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6 Climate warming disrupts mast seeding and its fitness benefits in European beech

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## 20 **Introductory paragraph**

21 Many plants benefit from synchronous year-to-year variation in seed production, called  
22 masting. Masting benefits plants because it increases the efficiency of pollination and satiates  
23 predators, which reduces seed loss. Here, using a 39 year-long dataset, we show that climate  
24 warming over recent decades has increased seed production of European beech, but decreased  
25 the year-to-year variability of seed production and the reproductive synchrony among  
26 individuals. Consequently, the benefits that the plants gained from masting has declined.  
27 While climate warming was associated with increased reproductive effort, we demonstrate  
28 that less effective pollination and greater losses of seeds to predators offset any benefits to the  
29 plants. This shows that an apparently simple benefit of climate warming unravels because of  
30 complex ecological interactions. Our results indicate that in masting systems, the main  
31 beneficiaries of climate-driven increases in seed production are seed predators, not plants.

32

## 33 **Introduction**

34 Anthropogenic environmental changes exert increasing pressure on forests world-wide<sup>1</sup>.  
35 Research on the effects of environmental change on trees has focused on the impacts on tree  
36 growth, carbon sequestration, mortality, or phenology<sup>2-4</sup>. There have been few studies of the  
37 impacts of environmental change on the reproductive ecology of trees, yet long-term changes  
38 in reproduction determine the ability of trees to disperse to shifting habitats and recolonize  
39 sites after disturbance<sup>5</sup>. What is more, reproduction of trees is likely to be sensitive to climate  
40 change, especially in the case of mast seeding (or masting) species – i.e. those that reproduce  
41 through spatially synchronous and temporally variable seed production – due to strong  
42 correlations of seed production with annual variation in weather<sup>6-8</sup>.

43 Numerous plant species, including the majority of forest-forming tree species in  
44 temperate zones, reproduce through mast seeding<sup>9,10</sup>. While masting plants are expected to be  
45 sensitive to global change<sup>11-13</sup>, the direction of that change is a source of controversy.  
46 Predictions range from an increase, to a decrease, to an unchanged strength of masting (i.e.  
47 interannual variability and synchrony) in response to climate change<sup>11,14,15</sup>, depending on the  
48 sensitivity of masting to climate and associated resources. However, the strength of masting is  
49 crucial in terms of plant fitness and forest regeneration, since masting is a life history trade-  
50 off between missed reproductive opportunities in low-seed years and enhanced pollination  
51 efficiency and decreased seed predation in mast years<sup>16-18</sup>. Studies that measure seed  
52 production, pollination efficiency, and seed predation for long enough to capture potential  
53 change are the key to understanding how anthropogenic climate change will affect plant

54 reproduction and thus global vegetation dynamics, but such studies are virtually non-existent.  
55 Here, we report on a unique 39-year study of 139 individuals of European beech (*Fagus*  
56 *sylvatica*) across twelve sites in England that documents how the success of this major  
57 European forest-forming tree species, including seed production, pre-dispersal seed predation  
58 by *Cydia fagiglandana* (Lepidoptera), and pollination success, has changed throughout the  
59 last four decades.

60 Mast seeding enhances plant fitness through economies of scale that decrease the cost  
61 of reproduction per surviving offspring<sup>12,19</sup>. This mainly happens through two mechanisms.  
62 The first is that large and synchronized flowering effort enhances pollination success, because  
63 pollination efficiency is increased when the density of flowers is high (density dependent,  
64 pollination efficiency hypothesis)<sup>16,20,21</sup>. Secondly, masting decreases seed predation by  
65 starving predator populations in years of low-seed production, and then satiating them in  
66 high-seed years (predator satiation hypothesis)<sup>22-24</sup>. Predator satiation is crucially dependent  
67 on the sequence of high and low years, whereas pollination efficiency is affected by the size,  
68 not sequence, of high-flowering years<sup>25</sup>. Therefore, the effects of global change will act  
69 differently on these two economies of scale, depending on how it alters plant reproductive  
70 variability and reproductive synchrony. This, in turn, depends on the causal relationship  
71 between masting and weather cues. Notably, if plants respond to the temperature difference  
72 between the two previous summers, as suggested by the  $\Delta T$  model, then masting should be  
73 relatively insensitive to increased mean temperatures (though sensitive to changes in  
74 temperature fluctuation)<sup>14</sup>. By contrast, if seed production is driven by interactions between  
75 plant internal resource dynamics and weather cues such as warm absolute temperatures, more  
76 frequent cueing will decrease synchrony among plants, reducing population-level year-to-year  
77 variation in seed crops<sup>17,26</sup>. Similarly, according to the environmental stress hypothesis,  
78 resource-augmented plants should increase mean seed production, and their reproduction  
79 should become less variable over time<sup>25,27</sup>. If global environmental change disrupts masting  
80 patterns, the long-term regeneration of masting plants may decrease at the same time as global  
81 warming requires increasingly rapid geographic range shifts to keep species within suitable  
82 climate zones<sup>28,29</sup>.

83

## 84 **Results**

85 Our 39-year dataset of seed production in 139 European beech trees indicated that  
86 mean reproductive effort increased during the study period, but mast seeding became  
87 progressively weaker (Fig. 1). Mean annual seed production per tree increased (Fig 1a,  $z =$

88 4.29,  $p < 0.001$ ), while the probability of a tree having a year of zero seed production  
89 decreased over time ( $z = -2.29$ ,  $p = 0.003$ ). Accordingly, sliding window analysis indicated  
90 that interannual variation in reproduction measured by the coefficient of variation (CV)<sup>30</sup>  
91 decreased 40% at the population level (CVp) from around 1.15 to 0.70 (Fig 1b,  $z = -4.93$ ,  $p <$   
92  $0.001$ ), and at individual-tree level (CVi) from around 1.30 to 0.80 (Fig 1c,  $z = -9.74$ ,  $p <$   
93  $0.001$ ). Furthermore, synchrony, measured by mean cross-correlation of seed production  
94 among trees, also decreased by 30% from over 0.85 to around 0.60, both at the within-site (Si)  
95 (Fig 1d,  $z = -4.66$ ,  $p < 0.001$ ) and among-site level (Sp) (Fig 1e,  $z = -7.27$ ,  $p < 0.001$ ). Thus,  
96 population-level variation in seeding across years decreased because individual trees varied  
97 less from year to year, and trees were more poorly synchronized.

98 The analysis of abiotic drivers of seed production supported mathematical models of  
99 the role of environmental cues/vetoes in mast seeding, which predict that more frequent  
100 occurrence of weather cues for reproduction should result in a decrease in both variability and  
101 synchrony of seed crops<sup>17,26</sup>. In the case of European beech, seed production correlates  
102 positively with warm summer temperature one year prior to seed dispersal (Supplementary  
103 Table 1), likely by promoting flower initiation<sup>8,31</sup> (the AIC analysis provided less support for  
104 the  $\Delta T$  model as the driver of masting in our population:  $\Delta AIC = 130.5$ , see Supplementary  
105 Table 1). Our analysis of temporal contributions attributed the temporal change in seed  
106 production largely to increasing temperatures (Fig. 2). Sensitivity of seed production to  
107 increasing growing season mean temperature was  $0.64 \pm 0.44$  [mean  $\pm$  s.e.m.] (seeds per 7-  
108 min count per tree  $\text{yr}^{-1}$  for each  $^{\circ}\text{C yr}^{-1}$ ), while sensitivity to increasing summer temperature a  
109 year prior to seed dispersal was  $1.30 \pm 0.90$  (seeds per 7-min count tree  $\text{yr}^{-1}$  for each  $^{\circ}\text{C yr}^{-1}$ ).  
110 This suggests that the increase in mean seed production was caused by two parallel  
111 mechanisms. First, warmer growing season temperatures are likely to enhance average seed  
112 output through lengthening of the growing season and increased photosynthesis<sup>32</sup>. Second,  
113 more frequent warm summers in recent years apparently trigger large flowering events more  
114 frequently, and simultaneously reduce the frequency of years with no reproduction. The  
115 resource budget model predicts that more frequent weather cueing should weaken the  
116 reinforcing dynamics of stored resources on among-tree synchrony of reproductive  
117 variation<sup>17,26</sup> – a pattern consistent with our data. While other variables, such as summer  
118 temperature two years before seed fall or nitrogen deposition in the past 5 years, significantly  
119 explained variance of annual seed production in our beech populations (Supplementary Table  
120 1), they did not correlate with the temporal trends in seed production (Fig. 2).

121           Unfortunately for the trees, desynchronization and more regular seeding weakened the  
122 masting benefits that economies of scale provided to European beech (see Supplementary  
123 Table 2 for outputs of all models). The proportion of pre-dispersal seed predation by *Cydia*  
124 sharply decreased with increasing ratio of the previous to the current year seed production  
125 (Fig. 3,  $z = -8.90$ ,  $p < 0.001$ ), indicating a strong starvation effect (numerical response) of  
126 beech masting on the moth population. The slope of that relationship did not change with  
127 time, but the intercept progressively increased with time ( $z = 9.72$ ,  $p < 0.001$ , Fig. 3). Thus,  
128 while masting still starved insects during years of low seed production, a lesser effect on  
129 predator numbers was seen in recent years (Fig. 3). Moreover, in accordance with the predator  
130 satiation hypothesis, weaker predator starvation resulted in less effective predator satiation:  
131 the proportion of predated seeds decreased with the number of seeds produced, but the slope  
132 of that relationship became less steep in recent years (interaction term seed production  $\times$  year:  
133  $z = 2.66$ ,  $p = 0.008$ , Fig. 3).

134           In the case of pollination efficiency economy of scale, the proportion of successfully  
135 pollinated seeds increased with the summed reproductive effort of conspecifics in the  
136 population, and that effect was stronger in years when the synchrony of flowering was higher  
137 (Fig. 3, Supplementary Table 2). In the model that included both summed conspecific  
138 flowering effort and synchrony, the effect of year was not significant ( $p = 0.07$ ). Thus, while  
139 large and synchronized reproductive effort always increased pollination efficiency, such large  
140 and synchronized flowering efforts happened less often in recent years, lowering the mean  
141 pollination efficiency (see below).

142           As a consequence of these weakened economies of scale, the estimated proportion of  
143 seeds predated by insects increased dramatically from 1% at the beginning of the study to  
144 over 40% in the final years (linear effect:  $z = 6.07$ ,  $p < 0.001$ , quadratic effect:  $p = -3.42$ ,  $p <$   
145  $0.001$ , Fig. 4). Simultaneously, the pollination efficiency decreased from 50% to 33% ( $z = -$   
146  $2.20$ ,  $p = 0.03$ , Fig. 4). Thus, the large temporal increase in total seed production (Fig. 4,  $\beta =$   
147  $0.04 \pm 0.01$  [SE]) became weaker once only pollinated seeds were considered ( $\beta = 0.03 \pm$   
148  $0.01$ ,  $z = 4.21$ ,  $p < 0.001$ ), and that positive trend almost disappeared for only pollinated and  
149 not predated seeds ( $\beta = 0.02 \pm 0.01$ ,  $z = 2.22$ ,  $p = 0.04$ , Fig. 4). Overall, the increased  
150 predation pressure and decreased pollination efficiency led to 2.6-fold decrease in the  
151 probability that a female flower becomes a sound seed. This probability was estimated to  
152 equal 47% (95% confidence interval: 31% – 65%) at the beginning of the study period, and  
153 decreased to 18% (7% – 36%) in 2010s (Fig. 4). This implies that the costs to European beech

154 per viable seed more than doubled during the last four decades as economies of scale became  
155 increasingly ineffective (Fig. 4d).

156

## 157 **Discussion**

158 Altered mean seed production induced by global changes has been reported in few previous  
159 studies, and has found both increase<sup>33,34</sup>, and decrease<sup>27</sup> in reproductive effort. How this  
160 translates into recruitment potential was, however, unknown since this crucially depends on  
161 parallel changes in variability and synchrony of reproduction and their consequences for seed  
162 predation and pollination efficiency<sup>7,13</sup>. Our study is the first to show that a long-term  
163 increase in mean seed production is accompanied by a decrease in synchrony and year-to-year  
164 variability of reproduction, and that these are associated with elevated costs. The apparently  
165 improved performance of European beech trees in a warmer world is offset by the breakdown  
166 of selectively beneficial strategies to avoid seed predators and improve pollination. Hence, the  
167 benefits of higher reproductive effort by the trees are largely offset by the effects of lower  
168 pollination success and higher pre-dispersal seed predation.

169         The temporal decrease in variability and synchrony of seed production provides the  
170 first documented natural experiment of how long-term changes in climate alter seed crop  
171 patterns and thereby alter the effectiveness of economies of scale. The predator satiation  
172 hypothesis consists of two parts, in which the starvation of seed predators in years of low seed  
173 production results in the satiation of reduced populations of predators in subsequent mast  
174 years<sup>35,36</sup>. More regular seeding of European beech, and the reduction in the frequency of seed  
175 failures in this study weakened the starvation effect which in turn lowered the effectiveness of  
176 pre-dispersal predator satiation. Such an effect is in line with past experimental and  
177 observational studies that found warming or nitrogen deposition was associated with  
178 increased mean seed production but also higher seed predation<sup>13,37</sup>. Furthermore, the  
179 disappearance of highly-synchronised mast years in recent years reduced the efficiency of  
180 pollination, and thus the proportion of successfully pollinated flowers. Together, the  
181 breakdown in economies of scale resulted in only small reproductive benefits to the studied  
182 trees, disproportionate to the size of the increase in long-term reproductive effort. Worryingly,  
183 successful beech regeneration also requires the successful starvation and satiation of *post-*  
184 dispersal seed predators, especially small mammals<sup>38,39</sup>. Here we show that predator satiation  
185 became less efficient in the case of a pre-dispersal insect seed predator, but if post-dispersal  
186 predator satiation also became less effective, as we would predict, the net effect on surviving  
187 seeds (Fig. 4) could easily be negative overall. This is an important area for further research.

188 Climate warming was the major driver of decreased variability and synchrony of  
189 reproduction in European beech. Even though our statistical analyses do not directly prove  
190 causality, the results support the dominant role of increased temperatures in explaining the  
191 trends in masting pattern. First, our analysis suggested that the trend in increasing seed  
192 production is driven by warming temperatures in the preceding summer, a well-documented  
193 cue for flowering in European beech<sup>8,31,40</sup>. The resource budget models of masting<sup>17,41</sup> predict  
194 that more frequent occurrences of the weather cue will decrease individual variability and  
195 desynchronize flowering by weakening the reinforcing effects that resource dynamics have on  
196 reproductive synchrony<sup>26,42</sup>, which jointly decrease population-level seed production  
197 variability. This mechanism is supported empirically in European beech, as we found that  
198 increased mean seed production is associated both with significantly lower CVi and with  
199 lower synchrony (Si). Second, the important effect on mean seed production of increasing  
200 mean temperatures during growing seasons supports the environmental stress hypothesis, that  
201 predicts masting plants will produce on average more seeds with lower variability when  
202 resource availability is high<sup>10,25,27</sup>. According to this hypothesis, plants growing under  
203 favourable conditions will be able to more rapidly accumulate the resources required for  
204 reproduction and, therefore, present a more regular pattern in seed production – a pattern  
205 consistent with the lower CVi in our data. The environmental stress hypothesis does not  
206 explicitly predict the effect of resource augmentation on reproductive synchrony.  
207 Nevertheless, warmer growing season temperatures and associated increases in resource  
208 availability potentially makes resources less limiting for reproduction, weakening the positive  
209 effect of plant internal resource dynamics on synchronising masting<sup>17,26,43</sup>.

210 The changes in masting patterns reported in this study will have profound implications  
211 for the long-term future of European beech. In northern Europe where beech is predicted to  
212 expand northwards under climate warming<sup>44</sup>, our results hint that a breakdown in masting  
213 might result in recruitment limitation. This emphasises the importance of including realistic  
214 reproduction processes within forest models<sup>45</sup>. Similar processes may explain observed  
215 declines in beech recruitment elsewhere in Europe<sup>46,47</sup>. More generally, our results imply  
216 potential climate-driven changes in the dynamics of beech-dominated ecosystems, including  
217 the spread of Lyme disease and Hantavirus by rodents dependent on beech seeds<sup>48-50</sup>, habitat  
218 selection of ground-nesting birds<sup>51</sup>, and population dynamics of small mammal predators<sup>52</sup>.  
219 Similar changes are likely to occur in other masting species, with other negative conservation  
220 consequences<sup>53</sup>, but such long-term datasets as the one reported here are extremely rare<sup>27</sup>.  
221 Thus, experiments to better understand the mechanisms underlying masting, and consequently

222 better predict the consequences of a changing climate for plant reproductive patterns and  
223 global vegetation dynamics, should become a research priority<sup>54</sup>. The net benefits of climate  
224 warming in the European beech system studied here accrue largely to an invertebrate seed  
225 predator, which suggests that ecological interactions may determine the real-world  
226 consequences of global change.

227

## 228 **Methods**

229 **Study species.** European beech (*Fagus sylvatica* L.) is a major forest-forming species in  
230 temperate Europe. The seeds are eaten and dispersed by a suite of vertebrates<sup>37,55</sup>, and  
231 destroyed by a seed-eating moth, *Cydia fagiglandana* Z. (Tortricidae). Because fruit and seed  
232 coats develop if pollination occurs and unpollinated fruits lack a seed (kernel)<sup>56</sup>, relatively  
233 accurate estimates of pollination can be made from seed production data. European beech  
234 produces flowers in the spring, which are fertilized and develop into mature fruit in the same  
235 year as they were pollinated. Flower induction happens in the summer prior to the flowering  
236 year.

237

238 **Data collection.** We sampled seed production in 139 beech trees located at 12 sites spaced  
239 across England annually for 39 years (1980 – 2018) (Supplementary Figure 1). The ground  
240 below each tree was searched for seeds for 7 minutes, and seeds were later classified as  
241 sound, or empty with formed pericarps (not pollinated), or damaged by *Cydia* sp. moth.  
242 Detailed description of sites and procedures is given in<sup>56</sup>.

243 Nitrogen deposition data for each site was estimated using the FRAME model (Fine  
244 Resolution Atmospheric Multipollutant Exchange<sup>58</sup>), an atmospheric chemistry and transport  
245 model, to produce estimates of N deposition<sup>59</sup>. Deposition data was available at a 5 x 5km  
246 resolution and produced estimates of both total reduced and oxidised N (kg N ha<sup>-1</sup> yr<sup>-1</sup>) over  
247 deciduous forest for three snapshots (1970, 1990, 2010). Linear interpolation was used to  
248 estimate annual deposition. Data was provided by CEH Edinburgh. Mean monthly maximum  
249 temperature and monthly sum precipitation for each site was obtained from the corresponding  
250 0.25° grid cell of the E-OBS dataset (version 19.0e)<sup>60</sup>.

251

## 252 **Analysis.**

253 **Trends in seed production.** We started our analysis by asking whether and how seed  
254 production patterns of European beech changed over the last 39 years. We built a zero-  
255 inflated, negative binomial family generalized linear mixed model (GLMM) with



256 autoregressive order-1 autocorrelation structure, and included total yearly seed production per  
257 tree as a response while year was included as fixed effect in both in count and logit part of the  
258 model. The model included tree ID and site as random intercepts.

259 **Temporal contributions and sensitivities of changes.** To attribute the temporal trends in  
260 seed production to its possible drivers, we used the temporal contribution method<sup>61,62</sup>. First,  
261 using the tree ID and site as the random intercepts and an autoregressive order-1  
262 autocorrelation structure, we modelled seed production as a function of weather cues  
263 identified as important for beech seeding in past studies<sup>63,64</sup>, i.e. mean max temperature and  
264 summed precipitation in summer (June and July) one and two years before seed dispersal. We  
265 also included mean temperature in the growing season (May-August) and nitrogen deposition,  
266 i.e. the cumulative totals of the previous 5 years to test whether resource augmentation drives  
267 the trend. We then used the full model to predict the change of the response variables during  
268 the study period (1980–2018). We first calculated the observed trend (slope estimate  $\pm$   
269 standard error of the slope estimate) in our data using GLMMs with random intercepts and  
270 temporal autocorrelation structure (see above, Trends in seed production). We then calculated  
271 the trend predicted by the full model and the trends predicted by the same model but  
272 maintaining the predictors constant one at a time (e.g., summer temperature is held constant,  
273 using the median values per site, while all other predictors change according to the  
274 observations). The difference between the observed trend and when one variable was  
275 controlled was the contribution of that predictor variable to the change in the response  
276 variable. The difference between all individual contributions and the observed trend were  
277 considered to be unknown contributions. Finally, we calculated the average seed production  
278 sensitivities to predictor changes by dividing the temporal contributions by the trends of the  
279 predictor variables. All errors were calculated using the error-propagation method<sup>61</sup>.

280 **Changes in masting behaviour (time series).** To explore whether changes in mean seed  
281 production were accompanied by changes in annual variation and among-plant synchrony in  
282 reproduction we calculated variability and synchrony on a 10-year sliding window with 1-  
283 year step size from 1980 to 2018 for each tree (for plant-level analysis) or site (for site-level  
284 analysis) separately. We used the coefficient of variation (CV) as a measure of temporal  
285 variability, and the mean Pearson cross-correlation as a measure of reproductive synchrony.  
286 CV was calculated both at tree- (CV<sub>i</sub>) and population-level (CV<sub>p</sub>)<sup>30</sup>. Similarly, synchrony  
287 was calculated as a mean pairwise correlation of seed production of an individual plant with  
288 all other individuals observed at the site (within-site synchrony, S<sub>i</sub>), or as a mean pairwise  
289 correlation of mean site-level seed production with all other sites (among-populations

290 synchrony,  $Sp$ ). Next, these rolling masting metrics were included as a response in linear  
291 mixed models with autoregressive order-1 autocorrelation structure and tree ID and site (for  
292  $CV_i$  and  $Si$ ) or only site ( $CV_p$  and  $Sp$ ) included as random intercepts.

293 **Economies of scale.** We explored whether beech masting provides fitness benefit through  
294 economies of scale, and whether that benefit changed with time. To do so, we built three  
295 binomial family GLMMs: two with proportion of seeds predated (predator satiation economy  
296 of scale), and another with proportion of seeds pollinated (pollination efficiency economy of  
297 scale) included as a response, all per tree per year. In all models, we used tree ID and site as  
298 random intercepts, observation-level random effect to account for overdispersion, and  
299 autoregressive order-1 autocorrelation structure. In the first predator satiation model, the fixed  
300 effect included tree-level yearly seed production (satiation effect or functional response of the  
301 predator), while in the second, the fixed effect included the ratio of the number of seeds  
302 produced in the current year to the number produced in the previous year (starvation effect or  
303 the numerical response of the predator). In the pollination efficiency model, fixed effects  
304 included summed number of total seeds produced by all conspecific trees at a particular site,  
305 the within site within year synchrony of seeding (calculated as coefficient of variation), and  
306 their interaction term. In all models, we also included the quadratic terms of fixed effects  
307 which were retained or dropped based on the standard AIC criteria<sup>65</sup>. Finally, to test for  
308 temporal patterns in economies of scale we included the second-order interactions of the  
309 above-listed fixed factors with year. These were removed from the final models if not  
310 significant.

311 **Temporal changes in pollinated and unpredated seeds, and costs of reproduction.** In the  
312 final step, we explored how the proportion of pollinated and predated seeds changed over  
313 time, how this translated into the production of “pollinated”, and “pollinated and not  
314 predated” seeds, and how all these affected beech reproductive costs. The temporal change in  
315 proportion of predated and pollinated seeds was tested using binomial GLMMs with similar  
316 structure as in tests of economies of scale, but using year as a fixed factor. In the case of  
317 proportion of predated seeds, we also included the previous year seed production as a  
318 covariate as this strongly affects *Cydia* population dynamics (see Results). In turn, temporal  
319 change in the production of “pollinated”, and “pollinated and not predated” seeds was  
320 modelled similarly as in the models exploring temporal changes in total seed production, but  
321 we used tree-level number of pollinated or pollinated and not predated seeds as a response.  
322 The change in reproductive costs was calculated as  $1-S$ , where  $S$  was calculated as probability  
323 that a seed is pollinated times probability that it will avoid *Cydia* predation. We used

324 parameter estimates from the above-described GLMMs and obtained standard errors with  
325 parametric bootstrapping, that is, sampling from the distributions defined by the mean and  
326 standard error of each coefficient to obtain a joint distribution for the derived variables.

327 All statistics were run in R (version 3.4.1), mixed models were fitted via glmmTMB<sup>66</sup>.  
328 Model validation was run with the DHARMA package<sup>67</sup>. We used the windowscanr package  
329 for rolling window analysis<sup>68</sup>. In models in which we detected heteroscedasticity of residuals,  
330 the dispersion was modelled as a function of fixed factors using the dispformula function.

331

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344

345 **Authors' contributions.** MB conceived the study and drafted the manuscript; MB led the  
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347 authors interpreted the results, revised the text, and provided critical feedback and helped  
348 shape the final text.

349

350 **Conflict of interest.** Authors declare no competing interests as defined by Nature Research,  
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353

### 354 **Data availability.**

355 The data that support the findings of this study are available on request from the  
356 corresponding author (MB).

357

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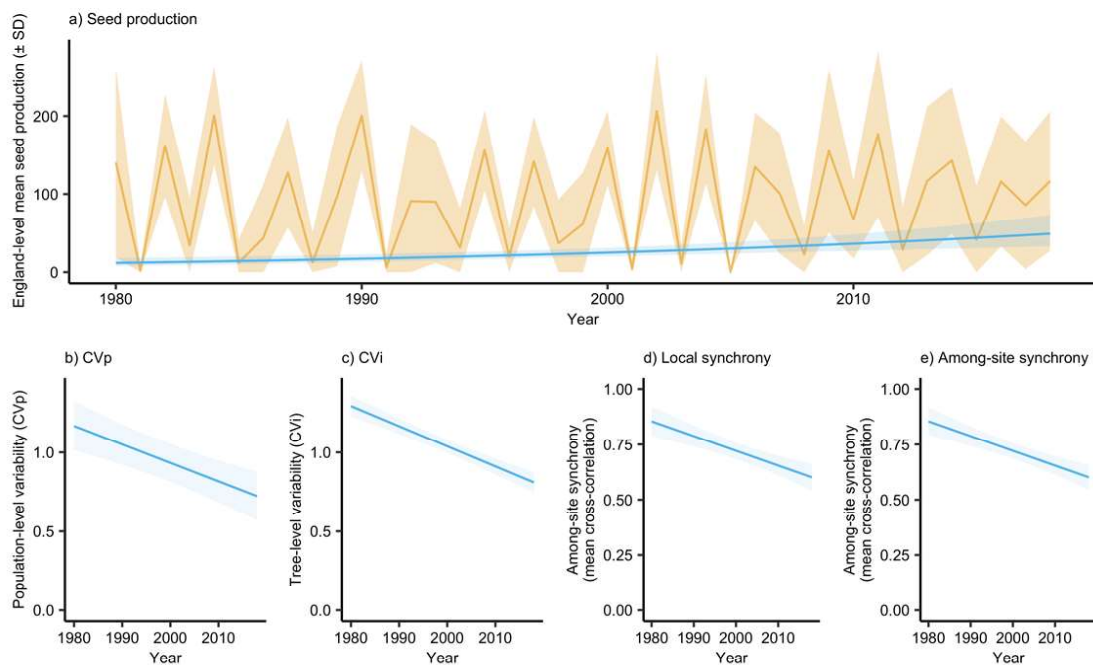
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521 Figure 1. Temporal trends in European beech (*Fagus sylvatica*) seed production in England,  
 522 population- and individual-level variability (CV), and within- and among-site synchrony of  
 523 reproduction for 12 sites and 139 trees (1980–2018). (a) Observed population-level seed  
 524 production per year per 7-minute search periods, and fitted long term mean. Significant fitted  
 525 trends in temporal change in (b) population-level CVp, (c) mean individual CVi, (d)  
 526 synchrony among trees within a site (Si), and (e) synchrony among sites (Sp). Trends were  
 527 calculated using GLMMs, with the site and trees as random intercepts and year as a fixed  
 528 effect. Models also included an autoregressive order-1 autocorrelation structure. Shading  
 529 around prediction lines indicates the 95% confidence intervals. See Methods for further  
 530 details.

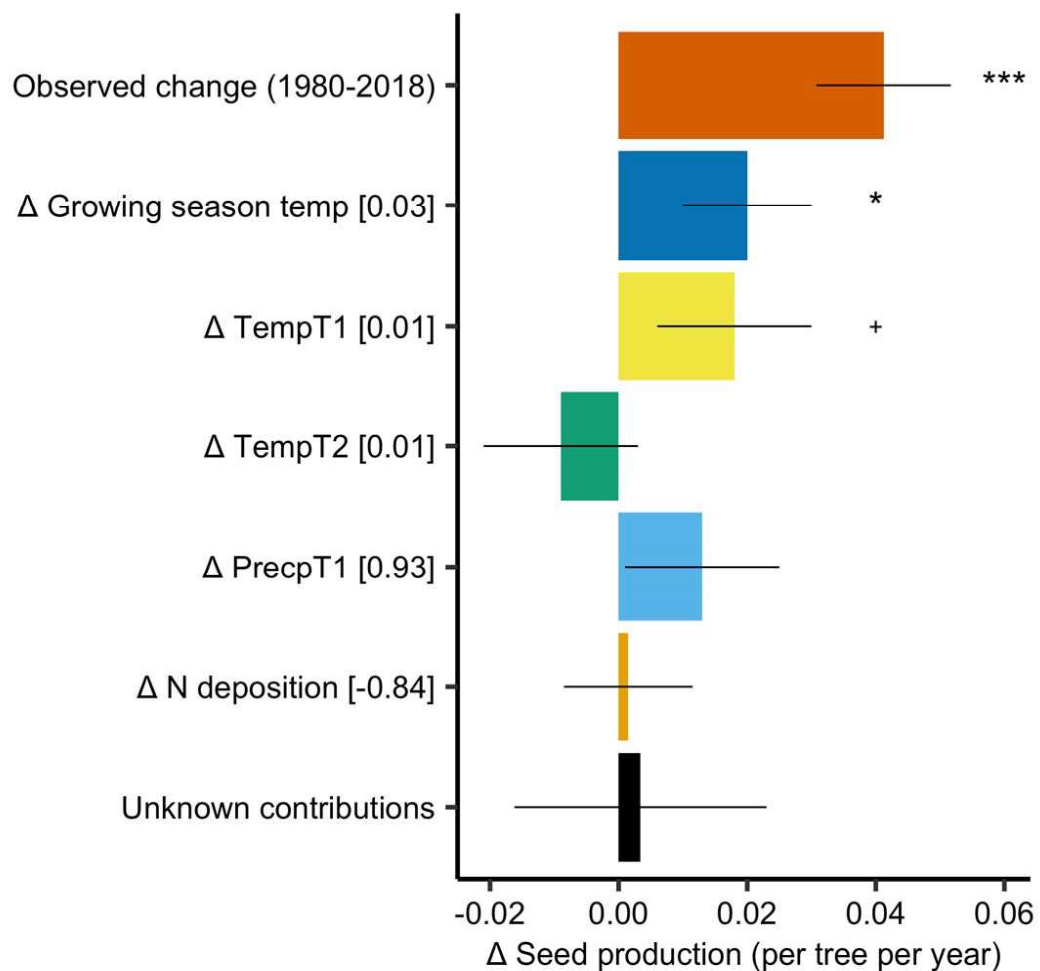


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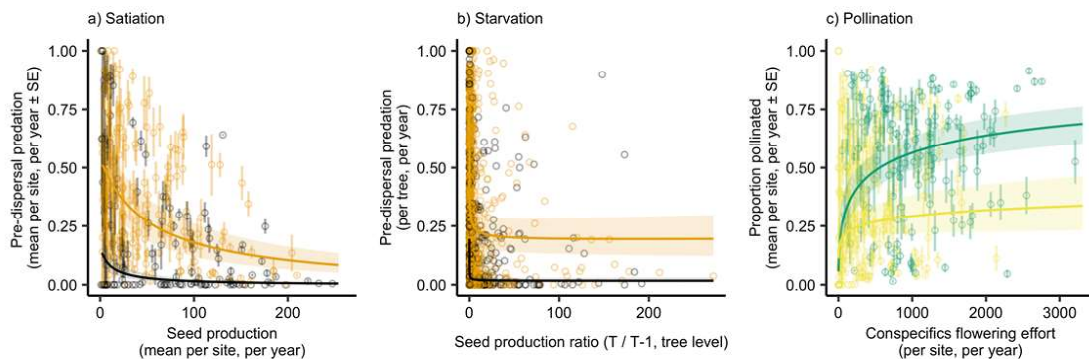
534 Figure 2. Temporal contribution of the predictor variables. The analysis, based on 12 sites and  
 535 139 trees (1980–2018), suggested that increasing temperature is the main contributor to the  
 536 observed increase in European beech (*Fagus sylvatica*) seed production (in seeds per tree per  
 537 year per 7-minute search periods). The difference between the modelled contributions and the  
 538 observed trends has been considered as an unknown contribution to the temporal variation  
 539 seed production. The temporal trends of the predictors are shown in square brackets. Error  
 540 bars for associated contributions indicate standard errors. TempT1 is the mean max June-July  
 541 temperate in the year prior seed dispersal, while TempT2 two years before. PrecipT1 is  
 542 summed June-July precipitation in the year prior seed dispersal. Units are °C for temperature,  
 543 kg ha<sup>-1</sup> yr<sup>-1</sup> for N deposition, mm for precipitation. See Methods for information about the  
 544 methodology used to calculate the contributions. Significance levels (two-sided t-test): + P =  
 545 0.10; \*P = 0.04; \*\*\*P < 0.001.



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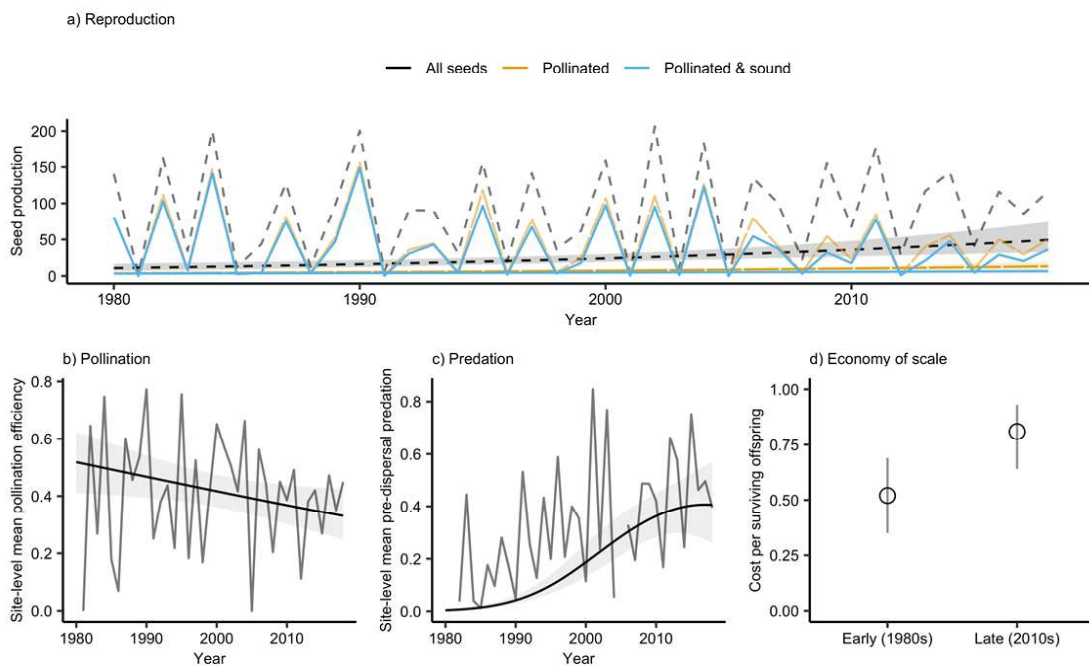
549 Figure 3. Weakening benefits to European beech from mast seeding. The proportion of seed  
550 production of each tree infested by *Cydia* sp. moths vs. (a) the current seed production per  
551 tree, and (b) the ratio of seed production in the current vs. the previous year. Different color  
552 lines show predictions for early (before 2000, black) and late (after 2000, yellow) monitoring  
553 periods. In later years, predation was higher for a given level of seed crop variation. (c) The  
554 proportion of successfully pollinated seeds on a plant vs the summed reproductive effort of all  
555 other conspecific trees at a particular study site. Different color lines show estimates for low  
556 ( $CV > 0.5$ , yellow) and high ( $CV < 0.5$ , green) within-site synchrony of flowering. When sites  
557 were more highly synchronous, pollination increased for a given flowering effort. Synchrony  
558 was calculated as CV of within-site among-tree flowering effort (thus, smaller value indicates  
559 higher among-tree synchrony of seeding). The lines are based on the significant binomial  
560 GLMMs predictions, while shading indicates the 95% confidence intervals, and is based on  
561 39-yr data set of 139 beech trees spaced across 12 sites in England. All models included the  
562 interaction term between the predictor showed at the x-axis and year. In the case of  
563 pollination efficiency, once synchrony and flowering effort were included, year effect became  
564 not significant (see Table S2).



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567 Figure 4. Temporal trends in European beech (a) total and effective seed production, (b)  
 568 pollination efficiency, (c) seed predation, and (d) economies of scale, for 12 sites and 139  
 569 trees (1980–2018). Trends were calculated using GLMMs, with the site and trees as a random  
 570 intercepts and year as a fixed effect. Models also used an autoregressive order-1  
 571 autocorrelation structure. Shading indicates the 95% confidence intervals of the means. In (a)  
 572 temporal trend was calculated based on either all seeds produced, only the fraction of  
 573 pollinated seeds, or only pollinated and not-predated seeds. See Methods for further details.  
 574 D) shows means and 95% confidence intervals.  
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