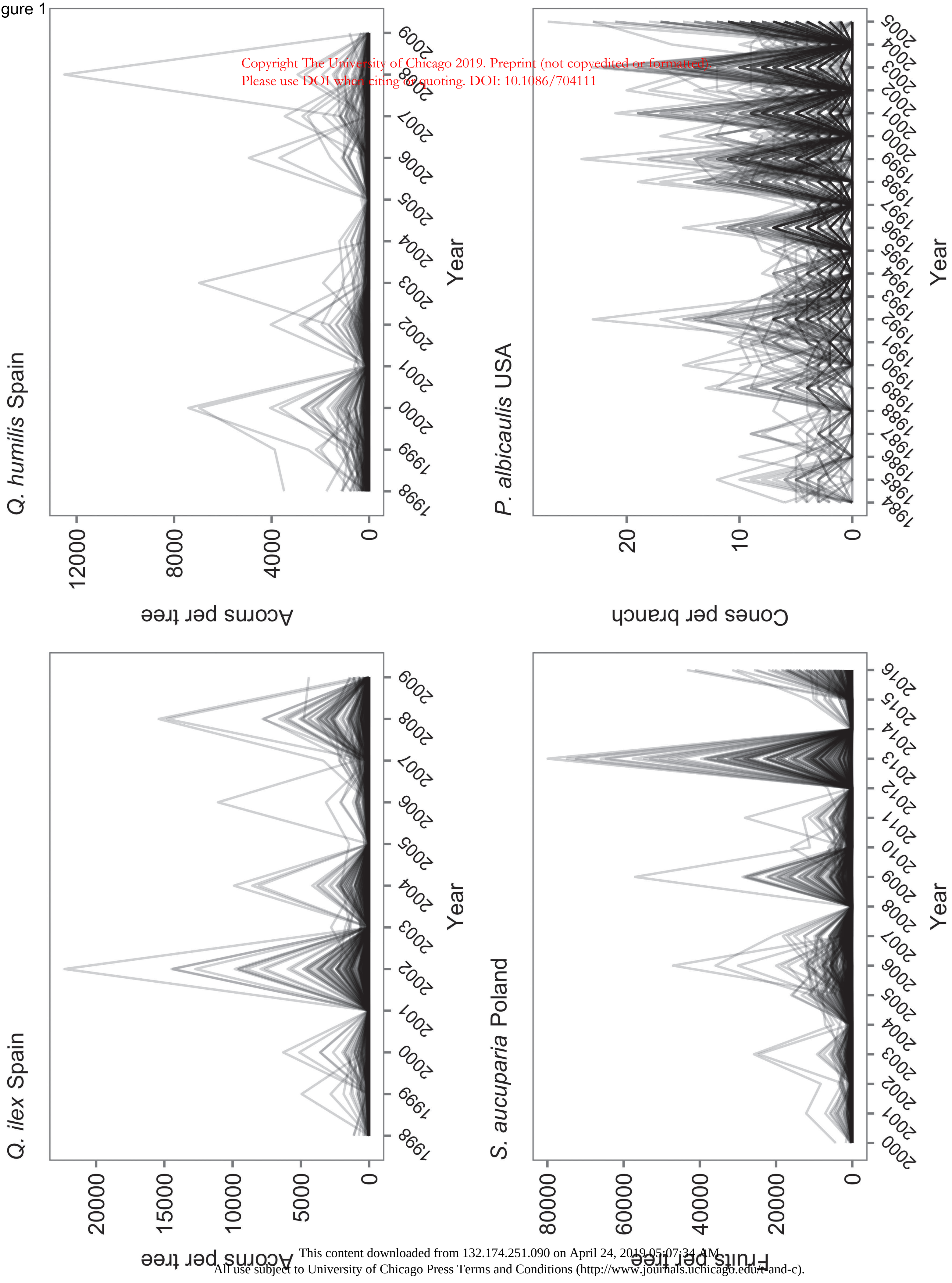

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Figure 2

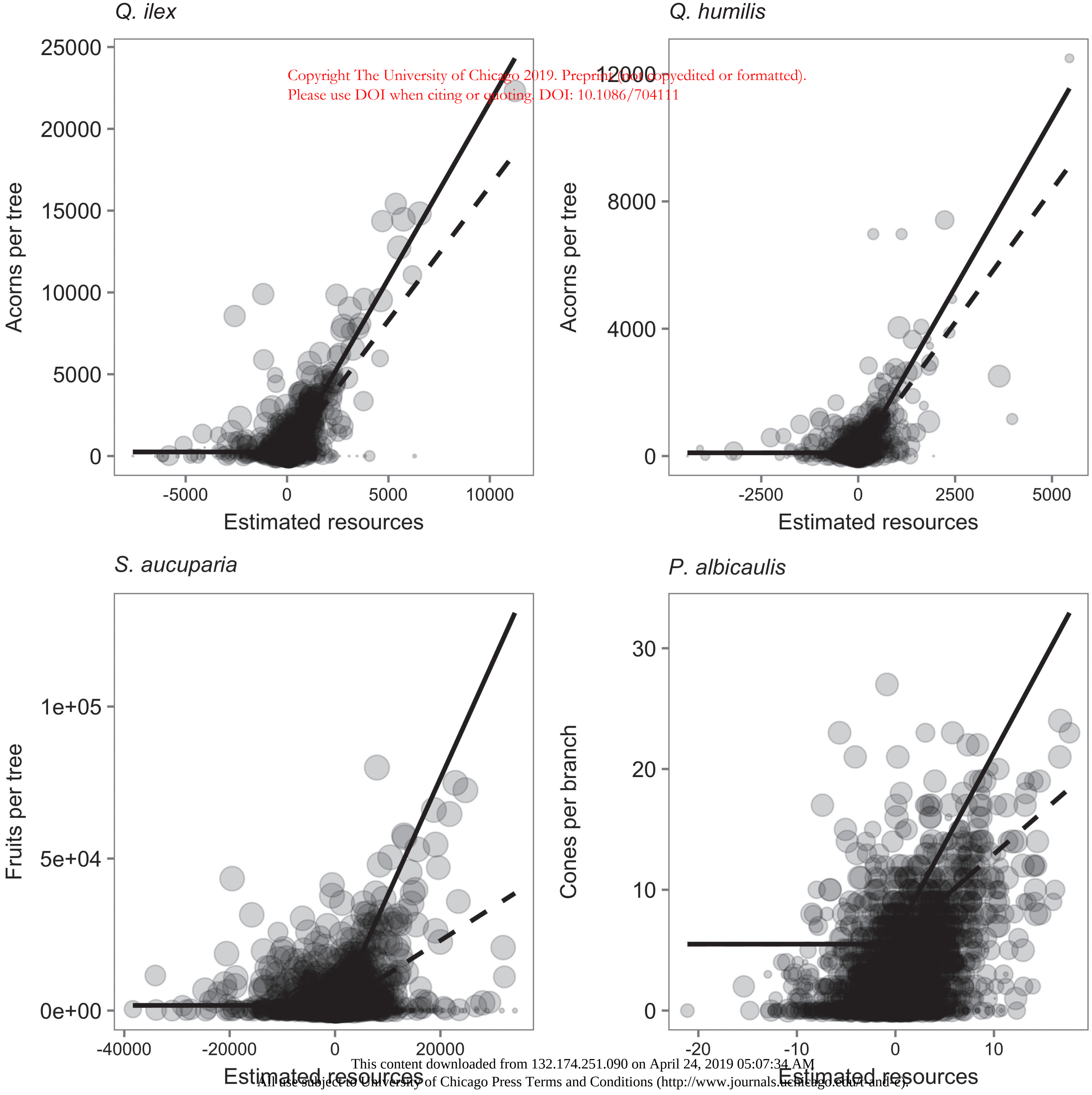

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Figure 3

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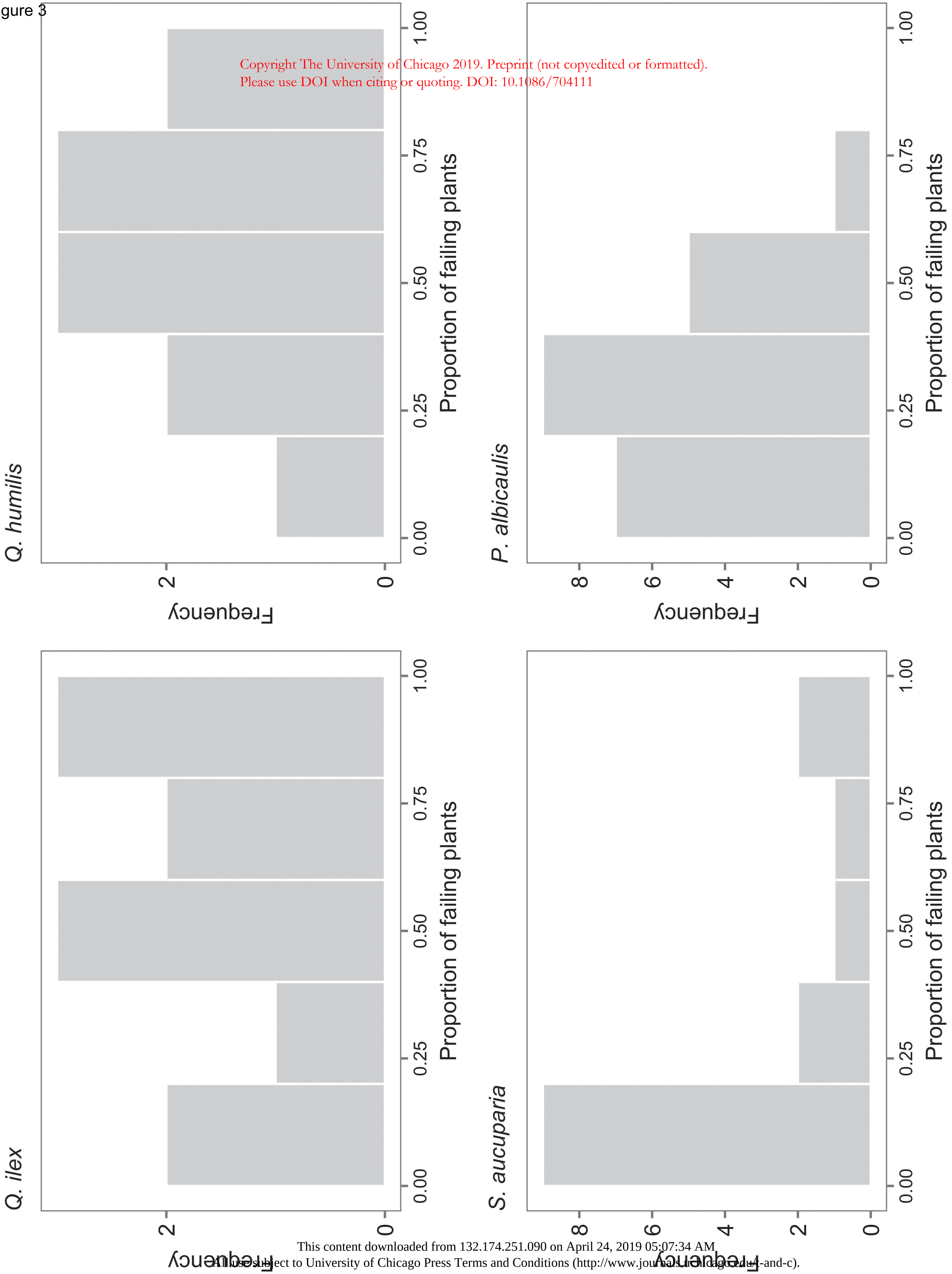

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Figure 4

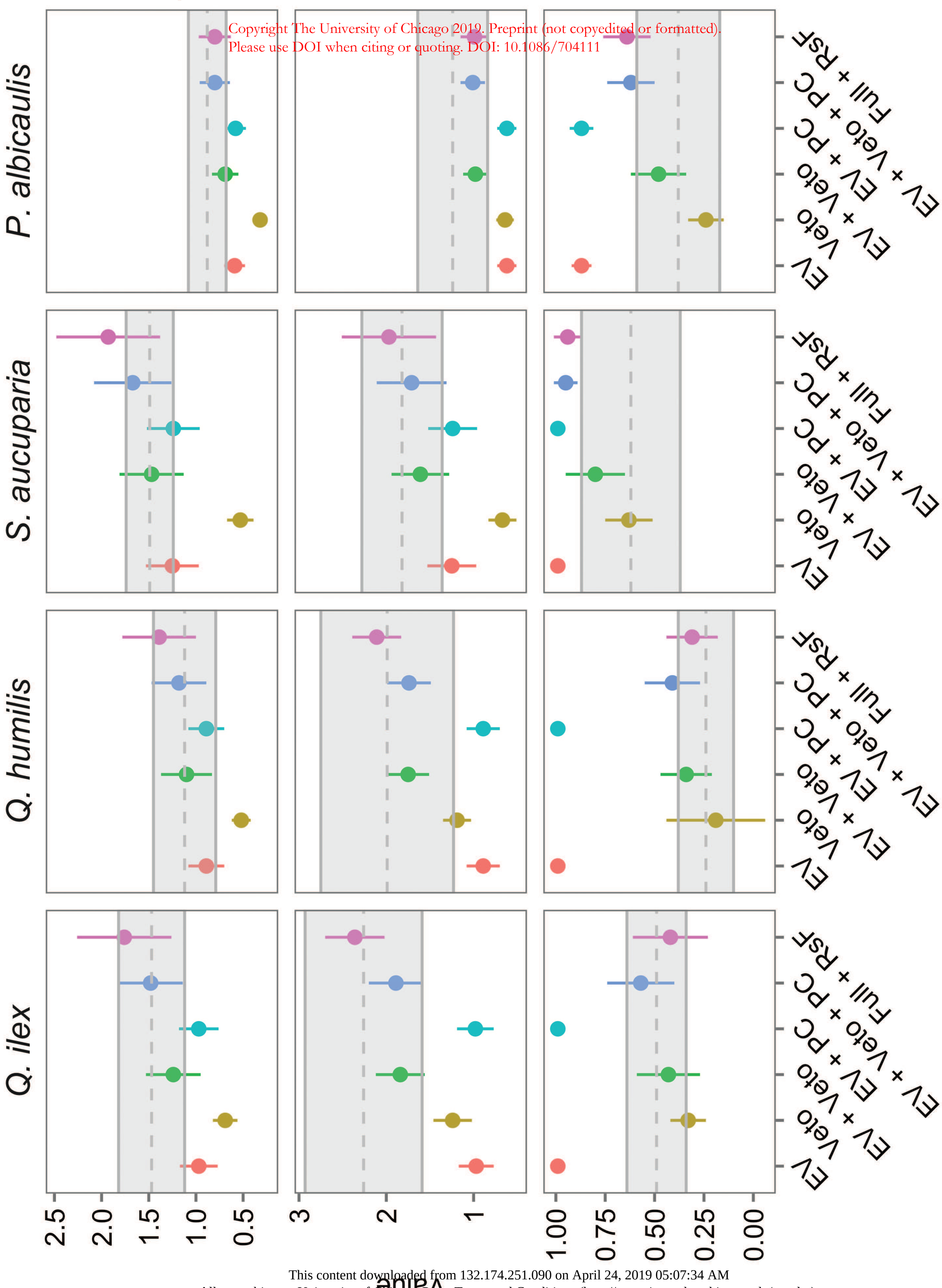

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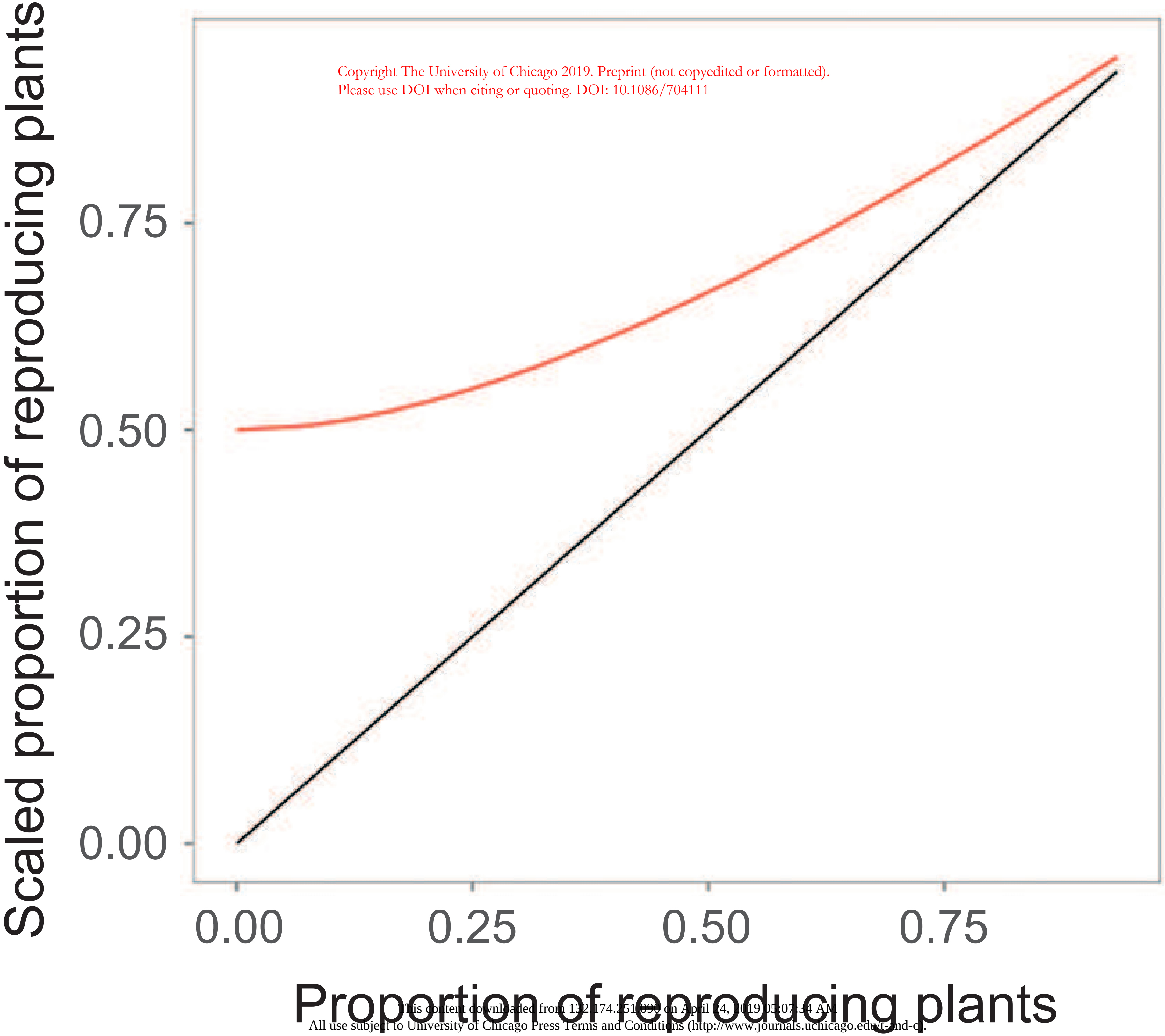
Figure A1



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