

1 **Title:**

2 **Increasing spring temperatures favor oak seed production in temperate areas**

3 **Authors:**

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13

14 **ABSTRACT (130/150 words)**

15 The changes in reproductive phenology (i.e. timing of flowering and fruiting) observed  
16 in recent decades demonstrate that tree reproduction has already been altered by climate  
17 change. However, understanding the impact of these changes in reproductive success and  
18 fitness remains a major challenge for ecologists. We describe here a previously unreported  
19 phenomenon: a significant increase in the reproductive effort (seed production) of temperate

20 oaks with increasing spring temperature, observed over the last two decades. This sensitivity  
21 of seed production to temperature was confirmed by a “space-for-time” substitution based  
22 on elevation gradients. Our findings suggest that global warming may enhance oak  
23 reproductive effort in temperate ecosystems. Nevertheless, while fitness can be enhanced by  
24 higher levels of seed production, it also depends on the frequency and synchronization of mast  
25 seeding production, which may also be influenced by climate change.

## 26 **MAIN TEXT (1925/3000 words)**

27         Forests are important for biodiversity and as a terrestrial carbon sink<sup>1</sup>, and contrasting  
28 responses to climate change have been identified. For instance, growth and survival, two of  
29 the main components of tree fitness, have been found to be substantially altered by climate  
30 change<sup>2,3</sup>. In cold and mild areas, such as boreal and temperate forests, global warming is  
31 extending tree growing seasons<sup>4,5</sup> and promoting wood production and tree growth<sup>3</sup>,  
32 whereas, in warmer and drier areas, negative impacts on tree growth<sup>6</sup> and survival<sup>7,8</sup> have  
33 been observed. In addition to the reported impact on growth, and, to a lesser extent, forest  
34 dieback, we need to know how tree reproduction, one of the most important components of  
35 plant fitness, is being affected by climate change, and its likely response.

36         Reproduction is critical for the maintenance and demography of populations, and  
37 should therefore be assessed carefully when modeling population responses to climate  
38 change<sup>9</sup>. Seedling regeneration and survival are directly linked to variations in seed  
39 production<sup>10,11</sup> and the assessment of changes in regeneration from seeds in response to  
40 temperature has become a major challenge. There is, therefore, an urgent need to assess the

41 impact of climate change on tree reproduction, to improve our understanding of the likely  
42 effects of this phenomenon on tree population dynamics.

43 An impact of climate change on the timing of reproduction has been reported for  
44 numerous organisms<sup>12,13</sup>. Indeed, reproductive phenology is known to be sensitive to  
45 environmental cues, such as temperature<sup>14,15</sup>, so climate change is likely to alter the intensity  
46 of seed production. However, the impact of climate change on reproductive effort is difficult  
47 to quantify, particularly in forest trees, which display the synchronized, intermittent  
48 production of large amounts of seeds. This phenomenon, commonly observed in oak species  
49 at the population scale, is called “masting” or “mast-seeding”<sup>16,17</sup>. Most studies of tree seed  
50 production over long time series have focused on single sites or small numbers of sites in  
51 limited areas. The specific features of masting have, thus, made it difficult to assess the  
52 sensitivity of seed production to temperature. Moreover, as pointed out by Crone and Rapp<sup>18</sup>,  
53 the large numbers of isolated studies and of weather variables tested have highlighted  
54 contradictory correlations with seed production, even for related species. As a result, to avoid  
55 artifacts caused by masting, the monitoring of seed production should be replicated in space  
56 and time, in ecologically independent forests.

57 In this study, we analyzed extensive sets of tree reproduction data for two temperate  
58 European white oak species (the sessile oak (*Quercus petraea*) and the pedunculate oak (*Q.*  
59 *robur*)), to determine whether seed production had changed over the last two decades in  
60 response to global warming. We monitored seed production in 28 forests of *Q. petraea* and  
61 *Q. robur* distributed throughout France over a period of 14 years. In parallel, a “space-for-  
62 time” substitution was used to quantify the temperature sensitivity of acorn production over  
63 elevation gradients. These analyses demonstrated significant temperature-induced trends in

64 seed production over the last two decades, suggesting that climate change enhances oak  
65 reproductive effort in temperate ecosystems.

## 66 **Results and Discussion**

### 67 **Temporal trend in seed production**

68 We examined temporal changes in the seed production of two oak species across France  
69 over recent decades (1994 to 2007). We observed a significant increase over time in  
70 reproductive effort for *Q. petraea* (Figure 1a) but not for *Q. robur* (Figure 1b). On average,  
71 acorn production ( $M_{\text{acorn}}$ ) in *Q. petraea* populations increased by 19.8 kg [8.3, 31.3] per  
72 hectare per year (Table 1). A similar trend was observed for *Q. robur*, but the correlation  
73 ( $M_{\text{acorn}}/\text{Year} = 14.1 \text{ kg}\cdot\text{ha}^{-1} [-1.7, 29.8]$ ) was not significant (Table 1). Similar positive temporal  
74 trends have been reported in a few other studies. A limited number of reports for *Pinus*  
75 *engelmannii*<sup>19</sup> and in *Nothofagus solandri*<sup>20,21</sup> have demonstrated temporal shifts. In these  
76 studies, the monitored populations were located at high elevations, at which reproduction  
77 appears to be more sensitive to environmental change<sup>20,21</sup>. However, in most cases, no  
78 temporal trend in fruit production, for example, was observed<sup>22,23</sup> and such trends have rarely  
79 even been sought, due to the scarcity of adequate, long-term datasets. In our study, the many  
80 populations surveyed were found in temperate lowland forests located over a large area and  
81 at an elevation of between 55 and 330 m above sea level. The mean synchrony of seed  
82 production (Spearman's coefficient) among the populations was very low for both species  
83 ( $0.11 \pm 0.016$  for *Q. petraea* and  $0.15 \pm 0.052$  for *Q. robur*), demonstrating the lack of  
84 synchrony between populations over this large scale (the differences in seed production  
85 dynamics between the populations monitored are shown in Supplementary Figure S1). As the

86 populations were independent, any temporal change in reproductive effort can be seen as a  
87 robust overall pattern rather than a local trend in a marginal population. Many studies have  
88 explored the potential drivers of plant reproduction<sup>18,24,25</sup>, but only a few have investigated  
89 changes in reproductive effort in response to global warming, due to a general lack of  
90 statistical power<sup>26,27</sup>. In the context of climate change, the temporal trends observed here may  
91 reflect the effects of recent warming over the last few decades. Consistent with this view, we  
92 observed a significant increase in temperature over time at the sites studied (Supplementary  
93 Figure S2), potentially sufficient to account for the positive temporal trend observed.

#### 94 **Reproductive effort in oak is increasing with increasing spring temperatures in** 95 **temperate areas**

96 Temperature and rainfall are routinely recorded and are considered the most relevant  
97 climatic variables driving seed production<sup>24</sup>, but their effects seem to differ between tree  
98 species and ecosystems<sup>23</sup>. Tree reproductive effort has been studied mostly in Mediterranean  
99 oak species and monitored mostly in Southern Europe and California<sup>28</sup>. For most of these  
100 species, a warmer, drier summer season results in lower levels of seed production<sup>29,30</sup>.  
101 Interestingly, the main driver appears to be water deficit rather than temperature *per se*<sup>31,32</sup>.  
102 By contrast, we found that, in both *Q. petraea* and *Q. robur*, seed production was positively  
103 correlated with spring temperature (Figure 2a, 2b, Table 1), which is known to have a strong  
104 effect on flowering and pollination<sup>14,15</sup>. No study has ever reported positive temporal clines  
105 for acorn production, but positive correlations with spring temperature have been found in  
106 California for three Mediterranean oak species, *Q. lobota*, *Q. douglasii* and *Q. kelloggii*<sup>33</sup>, and  
107 three temperate oak species, *Q. alba*, *Q. rubra* and *Q. velutina*<sup>17</sup>. In our study, despite the  
108 broad distribution of the populations, the positive correlation with spring temperature

109 observed could be explained mostly by temperature variability over time rather than  
110 temperature variability over space (Supplementary Table 1). The trend towards an increase in  
111 seed production over time observed for both species was therefore directly correlated with  
112 the increase in spring temperature observed over the last two decades (Supplementary Figure  
113 S2). Climate change has had a negative impact on reproduction in Mediterranean oaks in  
114 Europe, but we show here that the increase in spring temperature has favored reproduction  
115 in temperate oaks.

116 We then examined seed production along elevation gradients in Southern France, to refine  
117 the temperature-seed production relationship. Our findings confirm the strong positive  
118 correlation between seed production and spring temperature in *Q. petraea* (Table 1). The gain  
119 in acorn production per one-degree rise along the elevation gradient ( $M_{\text{acorn}}/T_{\text{Ap-Ma}} = 334.2$   
120  $\text{kg}\cdot\text{ha}^{-1}$ ) was three times greater than that along the spatio-temporal gradient ( $M_{\text{acorn}}/T_{\text{Ap-Ma}} =$   
121  $111.89 \text{ kg}\cdot\text{ha}^{-1}$ ). This difference may reflect differences in temperature values and gradients  
122 between the two designs. Indeed, the range of spring temperature variation was lower for the  
123 spatio-temporal gradient ( $6.2^\circ\text{C}$ ) than for the elevation gradient ( $10.8^\circ\text{C}$ ).

#### 124 **What is the impact on tree fitness?**

125 Our observations suggest that climate change may increase the fitness of temperate oaks.  
126 An increase in seed production is beneficial to the tree, as it increases seed dispersal<sup>34,35</sup>,  
127 thereby increasing the number of potential offspring and, consequently, their establishment.  
128 In addition, acorn mass increases with increasing temperature, by about 0.15 g per degree  
129 [0.09, 0.22] (Figure 3). This gain may increase the resistance of acorns to environmental stress  
130 (predation by insects, frost) and enhance germination<sup>36,37</sup>. However, reproduction in many

131 tree species, including oaks, is characterized by masting or mast-seeding, with synchronized  
132 large-scale seed production at the population scale (Supplementary Figure S1). This process is  
133 considered to be an adaptive response to the selective pressure exerted by predators<sup>16,17</sup>.  
134 Masting limits seed predation and promotes seed dispersal, thereby ensuring high rates of  
135 offspring survival and optimizing resource allocation to reproduction<sup>24,38</sup>. Changes in masting  
136 associated with climate change may, therefore, have a negative impact on the fitness of tree  
137 populations.

138       There is an ongoing controversy about the influence of climate change on reproduction.  
139 On the one hand, climate is considered to be a cue for variations in seed production<sup>26</sup>, and on  
140 the other, it is considered a proximal driver<sup>39,40</sup>. Kelly *et al.*<sup>26</sup> recently suggested that the  
141 difference in temperature between two consecutive years ( $\Delta T$ ) may act as the main signal for  
142 massive, synchronous seed production. As a gradual increase in mean temperature will not  
143 affect  $\Delta T$ , these authors suggest that climate change may not affect masting. However, other  
144 studies have contested this differential-temperature hypothesis. They have shown that  $\Delta T$   
145 effects do not apply to all species<sup>23,39</sup> and have suggested that this cue is relevant only  
146 because it combines the direct proximal effects of recent weather and the indirect effects of  
147 previous weather through previous seed set and resource limitation<sup>40,41</sup>. For instance,  
148 Övergaard *et al.*<sup>42</sup> observed, during 30 years of measurement in European beech forest (*Fagus*  
149 *sylvatica*), an increase in the frequency of mast events directly correlated with an increase in  
150 temperature. With increasing periodicity, the temporal variability characterizing mast-seeding  
151 and enabling the trees to control predator population size<sup>24,43</sup> might be greatly reduced<sup>27</sup>. Low  
152 inter-annual variability in seed crops may lead to an increase in predator population size,  
153 decreasing reduce offspring survival. This paradoxical consequence of climate warming for

154 temperate tree reproduction highlights the need for improvements in our understanding of  
155 the proximal mechanisms underlying masting in trees, for prediction of the response of forest  
156 ecosystems to climate change.

157 This study focused on temperate forests dominated by deciduous oak species and cannot  
158 be extended to other forest types. However, we can compare the time and temperature  
159 trends of acorn production observed in oaks with the patterns reported for whole biomass  
160 growth in trees<sup>44,45</sup>. There is a clear congruent increase in vegetative growth and reproductive  
161 growth (our results) in *Q. petraea* and *Q. robur* in recent decades in central Europe. Such  
162 trends can be seen as two facets of the overall consequence of the same causes relating to  
163 global changes in recent decades. An increase in temperature extends the period of vegetative  
164 growth<sup>4,5</sup> and enhances tree growth<sup>46</sup>. In addition to increasing temperature, increases in the  
165 carbon dioxide content of the atmosphere may also promote tree growth in some species,  
166 and increases in nitrogen (N) deposition have been shown to stimulate forest growth and  
167 carbon sequestration in Europe<sup>47</sup>. As reproduction in trees is also dependent on resource  
168 availability<sup>48,49</sup>, the combined effects of temperature, carbon dioxide, and nitrogen deposition  
169 may also contribute to the increase in seed production. However, the congruent pattern of  
170 vegetative and reproductive growth may be negatively affected by extreme events and  
171 disturbances, such as firestorms or the spread of insects and diseases, which may also be  
172 triggered by global changes<sup>50</sup>.

173 Global warming has had a positive effect on temperate oak growth. However, the  
174 response of tree reproduction to environmental changes remains unclear, mostly due to our  
175 limited understanding of masting processes. Long-term studies of reproductive investment  
176 over large areas would be required to assess the global impact of climate change on trees.



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#### 288 AUTHORS' CONTRIBUTIONS:

289 T.C and S.D. conceived the idea for this work. T.C., C.F. and M.N. assembled the dataset and  
290 analyzed the data. T.C. and S.D. wrote the manuscript and A.K., S.V. and C.F. revised the  
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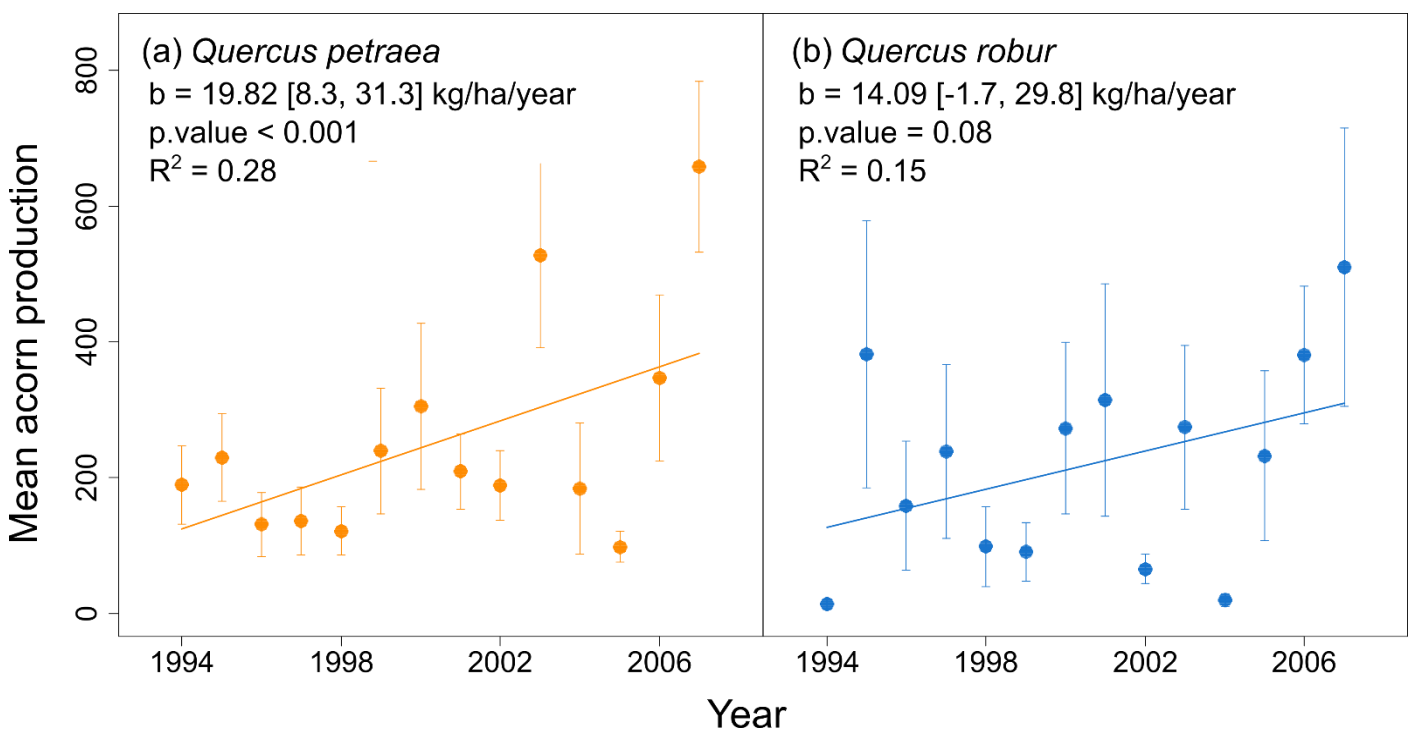
301

302 **Table 1: Temperature sensitivity of reproductive efforts in oaks** | Slopes of the linear mixed-  
 303 effect regression between acorn production in kilograms per hectare ( $M_{\text{Acorns}}$ ) and year  
 304 (temporal gradient, ( $M_{\text{Acorns}}/\text{Year}$ )), and for every 100 m increase in elevation (spatial gradient,  
 305  $M_{\text{Acorns}}/\text{Alt}_{100\text{m}}$ ), and the mean temperature in April and May in °C ( $M_{\text{Acorns}}/T_{\text{Ap-Ma}}$ ) in both  
 306 studies. The 95% credibility intervals are indicated in square brackets. Reproduction in  
 307 *Quercus petraea* was monitored in both studies, whereas *Quercus robur* was monitored in the  
 308 temporal gradient study only. Significant correlations are indicated in bold.

Species	Temporal		Spatial	
	$M_{\text{Acorns}}/\text{Year}$	$M_{\text{Acorns}}/T_{\text{Ap-Ma}}$	$M_{\text{Acorns}}/\text{Alt}_{100\text{m}}$	$M_{\text{Acorns}}/T_{\text{Ap-Ma}}$
<i>Q. petraea</i>	<b>19.82 [8.3, 31.3]</b>	<b>111.89 [63.1, 146.0]</b>	<b>- 83.89 [-149.5, - 18.3]</b>	<b>334.2 [175.6, 589.2]</b>
<i>Q. robur</i>	14.07 [-1.7, 29.8]	<b>72.66 [19.6, 120.5]</b>	–	–

309

310 **Figure 1: Temporal variation in seed production for *Q. petraea* and *Q. robur*** | Temporal  
311 variation in seed production (kg ha<sup>-1</sup>) of 19 and 9 populations of *Q. petraea* (a) and *Q. robur*  
312 (b) respectively, monitored over 14 years and distributed throughout France. Each dot  
313 corresponds to the mean seed production across all populations per year (kilograms per  
314 hectare per year averaged over all sites). The slope of the regression line and its 95% credibility  
315 interval, calculated from a linear mixed-effects model [2], are given for both species, with the  
316 coefficient of determination (R<sup>2</sup>) between model [2] and mean production.

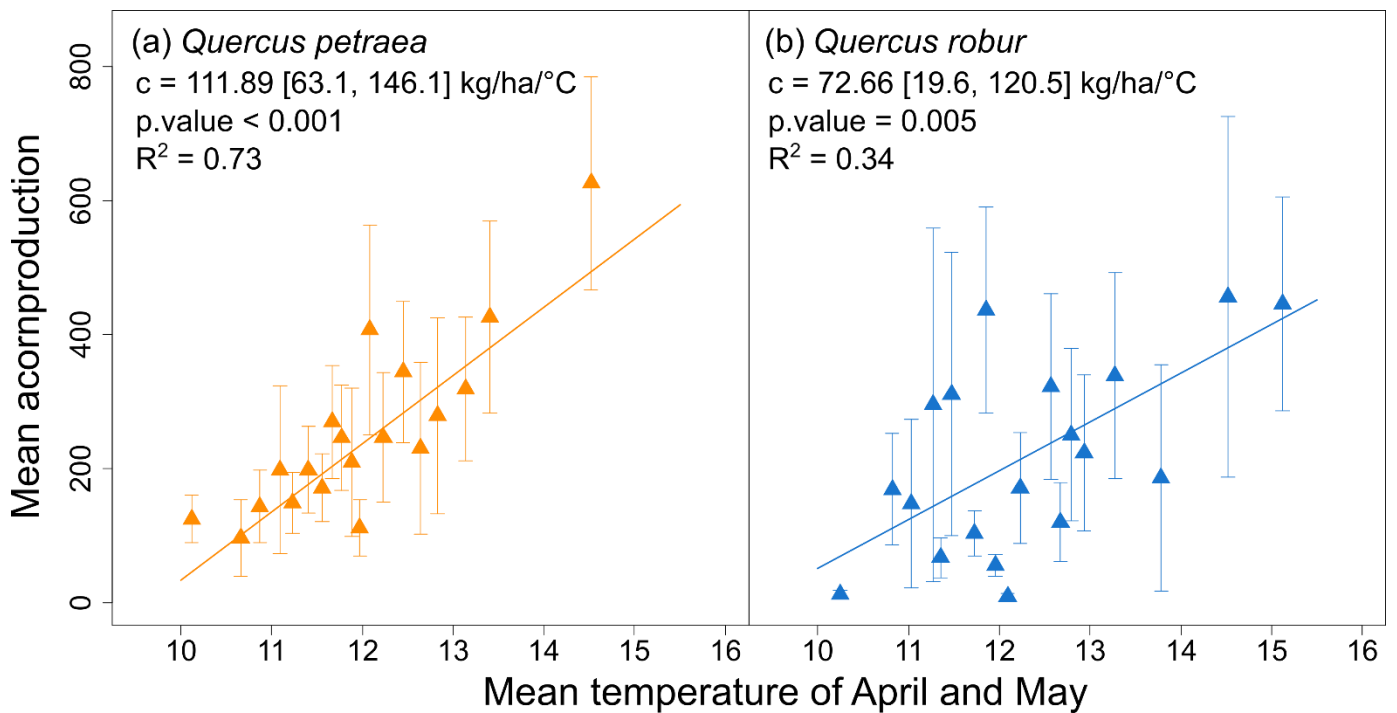


317

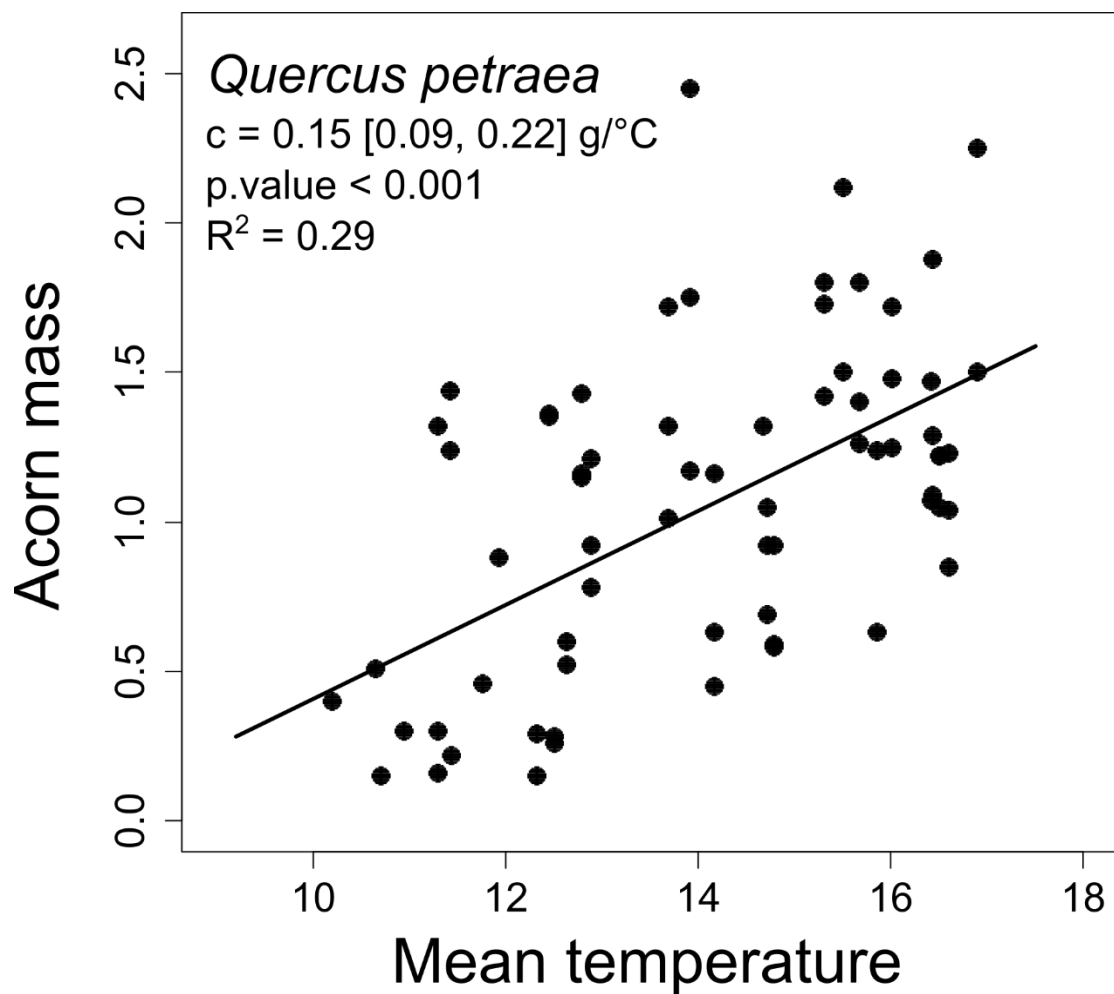


318 **Figure 2: Responses of seed production to spring temperature for both *Q. petraea* and *Q.***  
319 ***robur*** | Changes in acorn production per population and per year ( $M_{\text{Acorns}}$ ) for *Quercus petraea*  
320 (a) and *Quercus robur* (b) according to mean spring temperature. For both species, acorn  
321 production data for all populations and all years were binned into 19 temperature classes of  
322 the same size. Mean acorn production per bin is correlated with the temperature class  
323 median. The slope of the regression line and its 95% credibility interval, calculated from a  
324 linear mixed-effects model [3], and the coefficient of determination ( $R^2$ ) between the model  
325 [3] and the binned data are given for each species.

326



327 **Figure 3: Temperature trends in seed mass for *Quercus petraea*** | Trend in acorn mass (g)  
328 with mean temperature from April to November (°C) along the elevation gradient. Each dot  
329 corresponds to the mean value for acorn mass for a tree in a given year. The slope of the  
330 regression line and its 95% credibility interval, calculated from a linear mixed-effects model,  
331 and the coefficient of determination ( $R^2$ ) are indicated. April to November corresponds to  
332 reproductive cycle length in *Quercus petraea*: from flowering to acorn release.



## 334 **Materials and methods (1241/3000 words)**

### 335 **Study sites**

336 We analyzed variations in seed production for two European oak species (*Quercus*  
337 *petraea* and *Quercus robur*) along latitudinal and an elevation gradients. The latitudinal field  
338 survey concerned 19 *Q. petraea* populations and nine *Q. robur* populations distributed across  
339 France, for which seed production assessed during 14 years, from 1994 to 2007. Populations  
340 were distributed between latitudes of 43.2° and 50.2°N and longitudes of 0.04° and 3.7°E  
341 (Supplementary Table S2). The populations studied were mature oak stands with a mean age  
342 of 85.5 years  $\pm$  28.7 in 1994, at the start of monitoring. In each forest, acorns were collected  
343 at the population scale, in 10 5 m<sup>2</sup> litter bags, set up under the closed canopy and evenly  
344 distributed over an area of about half a hectare. Acorns were harvested twice during the fall  
345 (before and after leaf senescence). The mass of acorns produced was estimated for each  
346 population in kg ha<sup>-1</sup> through the measurement of dry mass. Daily mean, minimal and maximal  
347 temperatures (°C) and precipitation (mm) were extracted from the SAFRAN<sup>51</sup> spatially explicit  
348 database (8 x 8 km grid) for each site.

349 The elevation gradient survey was set up in the French Pyrenees, along a replicated  
350 transect in two parallel valleys: Ossau and Gaves (latitude 42° 47' N to 43° 45' N; longitude 00°  
351 44' W to 00° 06' E). Five natural mature populations of *Q. petraea* were monitored in each  
352 valley, at different elevations, from 131 m to 1630 m (Supplementary Table S3). At each site,  
353 nets were set up 1 m above the ground under the whole tree canopy, to collect all the acorns  
354 produced by an individual. In total 15, 13, 25 and 30 adult trees were monitored in 2012, 2013,  
355 2014 and 2015, respectively. The 30 trees had a mean height of 19.2  $\pm$  9.4 m and a mean

356 diameter of  $37.7 \pm 19.6$  cm. From 2012 onwards, the organic components (leaves, branches,  
357 fruits) falling from the trees were harvested every two weeks, from the end of September until  
358 the beginning of December. For each tree, the projected area of the canopy on the ground  
359 ( $SC_{OB_i}$ ) was calculated by first defining the canopy center (O) and then determining the  
360 distance from O to the outer limit of the canopy ( $B_i$ ), at 8 points,  $45^\circ$  apart ( $OB_{1-8}$ ). The surface  
361 area was calculated as:

362 
$$SC_{OB_i} = \frac{\pi}{i} \times \sum OB_i^2 [1]$$

363 The harvested litters were sorted in the laboratory, and total acorn production, total  
364 dry mass and mean acorn weight per tree and per year (g) were determined. Total seed  
365 production was normalized by dividing by the total projected surface area of the tree canopy.  
366 Air temperature was measured with a data logger (HOBO Pro RH/Temp, Onset Computer  
367 Corporation, Bourne, Massachusetts, USA) at all sites. Data were recorded hourly, from  
368 January 1 2012 to December 31 2015.

## 369 **Statistical analysis**

### 370 *Temporal trend*

371 We evaluated the change in seed production over time separately for the two species, with  
372 a linear mixed effects model:

373 
$$Y_{jt} = a_\mu + b_\mu t + (a_j + b_j t) + \varepsilon_{jt} [2]$$

374 where  $a_\mu$  is the overall intercept and  $b_\mu$  is the overall slope of line of acorn production over  
375 time (t),  $a_j$  is the random deviation associated with population  $j$ , and  $b_j$  is the population-

376 specific deviation in slope, and the residuals are denoted  $\varepsilon_{jt}$ . For both species, we compared  
377 the model [2] with a simpler model not including the random deviation in slope  $b_j t$ . We then  
378 used a likelihood ratio test (the Chi-squared test) to test the hypothesis that the temporal  
379 trend observed was homogeneous among populations. As the  $p$ -value values obtained, 0.91  
380 for *Quercus petraea* and 1.00 for *Quercus robur*, were greater than the significance threshold  
381 of 0.05, we did not reject the null hypothesis of a homogeneous temporal trend between  
382 populations. Moreover, slopes and confidence intervals were calculated with the simpler  
383 model (i.e.  $Y_{jt} = a_{\mu} + b_{\mu} t + (a_j) + \varepsilon_{jt}$ ).

384 We then evaluated the response of seed production to temperature:

$$385 \quad Y_{ijtT} = a_{\mu} + c_{\mu} T + (a_j + c_j T) + \varepsilon_{ijtT} \quad [3]$$

386 where  $c_{\mu}$  is the overall slope of the line of acorn production plotted against temperature (T)  
387 and  $\varepsilon_{ijtT}$  denotes the residuals. As before, we compared the model [3] with a simpler model  
388 lacking the random deviation of slope  $c_j T$ . We then used a likelihood ratio test (the Chi-  
389 squared test) to test the hypothesis that the observed correlation with temperature was  
390 homogeneous among populations. As the  $p$ -values obtained, 0.08 for *Q. petraea* and 0.12 for  
391 *Q. robur* were greater than the significance threshold of 0.05, we did not reject the null  
392 hypothesis that the observed correlation with temperature was homogeneous among  
393 populations.

394 We therefore used the simplest model [3] (i.e.  $Y_{ijtT} = a_{\mu} + c_{\mu} T + (a_j) + \varepsilon_{ijtT}$ ) to  
395 estimate the effect of temperature on seed production. For this purpose, we first compared  
396 this model with the null model (i.e. without the fixed effect of temperature  $c_{\mu} T$ ), using the  
397 Akaike criterion and hypothesizing that temperature has no effect on seed production. This

398 comparison was performed for the mean temperature of each month of the year. For April,  
399 March-April and April-May for *Q. petraea* and for April, and April-May for *Q. robur*, the Akaike  
400 criterion differed significantly between the models with and without a fixed effect of  
401 temperature (Supplementary Figure S3). The Akaike criterion values were lowest for  
402 temperatures recorded during the spring months, so we estimated slopes for different spring  
403 periods (Supplementary Table S4). For *Quercus petraea*, a significant relationship was found  
404 with the temperature in April (94.8 [61.5, 128.4] kg.ha<sup>-1</sup>), March-April (102.98 [56.6, 152.4]  
405 kg.ha<sup>-1</sup>), April-May (111.89 [63.1, 146.1] kg.ha<sup>-1</sup>) and May-June (41.59 [1.1, 86.1 kg.ha<sup>-1</sup>)  
406 (values given for each one-degree increase in temperature). For English oak, a significant  
407 increase was observed only for April (54.07 [14.4, 93.7] kg.ha<sup>-1</sup>) and April-May (72.66 [19.6,  
408 120.5] kg.ha<sup>-1</sup> (values given for each one-degree increase in temperature; Table 1,  
409 Supplementary Table S4).

410 As spring temperature was found to have increased over the last two decades  
411 (Supplementary Figure S2) and seed production was significantly correlated with temperature  
412 (Table 1, Figure 2), we considered the observed temporal trend in seed production in both  
413 species (Table 1, Figure 1) to be due principally to the increase in temperature. However, as  
414 the populations were distributed over a large area covering a large range of temperatures, we  
415 explicitly accounted for variability due to the year and population, with the following model:

$$416 \quad Y_{ijPY} = a_{\mu} + b_{\mu}P + c_{\mu}Y + (a_j) + \varepsilon_{ijPY} [4]$$

417 where  $b_{\mu}$  denotes the overall slope of the mean population temperature against year line (P)  
418 and  $c_{\mu}$  is the overall slope of mean yearly temperature against population line (Y) for acorn

419 production and  $\varepsilon_{ijPY}$  denotes the residuals. We used model [4], with the mean temperature  
420 of April-May (Supplementary Table S1).

#### 421 *Trend along the elevation gradient*

422 We then evaluated the sensitivity of reproduction to temperature along the elevation  
423 gradients in Pyrenees:

$$424 \quad Y_{ijkT} = a_{\mu} + c_{\mu}T + (p_j) + (n_{k(j)}) \varepsilon_{ijkT} [5]$$

425 where  $a_{\mu}$  denotes the overall intercept and  $c_{\mu}$  the overall slope of the line of acorn production  
426 against temperature (T),  $p_j$  and  $n_{k(j)}$  are the random deviations associated with population  $j$   
427 and the individuals within the population  $k$  and the residuals are denoted  $\varepsilon_{ijkT}$ . We tested the  
428 effect of temperature over the same period as above (Table 1, Supplementary Table S4).

429 Finally, we also evaluated the sensitivity of acorn size to temperature along the same  
430 elevation gradient, with the same model [5].

431 All the linear mixed effects models were fitted by the restricted maximum likelihood (REML)<sup>52</sup>  
432 method in the *lme4* R package<sup>53</sup>

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