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Climate Change Strengthens Selection for Mast Seeding in European Beech

Highlights

- Predation and pollination select for masting in European beech
- The population-level phenomenon (synchrony) is driven by individual-level selection
- Trees responsive to weather cues are more variable and better synchronized
- Climate change increased selection pressure for masting from seed predators

Authors

Michał Bogdziewicz, Dave Kelly, Andrew J. Tanentzap, Peter A. Thomas, Jonathan G.A. Lageard, Andrew Hackett-Pain

Correspondence

michalbogdziewicz@gmail.com

In Brief

Bogdziewicz et al. show how predator satiation and pollination efficiency select for high inter-annual variability and synchrony of reproduction in masting trees. Climate change increased the selection pressure for masting from predators, showing how natural selection is acting to restore fitness benefits of masting that decreased because of warming.

Climate Change Strengthens Selection for Mast Seeding in European Beech

Michał Bogdziewicz,^{1,2,8,*} Dave Kelly,³ Andrew J. Tanentzap,⁴ Peter A. Thomas,⁵ Jonathan G.A. Lageard,⁶ and Andrew Hacket-Pain⁷

¹Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umutłowska 89, 61-614 Poznan, Poland

²CREAF, Universitat de Autònoma Barcelona, Cerdanyola del Valles, 08193 Catalonia, Spain

³Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

⁴Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, Downing St., Cambridge CB2 3EA, UK

⁵School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK

⁶Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK

⁷Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool L69 7ZT, UK

⁸Lead Contact

*Correspondence: michalbogdziewicz@gmail.com

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SUMMARY

Climate change is altering patterns of seed production worldwide [1–4], but the potential for evolutionary responses to these changes is poorly understood. Masting (synchronous, annually variable seed production by plant populations) is selectively beneficial through economies of scale that decrease the cost of reproduction per surviving offspring [5–7]. Masting is particularly widespread in temperate trees [8, 9] impacting food webs, macronutrient cycling, carbon storage, and human disease risk [10–12], so understanding its response to climate change is important. Here, we analyze inter-individual variability in plant reproductive patterns and two economies of scale—predator satiation and pollination efficiency—and document how natural selection acting upon them favors masting. Four decades of observations for European beech (*Fagus sylvatica*) show that predator satiation and pollination efficiency select for individuals with higher inter-annual variability of reproduction and higher reproductive synchrony between individuals. This result confirms the long-standing theory that masting, a population-level phenomenon, is generated by selection on individuals. Furthermore, recent climate-driven increases in mean seed production have increased selection pressure from seed predators but not from pollination efficiency. Natural selection is thus acting to restore the fitness benefits of masting, which have previously decreased under a warming climate [13]. However, selection will likely take far longer (centuries) than climate warming (decades), so in the short-term, tree reproduction will be reduced because masting has become less effective at satiating seed predators. Over the long-term, evolutionary responses to climate change could potentially increase inter-annual variability of seed production of masting species.

RESULTS

Mast seeding is thought to be selectively beneficial because inter-annual variability and synchrony of seed production increase the fitness of plants through economies of scale that decrease the cost of reproduction per surviving offspring [5–7]. The two economies of scale with the most empirical support are positive density-dependent pollination success and predator satiation. The pollination efficiency hypothesis states that large and synchronized flowering effort enhances pollination success by increasing the density of flowers, especially in wind-pollinated plants [14–16]. Similarly, the predator satiation hypothesis states that masting decreases average seed predation by satiating predator populations in years of high seed production [17, 18] and sometimes also starving them in low-seed years [19–21]. Importantly, these two economies of scale differ in how they are affected on ecological timescales by patterns of seed

production. Predator satiation is crucially dependent on the sequence of high and low seed production years and the magnitude of the change from one year to the next, whereas pollination efficiency is affected only by the magnitude of each flowering year irrespective of the order in which they occur [22–24].

Pollination and predation should consequently select for different temporal patterns of reproduction. Pollination selects for population flowering efforts to be above the threshold for efficient pollination [14]. Where a species or population has insufficient resources to maintain flowering effort above this threshold during every flowering event, pollination should select for high variability across years. This strategy ensures that high pollination success is achieved because plants concentrate most of their reproductive allocation into fewer but larger flowering events [25, 26]. Importantly, selection for better pollination is not expected to lead to systematic changes in the temporal autocorrelation of seed production. In contrast, predation is

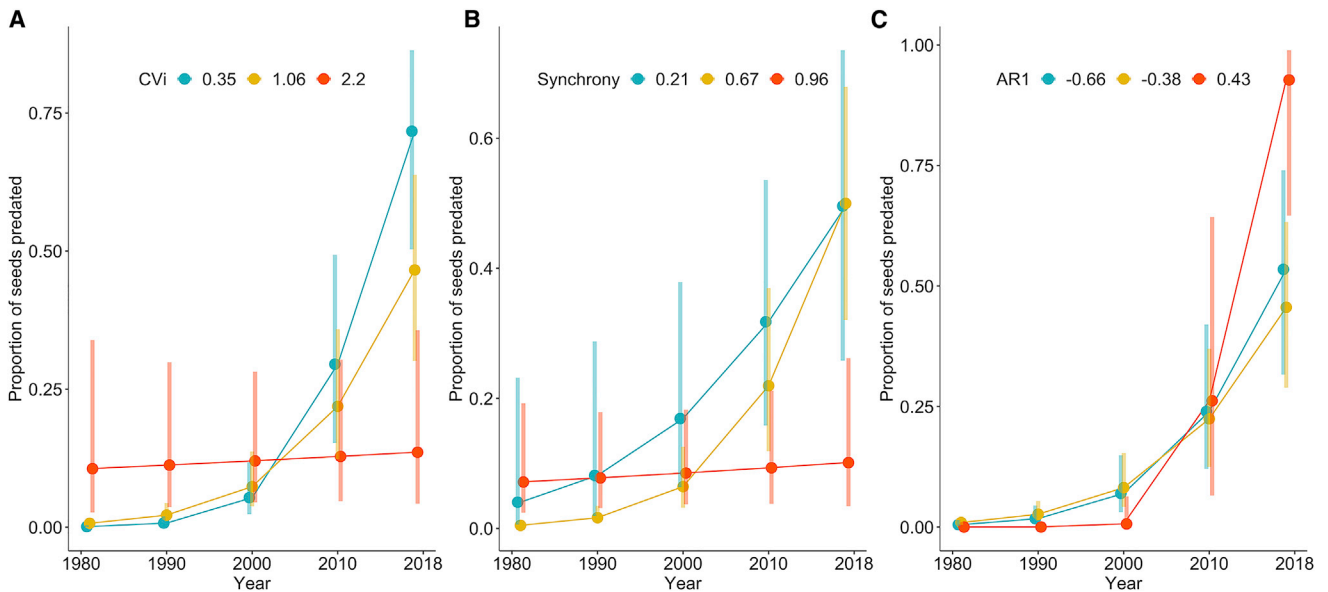


Figure 1. Temporal Increase in Predation Pressure Selects against Trees with Less Variable and Less Synchronized Reproduction

Temporal change in relationship between seed predation of beech by *C. fagiglandana* and (A) inter-annual variability CVi, (B) among-plant synchrony, and (C) lag1 temporal autocorrelation of seed production AR1. Points are estimated marginal means of seed predation for selected years from generalized linear mixed models and associated 95% confidence intervals (see also Table 1). For each metric (CVi, synchrony, and AR1), predictions are plotted for the minimum, mean, and maximum values (see color legend in each panel).

expected to select for strong negative temporal autocorrelation in seed production, i.e., with greater differences, on average, between successive years and high years not following each other [23, 25]. This strategy results in smaller predator populations and most seeds being produced in high-seed years when predation rates are lower [25]. Both pollination efficiency and seed predation should also select for high reproductive synchrony, because benefits accrue mostly to plants producing large reproductive efforts in phase with other individuals in the same population [27, 28].

In this study, we used 39 years of seed production data from 139 individual European beech (*Fagus sylvatica*) trees to test whether seed predation and pollination efficiency select for masting in this species. Our past studies on these populations have shown that inter-annual variation and synchrony in seed production have decreased in recent years, while the abundance of the main predispersal seed predator, *Cydia fagiglandana*, has increased [13]. In the early years of the study, seed predation rate was low (~1%) for all trees, irrespective of their masting behavior (Figure 1). However, by the end of the study, predation rate was higher overall (~40%). The increase in predation was largely attributed to increases in mean seed crops and increasing temperatures (Figure S1).

The temporal increase in seed predation, and temperature-related changes in masting patterns, had major consequences for predation-related changes in the relative fitness of plants with different masting patterns. Selection has increased against phenotypes with lower inter-annual variability in seed production (CVi), lower among-tree reproductive synchrony, and positive temporal autocorrelation (AR1) (Figure 1; Table 1; Table S1). For example, in 1980, the estimated predation rate equaled 4% for poorly synchronized plants (mean cross-correlation

~20%) and 7% for highly synchronized plants (mean cross-correlation ~90%). By 2018, estimated predation for plants with the same level of synchrony equaled 48% for poorly synchronized plants but only 10% for highly synchronized plants. Comparison of selection differentials (which estimate indirect selection) and selection gradients (which estimate direct selection) suggested that predation selected against positive AR1 values indirectly (Table 1; Table S1), through a negative correlation of AR1 with synchrony (Figure S1; Table S2). Thus, our analysis shows that climate change strengthens phenotypic selection under predator satiation for high inter-annual variability and high synchrony of reproduction in European beech, via both direct and indirect effects.

The selection driven by pollination efficiency was different from that under predator satiation, consistent with theory [23, 25]. We found that pollination efficiency also selected for high inter-annual variation and high synchrony in seed production but did not select for AR1 (Figure 2). Furthermore, rather than increasing over time as predator satiation did, this pollination selection effect was consistent through the 39 years of the study (Table 1). Pollination efficiency showed a generally positive relationship with inter-annual variation, but pollination efficiency peaked at CVi ~1.5 (Figure 2). Similarly, more synchronized trees achieved higher pollination efficiency (Figure 2). However, selection gradients from pollination efficiency models suggested that selection for high reproductive synchrony was not caused by direct selection but rather by positive indirect selection from the positive correlation with CVi (Figure S2; Table S2). Moreover, the observation that neither predation pressure nor pollination efficiency directly selected for AR1 aligns with the lack of an association between AR1 and hypersensitivity to the weather cues (see below). In other words, AR1 is a secondary feature of the

Table 1. Predator Satiation and Pollination Efficiency Select for Masting

Dependent Variable: Seed Predation			
Independent Variable	Effect Size (SE)	z-value	p Value
CVi	0.71 (0.17)	4.29	< 0.001
CVi × year	−0.03 (0.005)	−5.26	< 0.001
Synchrony	0.83 (0.17)	4.85	< 0.001
Synchrony ²	0.53 (0.11)	4.62	< 0.001
Synchrony × year	−0.04 (0.006)	−6.69	< 0.001
Synchrony ² × year	−0.02 (0.004)	−5.24	< 0.001
AR1	−0.04 (0.09)	−0.46	0.64
AR1 ²	−0.35 (0.11)	−3.09	0.002
AR1 ² × year	0.01 (0.003)	3.65	< 0.001
Year	0.12 (0.005)	19.92	< 0.001
Dependent variable: pollination success			
Independent variable			
CVi	0.24 (0.07)	3.56	< 0.001
CVi ²	−0.10 (0.03)	−3.53	< 0.001
Synchrony	0.15 (0.06)	2.55	0.01
AR1	−0.07 (0.05)	−1.33	0.18
Year	−0.02 (0.003)	−6.28	< 0.001

Selection differentials (*S*) for inter-annual variation (CVi), synchrony, and temporal autocorrelation of seed production (AR1) of 139 European beech trees were predicted with mixed-effects models. Fitness was measured by the proportion of predated or proportion of successfully pollinated seeds. Masting metrics were standardized to aid direct comparisons of effect sizes. Non-significant interaction and quadratic terms were dropped from the final models. Selection gradients (β) are given in Table S2, and correlations between masting metrics are in Table S1. See Analysis: Phenotypic selection for definitions of selection differentials and selection gradients.

reproductive time series that arises because of inter-annual variation and synchrony of seed production rather than a feature under direct selection itself.

Janzen [7] predicted that shared fluctuation in seed production (synchrony) is achieved by selection for hypersensitivity to a climate cue [29]. Such a system can evolve through selective amplification of initially modest synchrony, driven by either positive cues (e.g., warm summers), which let many plants produce larger seed crops, or negative cues (e.g., frosts), which constrain reproduction in some years and free resources for a larger effort the following year [30–32]. Through this process, individuals synchronized by weather events gain benefits through low seed predation or low pollen limitation. The eventual prediction of Janzen’s hypothesis [7] is that phenotypes that strongly respond to occasional weather signals should have higher inter-annual variation, higher synchrony of reproduction, and consequently higher individual fitness because they achieve larger economies of scale.

In support of Janzen’s predictions, beech trees more responsive to weather cues were better synchronized with their neighbors and gained larger economies of scale. The weather cue we used was site-level, mean maximum monthly (June and July) temperature in the year preceding masting

because it is a widely reported correlate of seed production in European beech, including in our populations [13]. Plants with a higher positive correlation coefficient with the cue tended to mature successfully higher proportions of seeds (regression slope: $\beta \pm SE = 1.04 \pm 0.3$, $p < 0.001$) (Figure 3A). The beech trees unresponsive to the cue had an estimated success of seed maturation (i.e., successful pollination and predator escape) of around 25%, half that of the most responsive plants (Figure 3A). Thus, individuals that are well correlated with the weather cue are under positive directional selection. Mechanistically, the higher responsiveness to weather cues was associated with higher synchrony (regression slope: $\beta \pm SE = 0.20 \pm 0.05$, $p < 0.001$) (Figure 3B) and higher inter-annual variation (regression slope: $\beta \pm SE = 0.46 \pm 0.12$, $p < 0.001$; Figure 3C) but was unrelated to temporal autocorrelation of seed production (regression slope: $\beta \pm SE = -0.09 \pm 0.07$, $p = 0.25$; Figure 3D). These results support the long-standing assumption that plant phenotypes that strongly respond to occasional weather signals should have higher inter-annual variation and higher synchrony of reproduction and consequently larger economies of scale.

DISCUSSION

Climate change strengthens selection for mast seeding. Our analysis suggests that warming temperatures increased seed predator abundance directly through its effects on the insect populations and indirectly by altering the masting behavior of beech trees (Figure S1) [13]. The climate-driven increase in predation pressure translated into stronger selection against individual trees that were poorly synchronized with their neighbors and had lower year-to-year variability. Assuming that masting traits are heritable [33, 34], stronger selection will lead to higher synchrony and variability of masting over time. This stronger natural selection is potentially good news for beech because it provides an eventual mechanism to restore the benefits of masting that have declined through climate change over the last four decades [13]. Unfortunately, the response is likely to be an order of magnitude slower than the original negative climate-driven changes. Masting benefits will only be restored when seedlings from the fitter trees replace the current canopy, a slow process given that these trees normally live for centuries and only become reproductively active after several decades [35]. Hence, our study shows the ultimate power of natural selection to respond to a warmer climate. Yet, such responses require far longer timescales than the climate changes that have provoked them.

Masting as a reproductive strategy is costly because it requires plants to delay reproduction [6, 36]. Such a strategy will evolve, however, if individual plants achieve greater fitness through variable seed production across years than they would through more constant annual production (so-called economies of scale) [22, 27, 37]. In support for the economies of scale, we found that seed predation and pollination efficiency selected for variability and synchrony of reproduction in European beech. Even though masting is a population-level phenomenon, it is selected at the individual-level because plants that are hyper-responsive to a weather cue tended to have higher inter-annual variability and higher reproductive synchrony. Consequently,

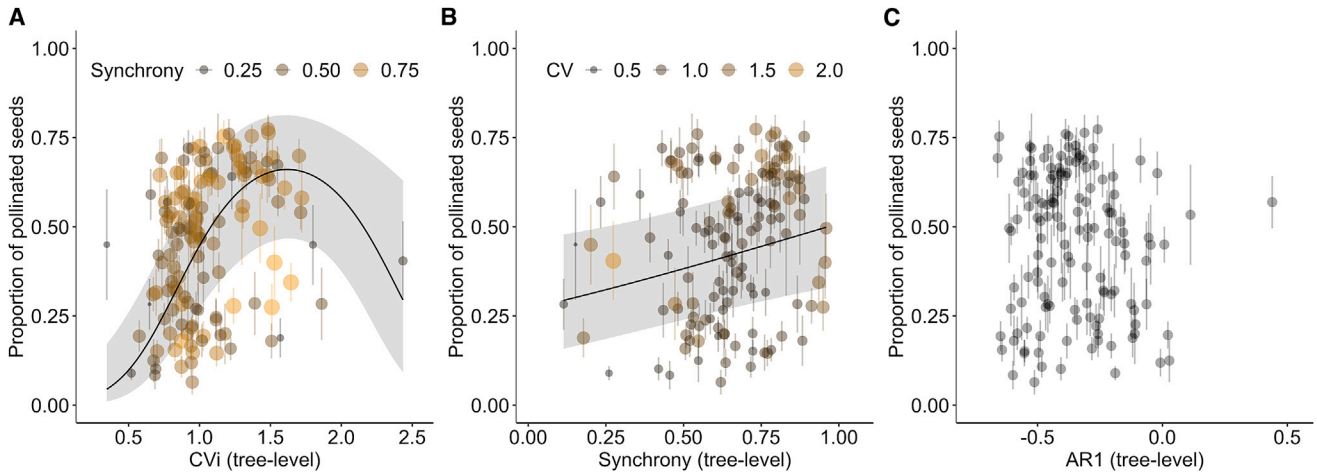


Figure 2. Pollination Efficiency Selects for High Inter-annual Variability and High Among-Plant Synchrony in Reproduction

Correlation between proportion of pollinated seeds and (A) inter-annual variability (CVi), (B) among-plant synchrony, and (C) lag1 temporal autocorrelation (AR1) of seed production. Prediction lines from generalized linear mixed models for 139 beech trees observed through 39 years, and ribbons are 95% confidence intervals for the model estimates. Only statistically significant relationships are plotted. Points represent tree-level means and associated standard errors. Refit of the model in (A) with the tree with CVi ~2.5 removed results in qualitatively the same pattern (see Figure S4).

these plants have higher seed maturation success. Overall, this provides empirical support for the notion that more variable and better synchronized individuals can gain larger reproductive

success and thus potentially invade and replace less strongly masting populations, a central process in models of masting evolution [36, 38].

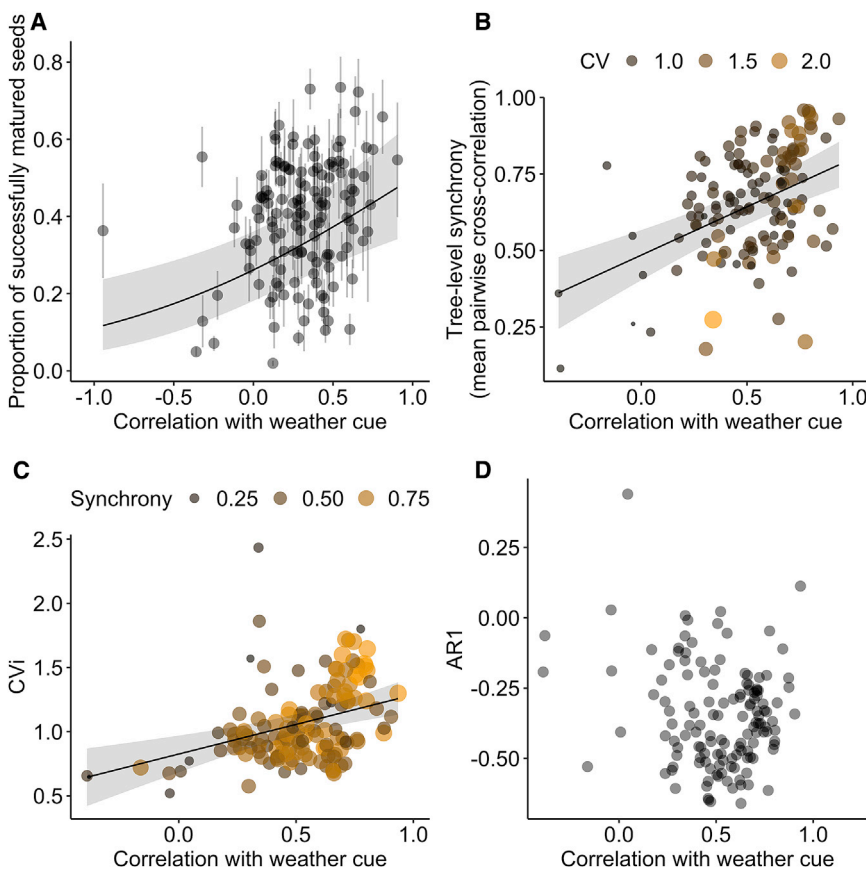


Figure 3. Economies of Scale Select for Masting through Favoring Plants that Respond to Weather Cues

We compared the tree-level correlation of yearly seed production with summer (June–July mean monthly maximum) temperature in the previous year with the (A) proportion of successfully matured seeds (pollinated and not predated), (B) among-plant synchrony, (C) year-to-year variability, and (D) temporal autocorrelation of seed production. Lines are from generalized linear mixed models for 139 beech trees observed through 39 years, and ribbons are 95% confidence intervals for the model estimates. Only statistically significant relationships are plotted. Points are tree-level observations with associated standard errors in (A).

Past theoretical studies suggested that natural selection can act either separately or concomitantly on different aspects of masting behavior [23, 39]. By separating pollination efficiency and seed predation as selective agents, we show that seed predators select directly for greater CVi and increased reproductive synchrony. In contrast, wind pollination selects for greater inter-annual variability but only indirectly for higher reproductive synchrony. Classical theory predicts that economies of scale can select for high inter-annual variability by favoring plant responses to weather cues [7, 40]. As Janzen noted, plants are not literally synchronized with each other, but each is responding independently to the same weather cue, and plants which do so can gain a large economy of scale [7, 40]. Our analysis lends empirical support for such an evolutionary process, showing that weather cues are associated with large economies of scale.

Our results suggest that climate change is an important contributor to evolutionary change in European beech. Thus, to predict the long-term reproductive patterns of trees in response to global climate change, we need to consider both the immediate phenotypic effects on reproduction [13] and the potential evolutionary responses to changes in natural selection [41, 42]. Our study suggests that these responses can reinstate masting intensity eroded by global warming through altering the relationship between adaptive optima and phenotypic means, albeit this process likely operates on centennial timescales. Therefore, over the long term, climate change has potential to increase inter-annual variability of reproduction in masting species and induce masting in species that so far have reproduced more regularly [43]. Many species, including trees, are unlikely to migrate quickly enough to track the rapidly changing climate of the future [41, 44, 45]. The adaptive potential documented here must therefore play an increasingly important role in ensuring their persistence *in situ*. In the near term, our results suggest tree reproduction will be reduced by climate change because masting has become less effective, which may further slow range adjustments. Ultimately, how reproduction in beech and other tree species evolves with climate change will determine the structure and diversity of twenty-first century forests, function of food webs, and ecosystem services important for human welfare [10, 12, 45].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.06.056>.

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AUTHOR CONTRIBUTIONS

M.B. conceived the study and drafted the manuscript. M.B. led the analysis with input from all authors. P.A.T., J.G.A.L. and A.H.-P. collected and managed the data. All authors interpreted the results, revised the text, provided critical feedback, and helped shape the final text.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
R software version 4.0.0 (2020-04-24)	The R Project for Statistical Computing	https://www.r-project.org/
glmmTMB_0.2.3 R package	[46]	https://cran.r-project.org/web/packages/glmmTMB/index.html
Other		
139 beech trees at 12 sites spaced across England	This paper	See Figure S3

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Michał Bogdziewicz (michalbogdziewicz@gmail.com)

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

The datasets generated during this study are available on request to the corresponding author. The study did not generate code.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study species and sites

Seed production of 139 beech trees located at 12 sites spaced across England ([Figure S3](#)) was sampled annually for 39 years (1980–2018). European beech (*Fagus sylvatica* L.) is a major forest-forming species in temperate Europe. It is wind-pollinated, and induces flower buds in the summer prior to the flowering year [35]. Flowers are produced in spring, and are fertilized and develop into mature fruit in the same year as they were pollinated. The seeds are then eaten and dispersed by a suite of vertebrates [47, 48], and destroyed by a seed-eating moth, *Cydia fagiglandana* Z. (Tortricidae). *C. fagiglandana* is the main pre-dispersal predator of beech seeds and has a univoltine cycle with five larval stages. Adults fly from July to September. Larvae grow within nuts feeding on the cotyledons until completing development, when they drill an exit hole through the seed coat to leave the nut. The insect species does not undergo prolonged diapause. Because fruit and seed coats develop irrespective of whether pollination occurs, but unpollinated fruits lack a seed (kernel) [49], relatively accurate estimates of pollination can be made from seed production data. Our previous study revealed that climate warming over recent decades has increased seed production of European beech at our sites, but decreased the inter-annual variability of seed production and the reproductive synchrony among individuals [13]. Consequently, the benefits that the plants gained from masting has declined – mean seed predation increased while mean pollination efficiency decreased over the last four decades.

METHOD DETAILS

Field studies of beech reproduction

The ground below each tree was searched for seeds for 7 min, and seeds were counted as sound, or empty with formed pericarps (not pollinated), or damaged by *Cydia fagiglandana* moths. Seeds killed by *Cydia* were filled with dark frass and had a round exit hole in the seed coat. This captured predispersal mortality (primarily by *Cydia*), and sampling within days of maximum seed fall each year minimized postdispersal loss of full seeds to predators [50]. Mean monthly maximum temperature for each site was obtained from the corresponding 0.25° grid cell of the E-OBS dataset version 19.0e [51].

QUANTIFICATION AND STATISTICAL ANALYSIS

Seed production and masting behavior

We calculated three individual-tree level masting metrics that are widely used to characterize reproductive patterns of plants [23, 52–54]: inter-annual variability of seed production of individuals (coefficient of variation, CVI); lag-1 autocorrelation of seed production at

the tree level (AR1), wherein negative numbers indicate populations that alternate between years of high and low seed production; and synchrony of seed production by plants, as measured by the average pairwise Pearson's correlation of seed production between individual plants in a site through time. Past studies in these populations revealed that inter-annual variability and synchrony of seed production declined over the last four decades (see *Study species*). We thus tested if the correlations between metrics persisted over time by splitting the dataset into two parts (first 20 years versus the last 19 years, since masting behavior can only be quantified on subsets of sufficient length), and calculating the metrics on each subset. We then analyzed intercorrelations between these three metrics using linear mixed models with study site included as a random intercept and metric by time interactions as fixed effects.

Temporal trends in seed predation

To attribute the temporal trends in seed predation to their possible drivers, we used the temporal contribution method [55, 56]. First, using the tree ID and site as random intercept terms and an autoregressive order-1 autocorrelation structure, we modeled seed predation as a function of beech seeding behavior and of temperature, i.e., variables that can affect *Cydia* population abundance. The temperature variables included mean temperature for the period between July and September, which covers the time of adult insect activity [57], and December and March, which can be important for wintering survival of larvae [46]. We also included current year seed production and the difference between seed production in the current versus the previous year, i.e., variables that affect predation by starving and satiating insects [13]. We first calculated the observed time trend in the predation rate (slope \pm standard error) in our data using binomial GLMM. We then calculated the trend predicted by the full model and the trends predicted by the same model but maintaining individual predictors constant (e.g., winter temperature is held constant, using the median values per site, while all other predictors change according to the observations). The difference between the observed trend and when one variable was constant was the contribution of that predictor variable to the change in the response variable. The difference between all individual contributions and the observed trend were considered to be unknown contributions. All errors were propagated using standard methods [55].

Phenotypic selection

We estimated phenotypic selection in beech populations using regression-based techniques developed by Lande and Arnold (1983). The method estimates the strength of natural selection by regressing fitness on the phenotype [58, 59]. In our study, fitness was measured as pollination efficiency and predation rate (see below). For each selection analysis described below, we built two types of models. We constructed univariate models for each masting metric to estimate selection differentials (S) for each reproductive trait (indirect selection). We also estimated selection gradients (β), which measure direct selection on each trait after removing indirect selection from all other traits in the analysis by using multiple regressions [58, 59]. In other words, selection differentials measure indirect selection, while selection gradients measure direct selection.

We tested whether pollination efficiency and predation selected for masting in European beech using generalized linear mixed models (GLMMs) with a binomial error term. Using the tree ID and site as the random intercepts and an autoregressive order-1 autocorrelation structure, we modeled the proportion of successfully pollinated seeds or proportion of predated seeds as a function of tree-level masting metrics: inter-annual variation (coefficient of variation, CVI), among-plant synchrony (mean Pearson pairwise cross-correlation), and tree-level lag1 temporal autocorrelation (AR1) in seed production. Directional and nonlinear selection differentials were estimated by including linear and quadratic effects of independent variables, respectively. We tested for heterogeneity in selection on masting across years by including an interaction term for each masting metric with year (as a continuous variable) as fixed effects in our models. Models included observation-level random intercepts to correct for overdispersion. The interaction and quadratic terms were removed from final models if not statistically significant.

We tested whether selection eliminates phenotypes that are insensitive to environmental cues that cause reproductive synchrony in two steps. In the first step, we tested whether higher individual tree-level correlations with mean summer (June-July) temperature one year before seedfall increased the probability of producing a viable seed (both pollinated and unpredated, combined). We used a binomial GLMM with tree ID and site as the random intercepts and an autoregressive order-1 autocorrelation structure. Mean summer (June-July) temperature in the previous year is a widely reported weather correlate of seed production in European beech, including in our populations [13, 60–62]. In the second step, we used linear mixed models with site as a random intercept to test the hypothesis that the positive response to the cue (i.e., individual tree-level correlations with mean summer temperature) correlates positively with reproductive synchrony, CVI, and AR1. We fitted all models in R version 3.6.1, and mixed models using the package `glmmTMB` v 0.2.3 [63].