

1 Community-wide masting improves predator satiation  
2 in North American oaks  
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14

## 15 **Abstract**

16 Mast seeding, a phenomenon observed in numerous perennial plant species, is highly variable  
17 reproduction across years, synchronized among individuals within a population. One major  
18 fitness advantage of masting lies in the reduction of seed predation rates, achieved through  
19 alternating phases of seed scarcity and abundance that starve and subsequently satiate seed  
20 consumers. Proximately, the variability in seed production frequently correlates with weather  
21 conditions. Convergent responses among species to weather fluctuations often lead to synchro-  
22 nized masting events across species, which may help with predator satiation, but this hypothesis  
23 has been rarely tested. Here, we address this gap by using 23 years of seed production and  
24 pre-dispersal seed predation monitoring in three North American oak species (*Quercus rubra*,  
25 *Quercus alba*, *Quercus montana*). We found that spring and summer weather patterns correlated  
26 with masting events in all three species, resulting in intraspecific synchrony levels ranging from  
27 0.21 to 0.38, depending on the species pair. Intraspecific masting synchrony facilitated efficient  
28 insect starvation in *Q. rubra* and *Q. alba*, while community-wide mast years were necessary for  
29 satiation in *Q. montana*. Our findings present a rare empirical test supporting the hypothesis that  
30 intraspecific masting synchrony enhances reproductive efficiency by minimizing seed losses to  
31 generalist seed predators.

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

## 35 **Introduction**

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

41 nutrient cycling (Bogdziewicz *et al.*, 2016; Hackett-Pain *et al.*, 2018; Mund *et al.*, 2020). At  
42 the ultimate level, mast seeding confers fitness benefits by enhancing reproductive efficiency  
43 through reduced seed predation rates or improved pollination efficiency (Kelly & Sork, 2002;  
44 Zwolak *et al.*, 2022). The alternation between seed scarcity and abundance associated with  
45 mast seeding diminishes seed predation rates by satiating seed consumers (Zwolak *et al.*, 2022),  
46 while pollination efficiency is bolstered by the concentration of flowering efforts in high-density  
47 events (Kelly *et al.*, 2001). On a proximate level, the variability in seed production is frequently  
48 linked to weather conditions, known as weather cues, which synchronize reproduction by either  
49 promoting or suppressing flowering and seed production (Kelly *et al.*, 2013; Koenig *et al.*, 2015;  
50 Journé *et al.*, 2024). Sympatric species often share similar weather cues, leading to synchro-  
51 nization in mast seeding events among species (Curran & Leighton, 2000; Koenig & Knops,  
52 2013; Koenig *et al.*, 2016; Wang *et al.*, 2017). Although community-level mast seeding has  
53 been hypothesized to confer fitness benefits by improving control of seed consumer populations,  
54 studies on this topic are scarce and results remain inconsistent.

55 One remarkable illustration of community-wide masting events is observed in Bornean dipte-  
56 rocarps, where hundreds of species synchronize their flowering at multi-year intervals (Ashton  
57 *et al.*, 1988; Satake *et al.*, 2021). In this system, community-wide masting appears essential for  
58 successful predator satiation, as species that mast asynchronously with the community struggle  
59 to evade seed consumption by generalist consumers (Curran & Leighton, 2000; Curran & Webb,  
60 2000). Intraspecific synchrony of masting in two Mediterranean oaks improves escape from  
61 weevil predation (Espelta *et al.*, 2008). However, tests from other systems remain limited. For  
62 instance, Shibata *et al.* (1998) used seven years of data on seed production and predation in four  
63 hornbeam (*Carpinus sp.*) species and found that predation rates decline with seed production  
64 when species are pooled together. Nevertheless, their analysis cannot distinguish whether satia-  
65 tion was enhanced through community-wide mast events or simple single-species masting. Seed  
66 predation in *Faramaea occidentalis* decreased when community-wide seed fall peaked, yet this  
67 effect was observed within, rather than across years (Schupp, 1990). In Japanese horse-chestnut  
68 (*Aesculus turbinata*), seed predation did not correlate with masting of other trees in the com-  
69 munity (Hoshizaki & Hulme, 2002). Generally, studies examining the effects of intraspecific

70 masting synchrony on seed predation are rare as they require long-term monitoring of multiple  
71 species within a community, encompassing both predation and seed production data.

72 In this study, we address this gap by using 23 years of seed production and pre-dispersal  
73 seed predation monitoring of three North American oak species: *Quercus rubra*, *Q. alba*,  
74 and *Q. montana*. Our system offers a well-suited platform to investigate whether intraspecific  
75 masting synchrony influences predator satiation. Firstly, these oak species exhibit synchronous  
76 masting, likely facilitated by convergent responses of acorn production to weather variation  
77 (Sork *et al.*, 1993; Bogdziewicz *et al.*, 2018b). Secondly, in *Q. alba* and *Q. montana*, pre-  
78 dispersal predator satiation is challenged by rapid bottom-up responses of seed consumers to  
79 seed availability (Bogdziewicz *et al.*, 2018a). Fluctuations in acorn availability, amplified by  
80 intraspecific masting synchrony, may foster starvation and satiation processes. Thirdly, weevils  
81 infesting acorns demonstrate the ability to switch among hosting oak species (Espelta *et al.*,  
82 2009; Muñoz *et al.*, 2014). Masting exerts a reduction in seed predation through two related  
83 mechanisms: starvation and satiation of seed consumers (Zwolak *et al.*, 2022). Both processes  
84 can benefit from intraspecific synchrony if plants share common seed predators. Starvation may  
85 prove more effective when consumers lack alternative hosts during poor-seeding years. Satiation  
86 can be enhanced if community-wide masting facilitates overwhelming seed consumption by  
87 consumers.

## 88 **Materials and Methods**

### 89 **Study system**

90 The three model oak species (*Quercus rubra* L., *Q. alba* L., *Q. montana*) are prominent hardwood  
91 species across Eastern North America known for their masting behavior (Fig. S1) (Bogdziewicz  
92 *et al.*, 2018b; Journé *et al.*, 2023). Across all three species, spring and summer temperatures  
93 exhibit a positive correlation with acorn production, although the importance of certain weather  
94 cues appears to vary across regions (Sork *et al.*, 1993; Cecich & Sullivan, 1999; Smith *et al.*,  
95 2021).

96 Curculio beetles are the primary pre-dispersal seed predators of our model oaks (Lombardo

97 *et al.*, 2008; Govindan *et al.*, 2012). This insect species is univoltine, producing a single brood  
98 of offspring per year. While weevil species exhibit some degree of host-specificity, they readily  
99 infest acorns of other oak species, albeit potentially resulting in lower larval mass gains (Muñoz  
100 *et al.*, 2014).

## 101 **Seed production and predation data**

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

## 110 **Data analysis**

111 **Masting synchrony, weather, and seed production** To quantify both within- and among-  
112 species synchrony in mast seeding among the three oak species, we used Spearman correlations  
113 (Koenig *et al.*, 2003). Within-species synchrony was determined by computing Spearman  
114 correlations on log-transformed acorn counts for each pair of trees of the same species within  
115 the same site. For among-species synchrony, correlations were computed among pairs of trees  
116 belonging to different species, again focusing on individuals monitored within the same site.

117 To investigate whether intraspecific masting synchrony arises from convergent responses of  
118 species to weather variation, we estimated relationships between seed production and weather  
119 using moving window analysis (Journé *et al.*, 2024). We employed a broad search for correlations  
120 to prevent bias towards selecting specific variables (e.g., spring weather) known to affect oak  
121 masting based on prior literature (Sork *et al.*, 1993), while potentially overlooking unknown  
122 weather effects that may diverge across the studied species. We implemented a moving beta  
123 regression between annual seed production (scaled between 0 and 1 at the individual level) and

124 mean temperature and precipitation, including tree ID and site ID as random intercepts. The  
125 window size was set at 30 days, with a 15-day step. From each model, we extracted the slope for  
126 the weather variable, providing a measure of the strength of the masting-weather relationship.  
127 Moving regression analysis was conducted separately for each species, in each case for both  
128 year T1 (one year preceding seed fall) and T0 (the year of seed fall), as weather effects on  
129 seed production extend across years, encompassing those occurring during pollination (T0) and  
130 flowering initiation (T1).

131 **Predator starvation and satiation** To assess whether community-wide seed production en-  
132 hances starvation and satiation of weevils, we constructed a series of six generalized linear mixed  
133 models (GLMMs) for each species. In each model, the proportion of predated seeds per tree  $i$   
134 per year  $y$  was used as the response variable, while individual tree number and site were used  
135 as random intercepts. The models were specified with binomial error terms and fitted using the  
136 `glmmTMB` package in R (Brooks *et al.*, 2017; R Core Team, 2023).

137 To test the scale (tree, population, community) at which starvation and satiation operate most  
138 efficiently, we introduced individual tree seed production ( $i,y$ ) in interaction with the ratio of  
139 the current year's seed production to that of the previous year. High values of this ratio indicate  
140 that a relatively poor seeding year was succeeded by a large one, which should correlate with  
141 reduced seed predation rates (Kelly & Sullivan, 1997; Kelly *et al.*, 2000). The calculation of the  
142 ratio involved dividing tree-level seed production by either: the previous year's seed production  
143 of the focal tree, the previous year's population-level seed production, or the previous year's  
144 community-level seed production. Each ratio represents a different scale of starvation operating  
145 at the tree, population, or community level.

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

153 criteria (Burnham *et al.*, 2011). Models are summarized in Table S1.

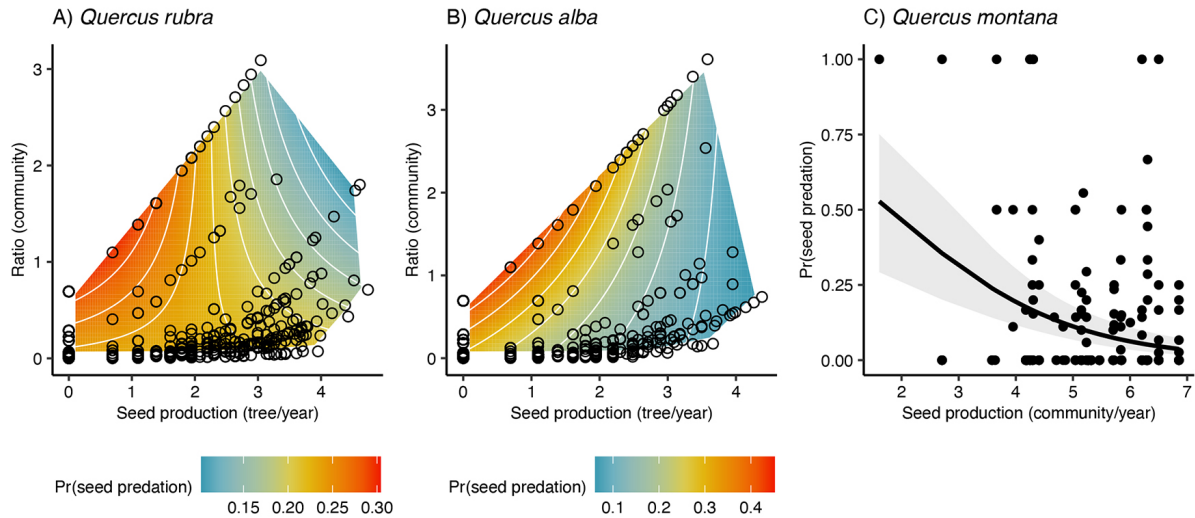
## 154 **Results**

155 In our model species, within-species synchrony of masting consistently exhibited positive values,  
156 ranging from 0.36 in *Q. alba*, 0.41 in *Q. rubra*, to 0.44 in *Q. montana*. Among species, the  
157 synchrony between *Q. rubra* and *Q. alba* was 0.21, between *Q. rubra* and *Q. montana* was 0.30,  
158 and between *Q. alba* and *Q. montana* was 0.38 (histograms plots in Fig. S4).

159 The moving window analysis revealed convergence in the correlations between weather  
160 variation on acorn production across the three oak species studied (Fig. S2, S3). In all three  
161 oaks, seed production demonstrated negative correlations with summer temperatures one year  
162 before seed fall, and positive correlations with summer temperatures in the year of seed fall  
163 (Fig. S2). Correlations with precipitation also exhibited remarkable consistency across species.  
164 The exception was observed in *Q. alba* and *Q. montana*, where spring precipitation correlated  
165 negatively with seed production, a pattern absent in *Q. rubra* (Fig. S3). Consequently, synchrony  
166 between *Q. alba* and *Q. montana* was higher than the synchrony observed between these two  
167 species and *Q. rubra* (Fig. S4).

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

179 In *Q. montana*, community-wide mast years enabled overwhelming weevils with an excess  
180 of seeds, leading to a 20-fold decline in seed predation rate, from 60% to 3%, between years with



**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 defined by observations (black points). C) Annual pre-dispersal seed predation rates vs community-wide seed production, points are observations, 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.

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

## 188 Discussion

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



**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	$\beta$	SE	<i>F</i>	p-value
<b><i>Quercus rubra</i></b>				
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	<b>0.026</b>
Seed production (tree) * Seed production (population)	-0.06	0.05	-1.17	0.240
<b><i>Quercus alba</i></b>				
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	<b>0.006</b>
Seed production (community)	0.10	0.18	0.55	0.582
Seed production (tree) * Ratio (community)	-0.24	0.12	-2.07	<b>0.039</b>
Seed production (tree) * Seed production (community)	0.05	0.06	0.74	0.459
<b><i>Quercus montana</i></b>				
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	<b>0.002</b>
Seed production (community)	-0.81	0.24	-3.38	<b>&lt;0.001</b>
Seed production (tree) * Ratio (population)	0.37	0.12	3.09	<b>0.002</b>
Seed production (tree) * Seed production (community)	0.09	0.09	0.96	0.336

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

198 Convergence in the effects of weather variation on seed production within communities of  
199 related species could stem from common ancestry or result from shared selection pressures.  
200 Supporting the importance of phylogeny, factors influencing seed production in oaks exhibit  
201 some degree of phylogenetic conservatism (Koenig *et al.*, 2016). However, the geographic  
202 origin of species also serves as a predictor of weather effects on seed production (Koenig *et al.*,  
203 2016). Moreover, the correlation of masting with weather variation often aligns across diverse  
204 plant species within specific geographic regions (Schauber *et al.*, 2002; Shibata *et al.*, 2002;  
205 Kelly *et al.*, 2013), suggesting that shared selection pressures among sympatric species may  
206 drive such convergence (Kelly *et al.*, 2013; Koenig *et al.*, 2016). The enhanced seed survival  
207 rates associated with community-level masting synchrony suggest that predation may indeed  
208 select for intraspecific synchrony in seed production.

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

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

224 Bogdziewicz *et al.*, 2022). Community-wide masting has been proposed as an effective strategy  
225 to counteract this challenge (Curran & Leighton, 2000), an argument supported by our study.  
226 As a synthesis is currently lacking, the extent of intraspecific masting synchrony remains un-  
227 clear. Nevertheless, evidence scattered across case studies suggests that such synchrony may  
228 be prevalent (Shibata *et al.*, 2002; Schauber *et al.*, 2002; Espelta *et al.*, 2008; Wang *et al.*,  
229 2017; Satake *et al.*, 2021). While further studies across diverse ecosystems are necessary before  
230 broader generalizations can be made, the convergence observed across diverse species implies  
231 the operation of strong selection pressures from generalist seed predators.

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239

## 240 **Author Contributions Statement**

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

244

## 245 **Declaration of interests**

246 No competing interests to declare.

247

## 248 **Data availability statement**

249 The data supporting the results are available at OSF:

250 [https://osf.io/uxfn2/?view\\_only=a86fd05a9b7041cb9faeb707be1aa94d](https://osf.io/uxfn2/?view_only=a86fd05a9b7041cb9faeb707be1aa94d)

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## References

- 252
- 253 Ashton, P.S., Givnish, T.J. & Appanah, S. (1988). Staggered flowering in the dipterocarpaceae:  
254 New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics.  
255 *Source: The American Naturalist*, 132, 44–66.
- 256 Bogdziewicz, M., Kuijper, D., Zwolak, R., Churski, M., drzejewska, B.J., Wysocka-Fijorek,  
257 E. *et al.* (2022). Emerging infectious disease triggered a trophic cascade and enhanced  
258 recruitment of a masting tree. *Proceedings of the Royal Society B: Biological Sciences*, 289,  
259 20212636.
- 260 Bogdziewicz, M., Marino, S., Bonal, R., Zwolak, R. & Steele, M. (2018a). Rapid aggregative  
261 and reproductive responses of weevils to masting of north american oaks counteract predator  
262 satiation. *Ecology*, 99, 2575–2582.
- 263 Bogdziewicz, M., Steele, M.A., Marino, S. & Crone, E.E. (2018b). Correlated seed failure as  
264 an environmental veto to synchronize reproduction of masting plants. *New Phytologist*, 219,  
265 98–108.
- 266 Bogdziewicz, M., Zwolak, R. & Crone, E.E. (2016). How do vertebrates respond to mast  
267 seeding? *Oikos*, 125, 300–307.
- 268 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A.  
269 *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated  
270 generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- 271 Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011). Aic model selection and multi-  
272 model inference in behavioral ecology: Some background, observations, and comparisons.  
273 *Behavioral Ecology and Sociobiology*, 65, 23–35.
- 274 Cecich, R.A. & Sullivan, N.H. (1999). Influence of weather at time of pollination on acorn  
275 production of quercus alba and quercus velutina. *Canadian Journal of Forest Research*, 29,  
276 1817–1823.

- 277 Curran, L.M. & Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed  
278 production of mast-fruiting dipterocarpaceae. *Ecological Monographs*, 70, 101–128.
- 279 Curran, L.M. & Webb, C.O. (2000). Experimental tests of the spatiotemporal scale of seed  
280 predation in mast-fruiting dipterocarpaceae. *Ecological Monographs*, 70, 129–148.
- 281 Espelta, J.M., Bonal, R. & Sánchez-Humanes, B. (2009). Pre-dispersal acorn predation in mixed  
282 oak forests: Interspecific differences are driven by the interplay among seed phenology, seed  
283 size and predator size. *Journal of Ecology*, 97, 1416–1423.
- 284 Espelta, J.M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. & Retana, J. (2008).  
285 Masting mediated by summer drought reduces acorn predation in mediterranean oak forests.  
286 *Ecology*, 89, 805–817.
- 287 Govindan, B.N., Kéry, M. & Swihart, R.K. (2012). Host selection and responses to forest  
288 fragmentation in acorn weevils: Inferences from dynamic occupancy models. *Oikos*, 121,  
289 623–633.
- 290 Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M. *et al.* (2018).  
291 Climatically controlled reproduction drives interannual growth variability in a temperate tree  
292 species. *Ecology Letters*, 21, 1833–1844.
- 293 Hoshizaki, K. & Hulme, P.E. (2002). *Mast seeding and predator-mediated indirect interactions*  
294 *in a forest community: evidence from post-dispersal fate of Rodent-generated caches.*, CABI  
295 Publishing, pp. 227–239.
- 296 Journé, V., Hacket-Pain, A. & Bogdziewicz, M. (2023). Evolution of masting in plants is linked  
297 to investment in low tissue mortality. *Nature Communications*, 14, 7998.
- 298 Journé, V., Szymkowiak, J., Foest, J., Hacket-Pain, A., Kelly, D. & Bogdziewicz, M. (2024).  
299 Summer solstice orchestrates the subcontinental-scale synchrony of mast seeding. *Nature*  
300 *Plants*.
- 301 Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology Evolution*, 9,  
302 465–470.

- 303 Kelly, D., Geldenhuis, A., James, A., Holland, E.P., Plank, M.J., Brockie, R.E. *et al.* (2013).  
304 Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate  
305 change. *Ecology Letters*, 16, 90–98.
- 306 Kelly, D., Harrison, A.L., Lee, W.G., Payton, I.J., Wilson, P.R. & Schaubert, E.M. (2000).  
307 Predator satiation and extreme mast seeding in 11 species of chionochloa (poaceae). *Oikos*,  
308 90, 477–488.
- 309 Kelly, D., Hart, D.E. & Allen, R.B. (2001). Evaluating the wind pollination benefits of mast  
310 seeding. *Ecology*, 82, 117–126.
- 311 Kelly, D. & Sork, V.L. (2002). Mast seeding in perennial plants: Why, how, where? *Annual*  
312 *Review of Ecology and Systematics*, 33, 427–447.
- 313 Kelly, D. & Sullivan, J.J. (1997). Quantifying the benefits of mast seeding on predator satiation  
314 and wind pollination in chionochloa pallens (poaceae). *Oikos*, 78, 143–150.
- 315 Koenig, W.D., Carbonero, M.D., Fernández-Rebollo, P., Knops, J.M.H., Marañón, T., Padilla-  
316 Díaz, C.M. *et al.* (2016). Is the relationship between mast-seeding and weather in oaks related  
317 to their life-history or phylogeny? *Ecology*, 97, 2603–2615.
- 318 Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. *et al.* (2003).  
319 Dissecting components of population-level variation in seed production and the evolution of  
320 masting behavior. *Oikos*, 102, 581–591.
- 321 Koenig, W.D., Knops, J.M., Carmen, W.J. & Pearse, I.S. (2015). What drives masting? the  
322 phenological synchrony hypothesis. *Ecology*, 96, 184–192.
- 323 Koenig, W.D. & Knops, J.M.H. (2013). Large-scale spatial synchrony and cross-synchrony in  
324 acorn production by two california oaks. *Ecology*, 94, 83–93.
- 325 Lombardo, J.A., Mccarthy & C, B. (2008). Forest management and curculionid weevil diversity  
326 in mixed oak forests of southeastern ohio. *Natural Areas Journal*, 28, 363–369.

327 Moore, J.E., Mceuen, A.B., Swihart, R.K., Contreras, T.A. & Steele, M.A. (2007). Determinants  
328 of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology*, 88, 2529–  
329 2540.

330 Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P. *et al.* (2020). It is not  
331 just a ‘trade-off’: indications for sink- and source-limitation to vegetative and regenerative  
332 growth in an old-growth beech forest. *New Phytologist*, 226, 111–125.

333 Muñoz, A., Bonal, R. & Espelta, J.M. (2014). Acorn - weevil interactions in a mixed-oak forest:  
334 Outcomes for larval growth and plant recruitment. *Forest Ecology and Management*, 322,  
335 98–105.

336 Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather,  
337 cues, and selection. *New Phytologist*, 212, 546–562.

338 Pesendorfer, M.B., Ascoli, D., Bogdziewicz, M., Hacket-Pain, A., Pearse, I.S. & Vacchiano,  
339 G. (2021). The ecology and evolution of synchronized reproduction in long-lived plants.  
340 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200369.

341 R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation  
342 for Statistical Computing, Vienna, Austria.

343 Satake, A., Yao, T.L., Kosugi, Y. & Chen, Y. (2021). Testing the environmental prediction  
344 hypothesis for community-wide mass flowering in south-east asia. *Biotropica*, 53, 608–618.

345 Schaubert, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B. *et al.* (2002). Masting  
346 by eighteen new zealand plant species: The role of temperature as a synchronizing cue.  
347 *Ecology*, 83, 1214–1225.

348 Schupp, E.W. (1990). Annual variation in seedfall, postdispersal predation, and recruitment of  
349 a neotropical tree. 71, 504–515.

350 Shibata, M., Tanaka, H., Iida, S., Abe, S., Masaki, T., Niiyama, K. *et al.* (2002). Synchronized  
351 annual seed production in 16 principal tree species in a temperate deciduous forest, japan.  
352 *Ecology*, 83, 1727–1742.

- 353 Shibata, M., Tanaka, H. & Nakashizuka, T. (1998). Causes and consequences of mast seed  
354 production of four co-occurring carpinus species in japan. *Ecology*, 79, 54–64.
- 355 Smith, S.J., McCarthy, B.C., Hutchinson, T.F. & Snell, R.S. (2021). Both weather and resources  
356 influence masting in chestnut oak (*quercus montana* willd.) and black oak (*q. velutina* lam.).  
357 *Plant Ecology*, 508, 120029.
- 358 Sork, V.L., Bramble, J. & Sexton, O. (1993). Ecology of mast-fruiting in three species of north  
359 american deciduous oaks. *Ecology*, 74, 528–541.
- 360 Wang, Y., Zhang, J., LaMontagne, J.M., Lin, F., Li, B., Ye, J. *et al.* (2017). Variation and  
361 synchrony of tree species mast seeding in an old-growth temperate forest. *Journal of Vegetation*  
362 *Science*, 28, 413–423.
- 363 Zwolak, R., Celebias, P. & Bogdziewicz, M. (2022). Global patterns in the predator satiation  
364 effect of masting: A meta-analysis. *Proceedings of the National Academy of Sciences of the*  
365 *United States of America*, 119, e2105655119.

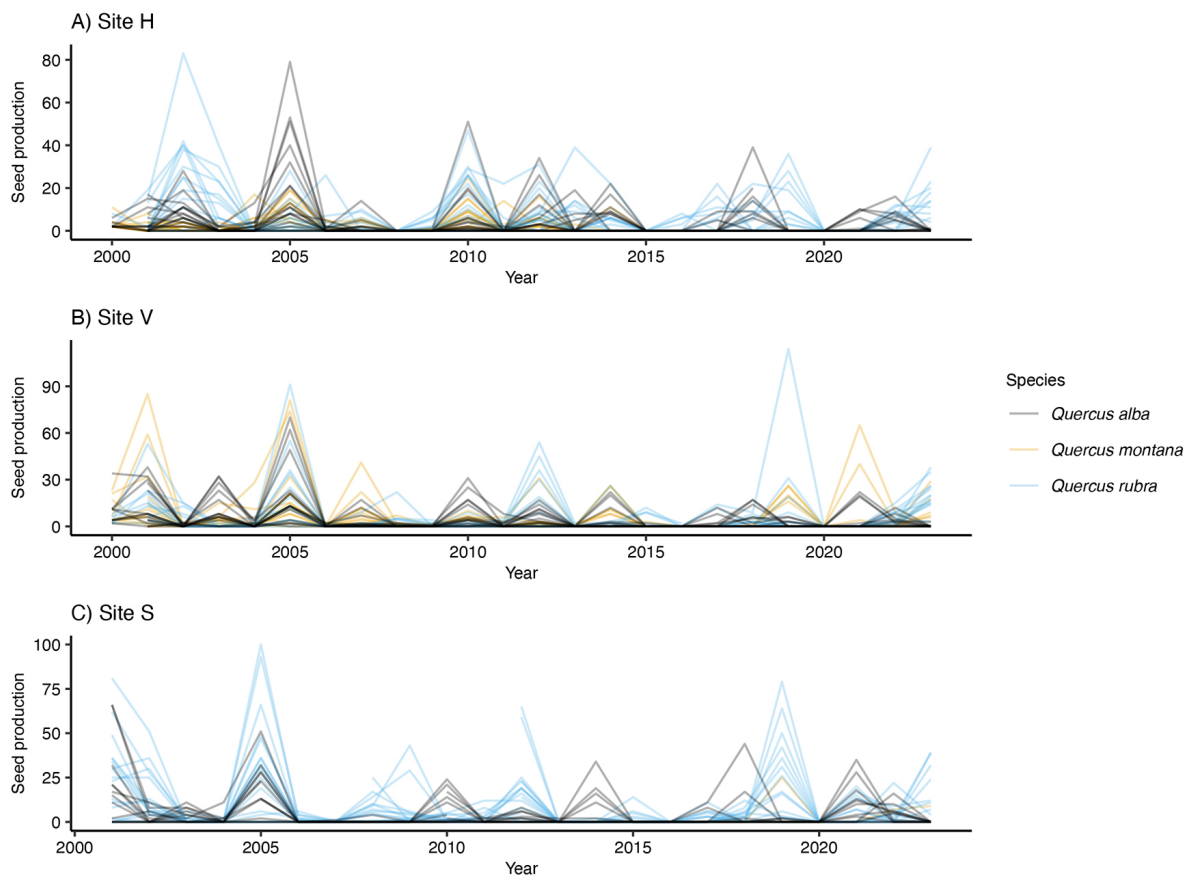


366 **Supporting Information**

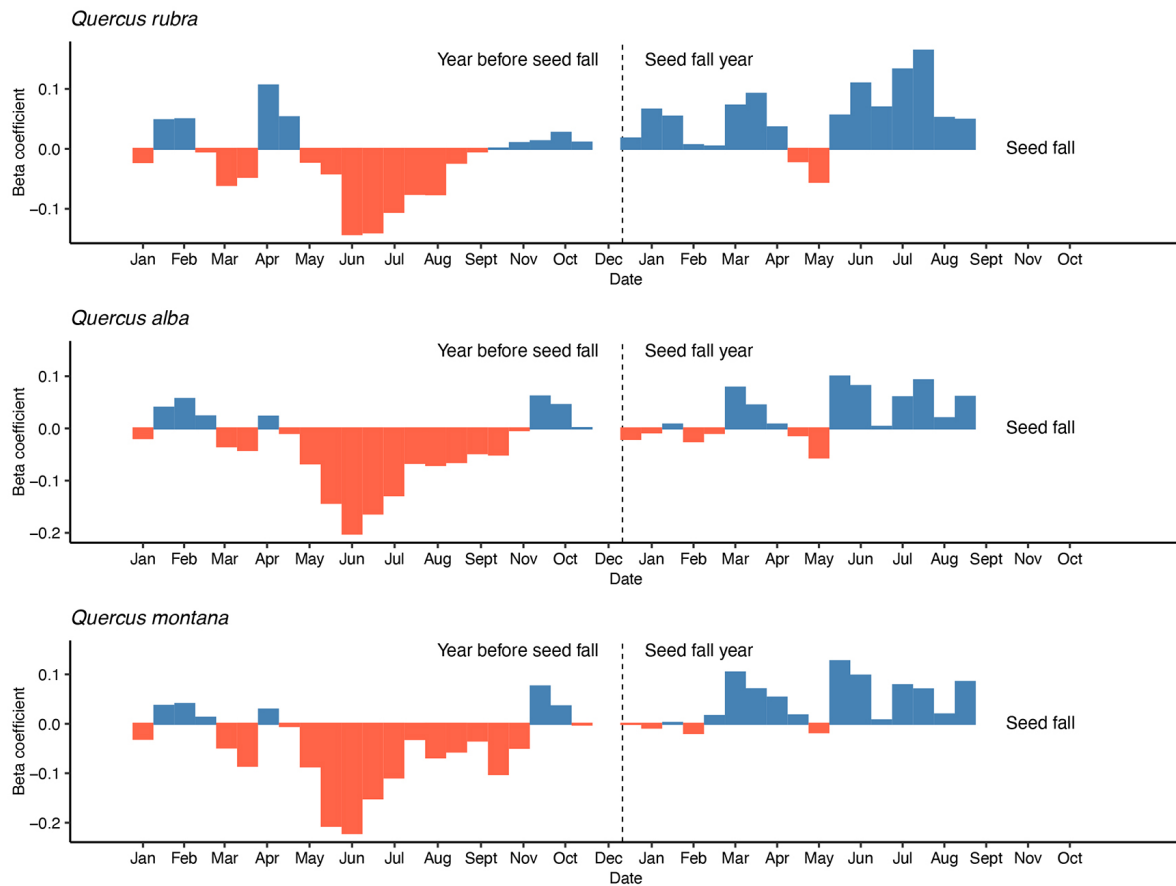
367 Szymkowiak et al. Community-wide masting improves predator satiation in North American  
368 oaks

**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.

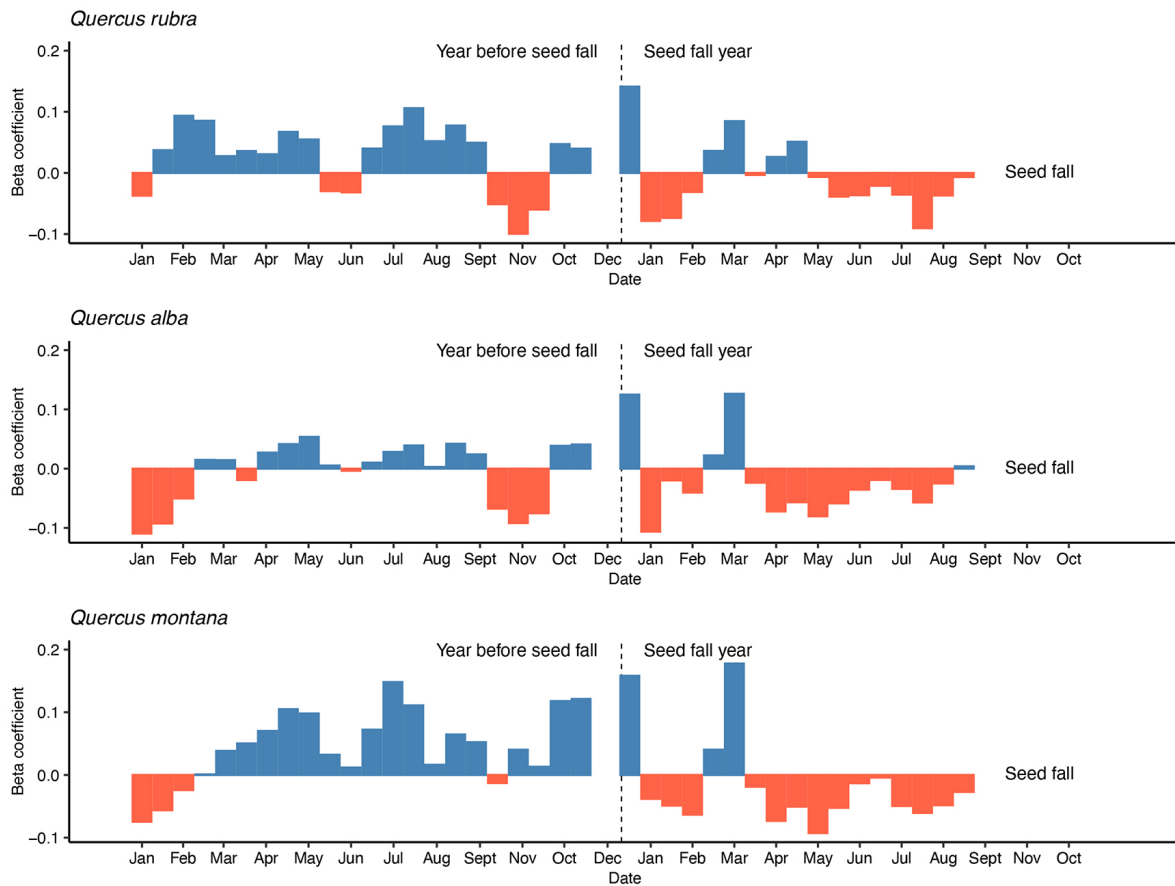
Model	AIC	ΔAIC	weight
<b><i>Quercus rubra</i></b>			
Seed production (tree) × Ratio (community) + Seed production (tree) × Seed production (population)	1674.9	0.0	0.705
Seed production (tree) × Ratio (tree) + Seed production (tree) × Seed production (population)	1677.1	2.2	0.229
Seed production (tree) × 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
<b><i>Quercus alba</i></b>			
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
<b><i>Quercus montana</i></b>			
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



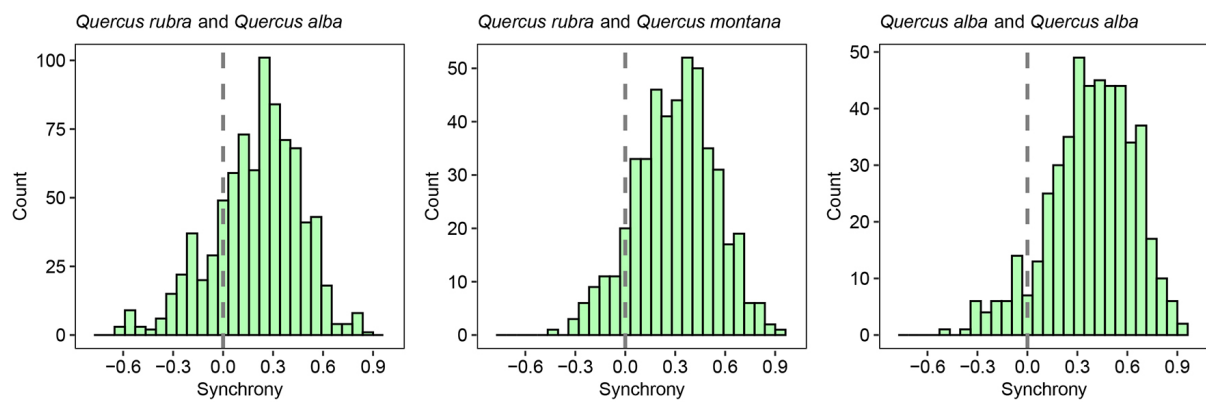
**Figure S1:** Annual patterns of tree-level seed production of the three oak species across the three study sites. Each line is one tree and colors represent the different species. At each site, we monitored 15 trees using seed traps. Among-species synchrony is provided in Fig. S4.



**Figure S2:** Beta coefficients from moving window analysis testing the relationships between temperature and masting in *Q. rubra*, *Q. alba*, and *Q. montana*. The graph shows slopes for the temperature effect 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 slopes are plotted according to the day of the year at the end of each 30-day window. Slopes are coded red for negative, and blue for positive.



**Figure S3:** Beta coefficients from moving window analysis testing the relationships between precipitation and masting in *Q. rubra*, *Q. alba*, and *Q. montana*. The graph shows slopes for the precipitation effect 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 slopes are plotted according to the day of the year at the end of each 30-day window. Slopes are coded red for negative, and blue for positive.



**Figure S4:** 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.