Community-wide masting improves predator satiation in North American oaks

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Abstract

Mast seeding, a phenomenon observed in numerous perennial plant species, is highly variable reproduction across years, synchronized among individuals within a population. One major fitness advantage of masting lies in the reduction of seed predation rates, achieved through alternating phases of seed scarcity and abundance that starve and subsequently satiate seed consumers. Proximately, the variability in seed production frequently correlates with weather conditions. Convergent responses among species to weather fluctuations often lead to synchronized masting events across species, which may help with predator satiation, but this hypothesis has been rarely tested. Here, we address this gap by using 23 years of seed production and pre-dispersal seed predation monitoring in three North American oak species (*Quercus rubra*, *Quercus alba*, *Quercus montana*). We found that spring and summer weather patterns correlated with masting events in all three species, resulting in intraspecific synchrony levels ranging from 0.21 to 0.38, depending on the species pair. Intraspecific masting synchrony facilitated efficient insect starvation in *Q. rubra* and *Q. alba*, while community-wide mast years were necessary for satiation in *Q. montana*. Our findings present a rare empirical test supporting the hypothesis that intraspecific masting synchrony enhances reproductive efficiency by minimizing seed losses to generalist seed predators.

keywords: density-dependence | economy of scale | masting | intraspecific synchrony | seed consumption | predator satiation

Introduction

Numerous perennial plant species exhibit mast seeding, a reproductive phenomenon characterized by highly variable reproduction across years and synchronized patterns among individuals within populations (Kelly, 1994; Pearse *et al.*, 2016; Pesendorfer *et al.*, 2021). Mast seeding is a prevalent mode of reproduction in perennial plants, with diverse effects on ecosystem functioning, including impacts on wildlife and plant population dynamics, carbon stocks, and

nutrient cycling (Bogdziewicz *et al.*, 2016; Hacket-Pain *et al.*, 2018; Mund *et al.*, 2020). At the ultimate level, mast seeding confers fitness benefits by enhancing reproductive efficiency through reduced seed predation rates or improved pollination efficiency (Kelly & Sork, 2002; Zwolak *et al.*, 2022). The alternation between seed scarcity and abundance associated with mast seeding diminishes seed predation rates by satiating seed consumers (Zwolak *et al.*, 2022), while pollination efficiency is bolstered by the concentration of flowering efforts in high-density events (Kelly *et al.*, 2001). On a proximate level, the variability in seed production is frequently linked to weather conditions, known as weather cues, which synchronize reproduction by either promoting or suppressing flowering and seed production (Kelly *et al.*, 2013; Koenig *et al.*, 2015; Journé *et al.*, 2024). Sympatric species often share similar weather cues, leading to synchronization in mast seeding events among species (Curran & Leighton, 2000; Koenig & Knops, 2013; Koenig *et al.*, 2016; Wang *et al.*, 2017). Although community-level mast seeding has been hypothesized to confer fitness benefits by improving control of seed consumer populations, studies on this topic are scarce and results remain inconsistent.

One remarkable illustration of community-wide masting events is observed in Bornean dipterocarps, where hundreds of species synchronize their flowering at multi-year intervals (Ashton *et al.*, 1988; Satake *et al.*, 2021). In this system, community-wide masting appears essential for successful predator satiation, as species that mast asynchronously with the community struggle to evade seed consumption by generalist consumers (Curran & Leighton, 2000; Curran & Webb, 2000). Intraspecific synchrony of masting in two Mediterranean oaks improves escape from weevil predation (Espelta *et al.*, 2008). However, studies examining the effects of intraspecific masting synchrony on seed predation are rare (Shibata *et al.*, 1998; Curran & Webb, 2000; Hoshizaki & Hulme, 2002; Espelta *et al.*, 2008) as they require long-term monitoring of multiple species within a community, encompassing both predation and seed production data.

In this study, we address this gap by using 23 years of seed production and pre-dispersal seed predation monitoring of three North American oak species: *Quercus rubra*, *Q. alba*, and *Q. montana*. Our system offers a well-suited platform to investigate whether intraspecific masting synchrony influences predator satiation. Firstly, these oak species exhibit synchronous masting, likely facilitated by convergent responses of acorn production to weather variation

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(Sork *et al.*, 1993; Bogdziewicz *et al.*, 2018b). Secondly, in *Q. alba* and *Q. montanta*, pre-dispersal predator satiation is challenged by rapid bottom-up responses of seed consumers to seed availability (Bogdziewicz *et al.*, 2018a). Fluctuations in acorn availability, amplified by intraspecific masting synchrony, may foster starvation and satiation processes. Thirdly, weevils infesting acorns demonstrate the ability to switch among hosting oak species (Espelta *et al.*, 2009; Muñoz *et al.*, 2014). Masting exerts a reduction in seed predation through two related mechanisms: starvation and satiation of seed consumers (Zwolak *et al.*, 2022). Both processes can benefit from intraspecific synchrony if plants share common seed predators. Starvation may prove more effective when consumers lack alternative hosts during poor-seeding years. Satiation can be enhanced if community-wide masting facilitates overwhelming seed consumption by consumers.

Materials and Methods

Study system

The three model oak species (*Quercus rubra* L., *Q. alba* L., *Q. montana*) are prominent hardwood species across Eastern North America known for their masting behavior (Fig. S1) (Bogdziewicz *et al.*, 2018b; Journé *et al.*, 2023). Across all three species, spring and summer temperatures exhibit a positive correlation with acorn production, although the importance of certain weather cues appears to vary across regions (Sork *et al.*, 1993; Cecich & Sullivan, 1999; Smith *et al.*, 2021).

Curculio beetles are the primary pre-dispersal seed predators of our model oaks (Lombardo *et al.*, 2008; Govindan *et al.*, 2012). This insect species is univoltine, producing a single brood of offspring per year. While weevil species exhibit some degree of host-specificity, they readily infest acorns of other oak species, albeit potentially resulting in lower larval mass gains (Muñoz *et al.*, 2014).

Seed production and predation data

Over 23 years (2001 - 2023), we monitored acorn production at three study sites in eastern Pennsylvania, USA. *Q. rubra* and *Q. alba* were monitored at all three sites, whereas *Q. montana* was absent from one site. The forests of all sites are continuous, dominated by oaks, hickories, and maples (Moore *et al.*, 2007). Acorn production monitoring involved the placement of two seed traps beneath each of 15 individuals of every species at every site. Throughout the analysis, crop size per tree per year is the aggregated acorn count from the two seed traps. Acorns collected via seed traps were bagged based on their tree of origin and transported to the laboratory. Within the laboratory, we evaluated weevil infestation levels for individual acorns across each species.

Data analysis

Masting synchrony, weather, and seed production   To quantify both within- and among-species synchrony in mast seeding among the three oak species, we used Spearman correlations (Koenig *et al.*, 2003). To this end, we computed Spearman correlations on log-transformed acorn counts for each pair of trees at the same site, either including only one species (within-species synchrony) or only heterospecifics (among-species).

To investigate whether intraspecific masting synchrony arises from convergent responses of species to weather variation, we estimated relationships between seed production and weather using moving window analysis (Journé *et al.*, 2024). We employed a broad search for correlations to prevent bias towards selecting specific variables (e.g., spring weather) known to affect oak masting based on prior literature (Sork *et al.*, 1993), while potentially overlooking unknown weather effects that may diverge across the studied species. We implemented a moving Spearman correlation between annual seed production and mean temperature and precipitation. The window size was set at 30 days, with a 15-day step. Note that only weather variables were calculated in windows, not acorn production. Moving correlation analysis was conducted separately for each species, in each case for both year T1 (one year preceding seed fall) and T0 (the year of seed fall), as weather effects on seed production extend across years, encompassing those occurring during pollination (T0) and flowering initiation (T1).

Predator starvation and satiation   To assess whether community-wide seed production enhances starvation and satiation of weevils, we constructed a series of generalized linear mixed models (GLMMs) for each species. These models included predictors that represented the three scales (tree, population, community) at which the starvation and satiation of seed predators can operate.

To test the scale (tree, population, community) at which starvation and satiation operate most efficiently, we introduced individual tree seed production (i,y) in interaction with the ratio of the current year's seed production to that of the previous year. Thus, the ratio represents the change in seed production between consecutive years, with high values indicating a large increase, which should correlate with reduced seed predation rates (Kelly & Sullivan, 1997; Kelly *et al.*, 2000). The calculation of the ratio involved dividing tree-level seed production by either: the previous year's seed production of the focal tree, the previous year's population-level seed production, or the previous year's community-level seed production. Each ratio represents a different scale of starvation operating at the tree, population, or community level.

To test whether population-wide or community-wide seed production enhances satiation, we used individual tree seed production (i,y) in interaction terms with either the summed acorn production of the focal species in a given site and year (reflecting population-wide masting) or with the summed acorn production of all species present at a given site and year (reflecting community-wide masting). The former interaction assesses whether satiation is enhanced by population-level synchrony (Bogdziewicz *et al.*, 2018a), while the latter examines whether satiation is improved by community-wide synchrony.

Together, we constructed six models for each species. In each model, the proportion of predated seeds per tree i per year y was used as the response variable, while individual tree number and site were used as random intercepts. The response was included through the cbind function in R that includes proportion as a matrix of the number of infested seeds and the number of seeds non-infested seeds. The models were specified with binomial error terms and fitted using the glmmTMB package in R (Brooks *et al.*, 2017; R Core Team, 2023). We ranked the models using standard AIC criteria (Burnham *et al.*, 2011). Models are summarized in Table S1.

Results

In our model species, within-species synchrony of masting consistently exhibited positive values, ranging from 0.36 (mean cross-correlation among pairs of trees within a site) in *Q. alba*, 0.41 in *Q. rubra*, to 0.44 in *Q. montana* (histograms in Fig. S2). Among species, the synchrony between *Q. rubra* and *Q. alba* was 0.21, between *Q. rubra* and *Q. montana* was 0.30, and between *Q. alba* and *Q. montana* was 0.38 (Fig. S3).

The moving window analysis revealed convergence in the correlations between weather variation on acorn production across the three oak species studied (Fig. S4, S5). In all three oaks, seed production demonstrated negative correlations with summer temperatures one year before seed fall, and positive correlations with winter temperatures in the year of seed fall (Fig. S4). Correlations with precipitation also exhibited consistency across species. The exception was observed in *Q. alba* and *Q. montana*, where summer precipitation correlated positively with seed production, a pattern absent in *Q. rubra* (Fig. S5). Consequently, synchrony between *Q. alba* and *Q. montana* was higher than the synchrony observed between these two species and *Q. rubra* (Fig. S3).

In *Q. rubra* and *Q. alba*, predator satiation benefited from community-level starvation of weevils (Fig. 1, Table 1). In both species, the rate of seed predation declined with increasing seed production levels, a decline that was improved (in *Q. alba*) or observed exclusively (in *Q. rubra*) during years in which large seed production followed after community-wide failure (ratio of tree-level seeding in the current year to previous year community-wide seed production) (Fig. 1). For instance, in *Q. rubra*, the seed predation rate decreased by 5.5-fold, dropping from 28% to 5% across low and high tree-level seed production rates, but only when last year's community-wide seed production was low (Fig. 1). Notably, models incorporating the difference calculated based on the previous year's community-wide seed production demonstrated a better fit to the data based on AIC (Table S1) compared to models involving the previous year's population-wide or individual-level seed production.

In *Q. montana*, community-wide mast years enabled overwhelming weevils with an excess of seeds, leading to a 20-fold decline in seed predation rate, from 60% to 3%, between years with sparse and abundant community-wide seed production (Fig. 1, Table 1). Models incorporating
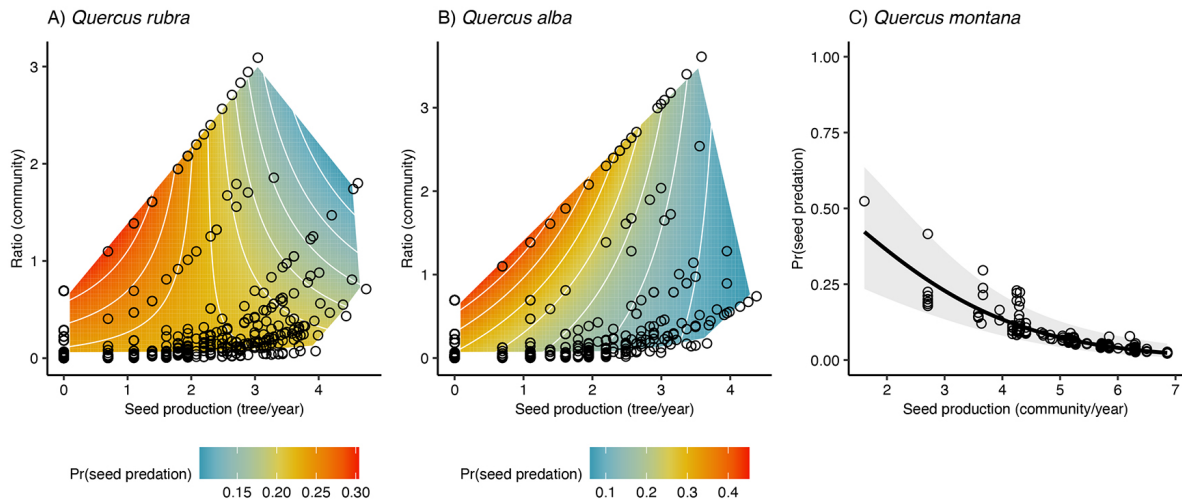
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Figure 1: Community-wide masting improves satiation in North American oaks. Surface plots at A) and B) show estimated pre-dispersal seed predation rates across combinations of tree-level seed production (per year) and the ratio of tree-level seed production to the previous year's community-wide seed production, with the convex hulls (parameter space across which predictions are computed) defined by observations (black points). C) Annual pre-dispersal seed predation rates vs community-wide seed production, points are partial residuals, while prediction line and associated 95% CI are extracted from GLMM. Models are summarized in Table 1. Seed production and predation were monitored for 23 years in each species, at three (*Q. rubra* and *Q. alba*) or two sites (*Q. montana*), with 15 individuals of each species monitored per site.

population-wide seed production rates exhibited poorer fit according to AIC (Table S1), and population-level seeding failed to emerge as a significant predictor of predation rates (p = 0.08), suggesting that synchronous single-species mast years of *Q. montana* alone are insufficient for weevil satiation. Furthermore, predation rates in this species increased with tree-level seed production, even when seed production was lower in the previous year compared to the present year (Table 1).

Discussion

Intraspecific masting synchrony facilitates predator satiation across the three North American oaks. Community-wide seed production failures (in *Q. rubra* and *Q. alba*) and mast years (*Q. montana*) correlated negatively with seed predation rates. Correlations between acorn production and weather variation in all three species led to relatively synchronous, community-wide masting events. In consequence, in *Q. rubra* and *Q. alba*, reduction of seed predation occurred through improved starvation, as community-wide failures left weevils with seeds from neither species to infest. Conversely, in *Q. montana*, only community-wide mast years proved capable of

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Table 1: Model summaries testing the relationships between seed predation rates and masting at tree, population, and community levels. Each model included the proportion of predated seeds as a response (per tree per year), while site and tree were included as random intercepts. Models were fitted with binomial error terms. These are top top-ranked models for each species according to standard AIC criteria (model selection Table S1). Seed production and predation were monitored for 23 years in each species, at three (*Q. rubra* and *Q. alba*) or two sites (*Q. montana*), with 15 individuals of each species monitored per site. Seed production (tree/population/community) - seed production per year per tree/population/community; Ratio (population/community) - seed production per tree year divided by population-/community- level seed production in the previous year.

Predictor	β	SE	F	p-value
Quercus rubra				
Intercept	-0.84	0.60	-1.39	0.166
Seed production (tree)	0.25	0.24	1.00	0.316
Ratio (community)	0.45	0.26	1.72	0.086
Seed production (population)	-0.08	0.13	-0.62	0.539
Seed production (tree) * Ratio (community)	-0.21	0.09	-2.22	**0.026**
Seed production (tree) * Seed production (population)	-0.06	0.05	-1.17	0.240
Quercus alba				
Intercept	-1.43	0.98	-1.46	0.145
Seed production (tree)	-0.65	0.38	-1.74	0.083
Ratio (community)	0.97	0.35	2.74	**0.006**
Seed production (community)	0.10	0.18	0.55	0.582
Seed production (tree) * Ratio (community)	-0.24	0.12	-2.07	**0.039**
Seed production (tree) * Seed production (community)	0.05	0.06	0.74	0.459
Quercus montana				
Intercept	-2.09	1.26	1.66	0.097
Seed production (tree)	-0.26	0.56	-0.46	0.647
Ratio (population)	-1.45	0.47	-3.07	**0.002**
Seed production (community)	-0.81	0.24	-3.38	**<0.001**
Seed production (tree) * Ratio (population)	0.37	0.12	3.09	**0.002**
Seed production (tree) * Seed production (community)	0.09	0.09	0.96	0.336

overwhelming weevils and diluting predation rates. Our long-term monitoring allowed us to test a widely hypothesized yet largely untested assumption: that intraspecific masting synchrony significantly influences predation rates of generalist seed consumers.

Convergence in the effects of weather variation on seed production within communities of related species could stem from common ancestry or result from shared selection pressures. Supporting the importance of phylogeny, factors influencing seed production in oaks exhibit some degree of phylogenetic conservation (Koenig *et al.*, 2016). However, the geographic origin of species also serves as a predictor of weather effects on seed production (Koenig *et al.*, 2016). Moreover, the correlation of masting with weather variation often aligns across diverse plant species within specific geographic regions (Schauber *et al.*, 2002; Shibata *et al.*, 2002; Kelly *et al.*, 2013), suggesting that shared selection pressures among sympatric species may drive such convergence (Kelly *et al.*, 2013; Koenig *et al.*, 2016). The enhanced seed survival rates associated with community-level masting synchrony suggest that predation may indeed select for intraspecific synchrony in seed production.

A past study on our populations indicated that masting in *Q. alba* and *Q. montana* does not lead to declines in pre-dispersal seed predation rates by weevils. The absence of predator satiation was linked to the rapid numerical response of insects to acorn availability (Bogdziewicz *et al.*, 2018a). However, as our current study suggests, the rapid bottom-up responses of insects can be overridden if fluctuations in seed production are intensified by intraspecific synchrony. In *Q. rubra* and *Q. alba*, community-wide failures played a crucial role in starving the insects. Asynchronous failures allow weevils to switch to other seed species if the focal species fail to reproduce, resulting in a higher abundance of insect population during subsequent large seeding years. Community-wide seeding failures likely facilitate more effective starvation of the insect population. With insects starting from lower numbers the following year, the bottom-up response proves insufficient to offset predator satiation. Conversely, *Q. montana* exhibits the lowest fecundity in our populations (Fig. S1). Thus, mast years fueled solely by seed production from the other two oaks suffice to satiate seed predators.

Generalist seed consumers are challenging to satiate due to their ability to switch to alternative food sources during poor-seeding years (Curran & Leighton, 2000; Koenig *et al.*, 2003;

Bogdziewicz *et al.*, 2022). Community-wide masting has been proposed as an effective strategy to counteract this challenge (Curran & Leighton, 2000), an argument supported by our study. As a synthesis is currently lacking, the extent of intraspecific masting synchrony remains unclear. Nevertheless, evidence scattered across case studies suggests that such synchrony may be prevalent (Shibata *et al.*, 2002; Schauber *et al.*, 2002; Espelta *et al.*, 2008; Wang *et al.*, 2017; Satake *et al.*, 2021). Further studies across diverse ecosystems are necessary to evaluate to what extent the selection pressures from generalist seed predators are responsible for the community-wide masting synchrony.

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Author Contributions Statement

All authors designed the study, SM and MS collected and curated the data, JSz performed the analysis, MB led the writing of the manuscript. All authors contributed critically to the interpretation of the analysis and drafts, and gave final approval for publication.

Declaration of interests

No competing interests to declare.

Data availability statement

The data supporting the results are available at OSF repository.

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Supporting Information

Szymkowiak et al. Community-wide masting improves predator satiation in North American oaks

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Table S1: Selection tables for models testing the relationships between seed predation rates and masting at tree, population, and community level in three oak species (*Q. rubra*, *Q. alba),* Q. montana. Each model included the proportion of predated seeds as a response (per tree per year), while site and tree were included as random intercepts. Models were fitted with binomial error terms. For each species, we fitted six models as presented. Seed production (tree/population/community) - seed production per year per tree/population/community; Ratio (tree/population/community) - seed production per tree year divided by population-/community- level seed production in the previous year. The interaction between seed production (tree) and Ratio (tree/population/community) tests for improvement of satiation through starvation at the three levels, from tree to community. The interaction between seed production (tree) and seed production at population or community levels tests for improvement of satiation through population- or community-wide synchronization of mast years. The top models are summarized in Table 1.

| Model	AIC	ΔAIC	weight
Quercus rubra			
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (population)	1674.9	0.0	0.705
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (population)	1677.1	2.2	0.229
Seed production (tree) × Ratio (population) + fecundity × Seed production (population)	1679.6	4.7	0.066
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (community)	1692.5	17.7	<0.001
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (community)	1697.1	22.2	<0.001
Seed production (tree) × Ratio (population) + fecundity × Seed production (community)	1698.9	24.0	<0.001
Quercus alba			
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (community)	1100.9	0.0	0.830
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (community)	1105.0	4.2	0.103
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (population)	1106.6	5.7	0.047
Seed production (tree) × Ratio (population) + Seed production (tree) × Seed production (community)	1110.2	9.3	0.008
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (population)	1110.2	9.4	0.008
Seed production (tree) × Ratio (population) + Seed production (tree) × Seed production (population)	1111.4	10.6	0.004
Quercus montana			
Seed production (tree) × Ratio (population) + Seed production (tree) × Seed production (community)	482.5	0.0	0.936
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (community)	489.8	7.3	0.024
Seed production (tree) × Ratio (population) + Seed production (tree) × Seed production (population)	489.9	7.4	0.023
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (community)	490.6	8.1	0.016
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (population)	500.9	18.4	<0.001
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (population)	502.6	20.1	<0.001
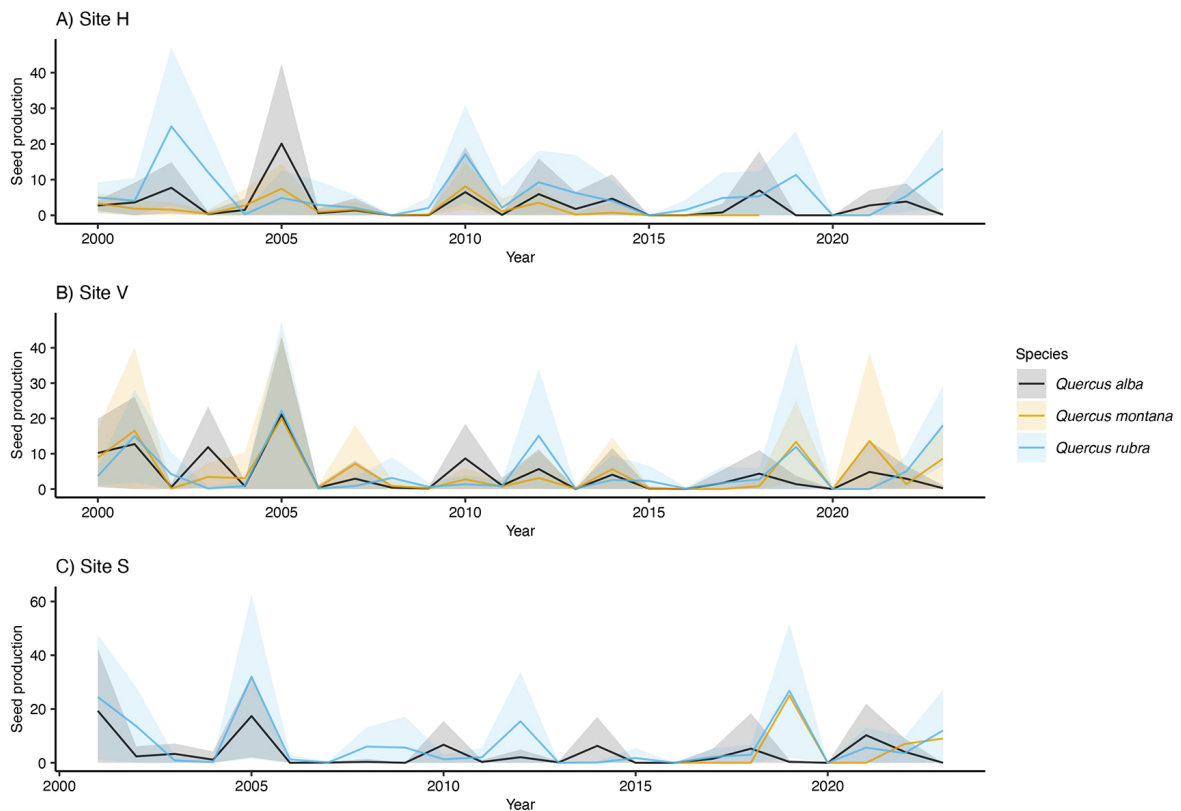
Figure S1: Annual patterns of seed production of the three oak species across the three study sites (acorns per tree, measured with two seed traps placed under each individual). Each line is mean annual seed production (±standrad deviation of the mean, shown by ribbons) and colors represent the different species. At each site, we monitored 15 trees using seed traps. Among-species synchrony is provided in Fig. S3.
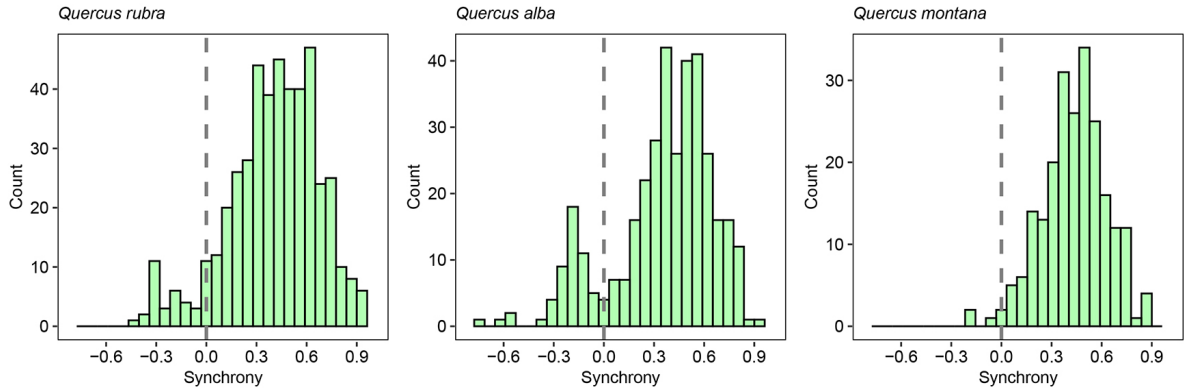
Figure S2: Within-species synchrony of seed production in *Q. rubra*, *Q. alba*, and *Q. montana*. Histograms show the distribution of Spearman correlation coefficients, calculated between seed production time-series of each tree and all conspecifics present at a particular site.
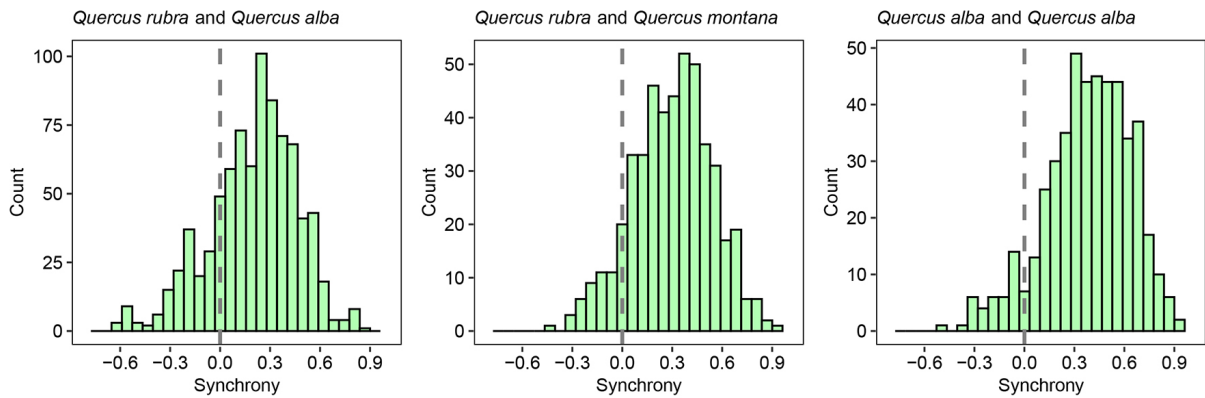

Figure S3: Between-species synchrony of seed production in *Q. rubra*, *Q. alba*, and *Q. montana*. Histograms show the distribution of Spearman correlation coefficients, calculated between seed production time-series of each tree and all heterospecifics present at a particular site.
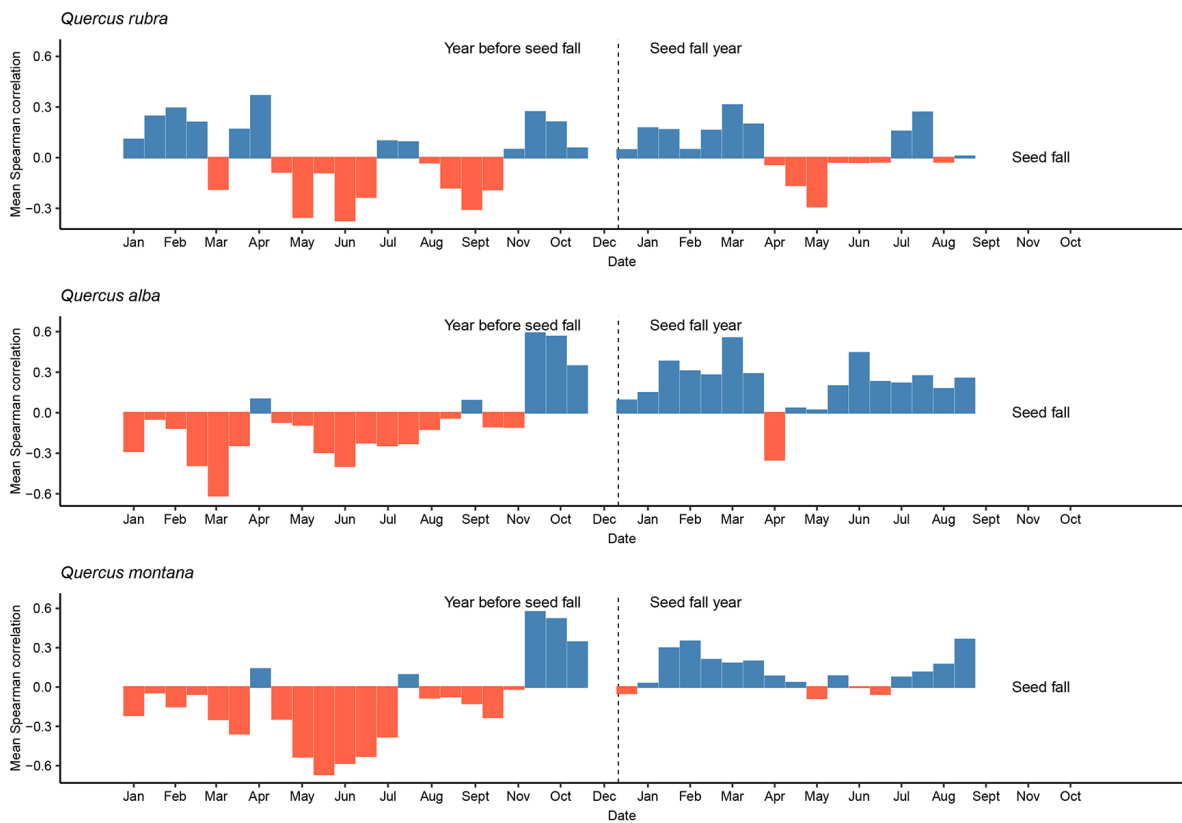
Figure S4: <mark>Mean Spearman correlation coefficients</mark> from moving window analysis testing the relationships between temperature and masting in *Q. rubra*, *Q. alba*, and *Q. montana*. The graph shows mean correlations for the temperature-seed production relationships in the year of seed fall (T0), and one year before (T1). The size of the window is 30 days, with a 15-day step, and correlations are plotted according to the day of the year at the start of each 30-day window. Correlations are coded red for negative, and blue for positive.
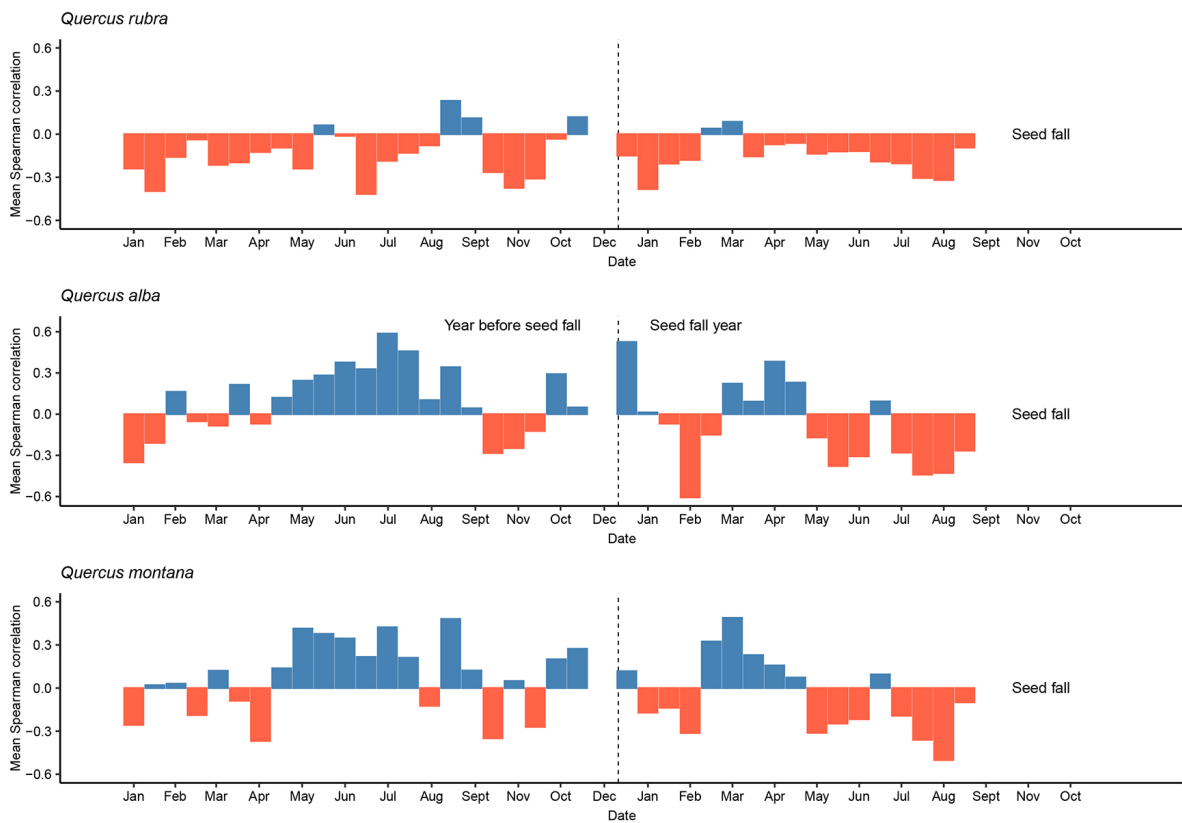
Figure S5: <mark>Mean Spearman correlation coefficients</mark> from moving window analysis testing the relationships between precipitation and masting in *Q. rubra*, *Q. alba*, and *Q. montana*. The graph shows mean correlations for the precipitation-seed production relationships in the year of seed fall (T0), and one year before (T1). The size of the window is 30 days, with a 15-day step, and correlations are plotted according to the day of the year at the start of each 30-day window. Correlations are coded red for negative, and blue for positive.