

1 **Effects of climate on reproductive investment in a masting species: assessment of**  
2 **climatic predictors and underlying mechanisms**

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4 Running title: **Climatic predictors of masting**

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32 **Summary**

33 **1.** Mechanisms by which climatic factors drive reproductive investment and phenology  
34 in mast seeding species are not completely understood. Climatic conditions may act as a  
35 proximate cue, stimulating the onset of reproduction and indirectly increasing fitness  
36 through benefits associated with synchronous reproduction among individuals.

37 Alternatively, climatic conditions may directly influence individual level allocation to  
38 reproduction and reproductive success through effects occurring independently of  
39 synchronous reproduction. We previously showed that mast seeding in a ponderosa pine  
40 (*Pinus ponderosa*) population was strongly influenced by spring mean temperature two  
41 years before seed cone maturation ( $T_{i-2}$ ). However, recent work shows that the  
42 difference in temperature between previous growing seasons ( $\Delta T$ ) is more predictive of  
43 reproductive investment in long-lived tree species.

44 **2.** Here we compared four candidate models that predict seed cone production in *P.*  
45 *ponderosa* based upon different climatic factors (including  $T_{i-2}$  and  $\Delta T$  models). After  
46 determining the best climatic predictor, we tested for a potential mechanism by which  
47 climate might directly influence seed cone production independent of benefits via  
48 synchrony, namely effects of temperature on trade-offs between current and past  
49 reproduction (determined by underlying resource availability).

50 **3.** We found that  $T_{i-2}$  (rather than  $\Delta T$ ) was the best predictor of seed cone production.  
51 We further show that this same climatic factor exerts a direct fitness benefit to  
52 individuals by reducing the strength of trade-offs between current and past reproductive  
53 efforts.

54 **4. Synthesis:** We demonstrate that a single climatic factor provides fitness benefits to  
55 individuals directly, by weakening reproductive trade-offs, and indirectly through the  
56 benefits associated with synchrony and mast seeding. This suggests a mechanism for the

57 origin and maintenance of masting: individuals initially respond to climatic cues that  
58 directly enhance reproduction (e.g. lower reproductive costs through weakened trade-  
59 offs) and this dynamic, expressed across multiple individuals, reinforces these benefits  
60 through the economies of scale associated with synchrony and masting.

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62 **Key-words:** Economies of scale, *Pinus ponderosa*, Plant population and community  
63 dynamics, reproductive trade-offs, resource limitation, seed cone production,  $\Delta T$  model

64

## 65 INTRODUCTION

66 Masting is a reproductive strategy defined as the episodic production of large,  
67 synchronous seed crops by a plant population (Silvertown 1980; Kelly 1994). Several  
68 fitness advantages have been associated with masting that entail economies of scale  
69 such as seed predator satiation (Janzen 1971; Kelly *et al.* 2000; Fletcher *et al.* 2010),  
70 improved seed dispersal (Norton & Kelly 1988; Kelly 1994), and increased pollination  
71 efficiency (Kelly, Hart & Allen 2001; Kon *et al.* 2005a; Rapp, McIntire & Crone 2013;  
72 Moreira *et al.* 2014), all of which have been invoked to explain the occurrence and  
73 maintenance of this reproductive phenomenon.

74 The reproductive dynamics of masting species are strongly influenced by  
75 climatic conditions previous to or during the initiation of reproduction, which influence  
76 allocation to reproduction and the degree of synchrony in seed production (Schauber *et*  
77 *al.* 2002; Kon *et al.* 2005b; Kelly *et al.* 2008; Smaill *et al.* 2011; Roland, Schmidt &  
78 Johnstone 2014). For example, high seed production is frequently linked to warm  
79 temperatures during the previous growing season (e.g. Schauber *et al.* 2002; Selås *et al.*  
80 2002; Kelly *et al.* 2008; Masaki *et al.* 2008). In addition, other studies have found that

81 drought in the early summer has positive effects on flowering the following year (e.g.  
82 Piovesan & Adams 2001; Krebs *et al.* 2012).

83         The mechanisms by which climatic factors drive reproductive patterns in  
84 masting species are not fully understood, but several non-mutually-exclusive scenarios  
85 are commonly considered. First, climatic conditions may act as proximate cues that  
86 directly stimulate the onset of reproduction and reproductive phenology (Kelly & Sork  
87 2002; Kelly *et al.* 2013). Under this scenario, the fitness advantage of individual plants  
88 responding similarly (in amount and timing) originates from the economies of scale  
89 associated with population-level reproductive synchrony (see above; Norton & Kelly  
90 1988; Kelly 1994). Nevertheless, it is difficult to explain the evolution of a reproductive  
91 response to a cue that provides no direct, individual-level benefit (Koenig *et al.* 2015).  
92 Second, other authors argue that climatic factors shape reproductive patterns at the  
93 individual level, and that any benefit of masting associated with economies of scale  
94 arises secondarily. Climatic factors may directly alter resource availability (Koenig *et al.*  
95 *al.* 1996; Richardson *et al.* 2005; Pearse, Koenig & Knops 2014; Koenig *et al.* 2015)  
96 such that there are individual-level fitness advantages of responding to climatic factors  
97 (Pearse, Koenig & Knops 2014; Koenig *et al.* 2015). For example, seasonality in  
98 precipitation or temperature have been shown to influence plant nitrogen and carbon  
99 availability (Allen & Platt 1990; Richardson *et al.* 2005; Smaill *et al.* 2011), as well as  
100 soil moisture (Abrahamson & Layne 2003; Richardson *et al.* 2005) which may in turn  
101 influence within-plant resource allocation patterns (Barringer, Koenig & Knops 2013;  
102 Pearse, Koenig & Knops 2014). As a consequence of such effects on resource  
103 availability, climatic conditions may strengthen or weaken trade-offs between current  
104 and past reproduction; such effects may be particularly strong in the case of masting  
105 species due to resource depletion during large reproductive events (Sala *et al.* 2012).

106 Finally, so called "pollen coupling" has been proposed to underlie masting in the  
107 absence of climatic drivers (see reviews by Miyazaki 2013; Crone & Rapp 2014), where  
108 inter-annual variation is driven by reproduction trade-offs among years, and synchrony  
109 occurs because out-cross pollen limitation renders asynchronous reproduction  
110 unsuccessful.

111 A recent analysis of long-term datasets of 15 species across five plant families  
112 proposed a new predictive model to explain how climatic conditions modulate  
113 reproductive investment and phenology in masting species (Kelly *et al.* 2013).  
114 Specifically, for 12 of the 15 species studied, a model using the difference in  
115 temperature from one previous growing season to the next ( $\Delta T$  model hereafter) as a  
116 predictor of reproductive investment better predicted (i.e. smaller Akaike information  
117 criterion and higher correlation coefficient) seed production relative to a model  
118 including the temperature from a single previous growing season as predictor (Kelly *et*  
119 *al.* 2013). The authors offered several reasons for why the  $\Delta T$  model exhibited a better  
120 fit relative to the model based upon a temperature from a single previous season. First, a  
121 model based on temperature from a single previous season is not capable of explaining  
122 why two previous consecutive warm years rarely cause two consecutive years of high  
123 seed production (i.e. climatic effects of previous consecutive years are not additive).  
124 Second, the  $\Delta T$  model predicts that long-term plant reproductive responses are not  
125 influenced by gradual increases in mean temperature (such as those produced by climate  
126 change) but rather by averaging effects of climatic conditions across multiple growing  
127 seasons. This would also explain why the frequency of high-seed years (i.e. mast years)  
128 remains relatively constant over large periods of time (Kelly *et al.* 2013). However, not  
129 all studies have been supportive of this model's predictions. For example, Koenig &  
130 Knops (2014) showed that acorn production of three out of four oak species was

131 correlated with spring and summer temperature and precipitation, but not with  
132 differences between previous growing seasons for each of these climatic variables.  
133 Accordingly, further tests are needed to determine the general applicability of the  $\Delta T$   
134 model, as well as to identify the climatic drivers that best predict reproduction in long-  
135 lived species and the mechanisms underlying such effects.

136         Using a long-term data set (31 years), we previously reported that masting  
137 behaviour in a population of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson)  
138 increases reproduction through two complementary mechanisms operating via  
139 synchrony and associated economies of scale. First, synchronized, high levels of  
140 reproduction reduced pollen limitation by increasing the rate of female cone fertilization  
141 (Moreira *et al.* 2014). Second, synchronous bouts of high cone production, followed by  
142 intervening years of low reproduction reduced seed cone herbivory through predator  
143 satiation (Linhart *et al.* 2014). Additionally, we found that production of mature seed  
144 cones in this population was strongly influenced by spring (May-July) mean  
145 temperature two years before cone maturation ( $T_{i-2}$  model hereafter) (Mooney, Linhart  
146 & Snyder 2011).

147         Here we sought to determine which climatic factors drive synchronous  
148 reproduction in *P. ponderosa* by comparing different competing models, and address if  
149 responses to such climatic factors provide direct, individual-level reproductive benefits  
150 independent of those previously shown to occur through synchrony (Mooney, Linhart &  
151 Snyder 2011; Linhart *et al.* 2014; Moreira *et al.* 2014). First, we compared four  
152 candidate models that predict mature seed cone production in *P. ponderosa* based upon  
153 different climatic factors: 1) a model using as predictor the difference between spring  
154 mean temperature two and three years before cone maturation ( $\Delta T$  model), i.e.  $T_{i-2} - T_{i-3}$   
155 (Kelly *et al.* 2013), 2) a model using as predictor the mean temperature two years before

156 cone maturation (i.e.  $T_{i-2}$ ; Mooney, Linhart & Snyder 2011), 3) a model using as  
157 predictor the temperature three years before seed cone maturation ( $T_{i-3}$ ), and 4) a model  
158 using as predictor the individual effects of spring temperature two years and spring  
159 temperature three years before cone maturation (2T model hereafter, i.e.  $T_{i-2}$  and  $T_{i-3}$ )  
160 (Kelly *et al.* 2013). Second, after determining which temperature predictor best  
161 explained seed cone production (based upon results from the above models), we tested  
162 for a potential mechanism by which such climatic variables could provide a direct  
163 reproductive advantage not associated with the economies of scale from synchronized  
164 reproduction. Specifically, we tested whether temperature influenced within-plant  
165 resource allocation patterns via reproductive trade-offs. In so doing, this study identifies  
166 the climatic factors influencing reproductive investment and phenology in a long-lived  
167 plant and proposes a mechanism by which masting originates and is maintained.

168

## 169 **MATERIAL AND METHODS**

### 170 **Pine species, study area, and data collection**

171 Ponderosa pine is native to western North America, but has a widespread distribution as  
172 a planted species throughout temperate areas of both the New and Old World  
173 (Richardson 1998). Episodic mast seeding events are common for this species (e.g.  
174 Mooney, Linhart & Snyder 2011; Linhart *et al.* 2014; Moreira *et al.* 2014). Female  
175 cones (“seed cones” hereafter) are usually found on the upper branches and are  
176 produced in early spring and require two growing seasons after pollination to mature,  
177 reaching their full size by mid-summer. Several months later, during the fall, seed cones  
178 open and release their seeds.

179         We carried out a long-term (31 years) field survey during which we monitored  
180 the reproduction of 217 individuals from a ponderosa pine population distributed over a

181 2-ha area on the south-facing slope of Boulder Canyon, at an elevation of 1740 m in the  
182 Front Range of the Rocky Mountains (near the town of Boulder, Colorado, 40° 00'  
183 48"N, 105° 18' 12"W; Linhart & Mitton 1985; Mooney, Linhart & Snyder 2011). To  
184 reduce among-tree variation in abiotic factors strictly associated to fine-scale  
185 environmental conditions at each tree location, we selected the experimental trees from  
186 an area with a uniform slope, soils, sun and wind exposure. At the beginning of this  
187 study, the age of the studied trees ranged from ca. 40 to over 280 years based upon  
188 trunk cores taken at 30-50 cm above ground level. We also measured the basal diameter  
189 of each tree at the beginning of this study.

190         We recorded seed cone production during each year (from July to October for 31  
191 years [from 1977 to 2008, except in 2004]) by visually counting the total number of  
192 mature seed cones (pollinated during the previous year and matured during the current  
193 year) found throughout the crown of each tree (Mooney, Linhart & Snyder 2011;  
194 Linhart *et al.* 2014; Moreira *et al.* 2014). Previous studies in conifers have documented  
195 that the number of seed cones per tree is a good predictor (positive correlate) of the  
196 number of seeds per tree (e.g. Zasada & Viereck 1970; El-Kassaby & Cook 1994; Krebs  
197 *et al.* 2001). Finally, we also gathered climatic data (monthly mean temperature and  
198 total monthly precipitation) for this population from the Colorado Climate Center at the  
199 Department of Atmospheric Science of Colorado State University  
200 (<http://ccc.atmos.colostate.edu/>, site = Boulder 50848) (Mooney, Linhart & Snyder  
201 2011).

202

### 203 **Statistical analyses**

204 *Comparison of climatic predictors of ponderosa pine reproduction.* In a previous study  
205 using the same population, we related mean monthly precipitation and temperature to

206 mature seed cone production (Mooney, Linhart & Snyder 2011). We found that  
207 increased mature seed cone production was associated with decreases in spring  
208 temperature (mean of May, June, July) two years before, increases in summer  
209 precipitation (mean of July, August, September) two years before, and increases in  
210 winter temperature (mean of December, January, February) during the previous year  
211 (Mooney, Linhart & Snyder 2011). To achieve normality of residuals in our models,  
212 seed cone data were log-transformed for the present analyses (see below). After log-  
213 transforming, spring temperature two years before was the only significant predictor of  
214 mature seed cone production. Additionally, because pollen and ovule meiosis  
215 corresponded with spring temperature two years before seed cone maturation (Mooney,  
216 Linhart & Snyder 2011), the effect of this climatic factor would likely be the best  
217 predictor of reproductive investment. For both these reasons, in the present study we  
218 only tested models that included predictors based upon spring temperatures (calculated  
219 as the mean of May, June and July monthly means; Mooney, Linhart & Snyder 2011).

220         We compared four candidate models using log-transformed seed cone data at the  
221 population level (Kelly *et al.* 2013; Pearse, Koenig & Knops 2014). First, we assessed  
222 the predictive power of the  $T_{i-2}$  model, where increased mature seed cone production  
223 was previously shown to be associated with decreases in spring (May-July) temperature  
224 two years before at the studied ponderosa pine population (Mooney, Linhart & Snyder  
225 2011). Second, we sought to compare the  $T_{i-2}$  model with a model based on the  
226 difference in temperature between  $T_{i-2}$  and the year preceding the initiation of  
227 reproduction ( $T_{i-2} - T_{i-3}$ ), i.e. the  $\Delta T$  model. Finally, for the sake of thoroughness, we ran  
228 two additional models, one including both  $T_{i-2}$  and  $T_{i-3}$  (2T model) and the other  
229 including  $T_{i-3}$  alone ( $T_{i-3}$  model) (Pearse, Koenig & Knops 2014). The four candidate  
230 models were compared using the Pearson  $r$  correlation coefficient and the corrected

231 Akaike information criterion ( $AIC_c$ ) (see Krebs *et al.* 2012; Kelly *et al.* 2013; Pearse,  
232 Koenig & Knops 2014). The  $AIC_c$  is a measure of the relative fit of a statistical model  
233 based upon the observed data. The model with the smallest  $AIC_c$  has the best fit because  
234 it minimizes the information loss (Burnham & Anderson 2002; Murtaugh 2014). In  
235 addition, this information criterion penalizes the model based upon the number of  
236 parameters included (Burnham & Anderson 2002; Murtaugh 2014).

237 *Mechanism of climatic effects on reproduction.* Following Pearse, Koenig &  
238 Knops (2014), we explored the mechanistic links between climatic factors and seed  
239 cone production by testing whether temperature influenced patterns of reproductive  
240 investment (via effects on resource availability and trade-offs). In so doing, we assessed  
241 whether there were individual-level effects of climate on plant reproductive investment  
242 that occurred independently of fitness benefits of population-level reproductive  
243 synchrony.

244 In particular, we tested for a trade-off between current and past female  
245 reproduction, and whether climatic factors influenced the strength of this trade-off. To  
246 test for such trade-off, we regressed current mature seed cone production onto mature  
247 seed cone production in the previous year. Then, to test for an effect of temperature on  
248 this trade-off, we performed a linear mixed model with seed cone production in the  
249 previous year,  $T_{i-2}$  (the spring mean temperature two years before seed cone maturation),  
250 and their interaction as predictors of mature seed cone production. Because reproductive  
251 trade-offs occur at the individual level due to resource limitation and allocation  
252 constraints, this mechanistic model was conducted at the tree level (Pearse, Koenig &  
253 Knops 2014). We used  $T_{i-2}$  in this model (instead of the other climatic predictors)  
254 because this climatic variable was the best predictor of mature seed cone production  
255 (see *Results*). The interaction term tested whether the relationship between current and

256 past reproduction was contingent upon the spring mean temperature two years before  
257 seed cone maturation (i.e. climate influencing reproductive investment via within-tree  
258 resource availability). A negative value for the interaction parameter indicates that as  $T_{i-2}$   
259 increases, the relationship between current seed cone production and past seed cone  
260 production becomes more negative (i.e. stronger trade-off between seed cone production  
261 in  $N_{i-1}$  and  $N_i$ ), or alternatively, that as  $T_{i-2}$  decreases (cooler previous springs), the  
262 trade-off becomes weaker. To account for effects of tree size which have previously  
263 been shown to influence the magnitude of reproductive trade-offs (i.e. larger trees have  
264 more available resources and are less likely to exhibit allocation constraints), we  
265 included basal tree diameter as a covariate in this statistical model (Almqvist, Jansson &  
266 Sonesson 2001; Smaill *et al.* 2011; Santos-del-Blanco & Climent 2014).

267 The test of mechanism (trade-offs) of temperature effects on reproduction was  
268 performed using linear mixed models with PROC MIXED in SAS 9.2 (SAS Institute,  
269 Cary, NC), using tree as a random factor to account for repeated measures taken from  
270 each tree throughout the sampling period (Moreira *et al.* 2014; Pearse, Koenig & Knops  
271 2014).

272

## 273 **RESULTS**

274 A total of 194,052 seed cones were produced at the site over the 31 years of study for a  
275 site-wide average of  $6,064 \pm 1,410$  cones per year (mean  $\pm$  SE). Seed cone production  
276 varied extensively among the 217 trees, ranging 0 to 26,040 seed cones produced  
277 throughout the 31 years sampled.

278

## 279 **Models of climatic predictors of seed cone production in ponderosa pine**

280 The  $\Delta T$ ,  $T_{i-2}$ , and 2T models all significantly predicted mature seed cone production by  
281 *P. ponderosa*, whereas the  $T_{i-3}$  model was not significant (Table 1). The Pearson  $r$   
282 correlation coefficients between climatic factors and mature seed cone production were  
283 negative and similar in magnitude for these three significant models (Table 1, Fig. 1),  
284 demonstrating a pattern of increase in mature seed cone production with (i) decreases in  
285 spring mean temperature two years prior to cone production ( $T_{i-2}$  model), (ii) decreases  
286 in the spring mean temperatures two and three years prior (2T model), and (iii)  
287 decreases in the change in spring mean temperatures from three years prior to two years  
288 prior ( $\Delta T$  model). However, the  $T_{i-2}$  and 2T models had smaller  $AIC_c$  values and thus  
289 provided a better fit relative to the  $\Delta T$  model (Table 1, Fig 1). These results indicate that  
290 the difference in temperature between previous growing seasons (as proposed by Kelly  
291 *et al.* 2013) was a less robust predictor of mature seed cone production compared with  
292 temperature two years before seed cone maturation ( $T_{i-2}$ ) or temperature two years  
293 before together with three years before maturation (2T). In addition, although the  $T_{i-2}$   
294 and 2T models had qualitatively similar  $AIC_c$  values, we use  $T_{i-2}$  for subsequent  
295 analyses because this model had a marginally better fit (0.6 lower  $AIC_c$ ). Moreover,  
296 while the AIC accounts for the number of terms in a model, the  $T_{i-2}$  model provided a  
297 more parsimonious explanation of mature seed cone production relative to the 2T model  
298 as the former included only one predictor and the latter included two.

299  $T_{i-2}$  ranged from 16.23 °C in 1995 to 21.62 °C in 2000. The mean  $T_{i-2}$  over the 31  
300 years of study was  $18.76 \pm 0.22$  (mean  $\pm$  SE). Importantly, for climate to drive masting,  
301 patterns of reproduction must be more variable than climate (Kelly 1994). Accordingly,  
302 we found that the coefficient of variation of seed cone production at the population level  
303 was 1.26 (Linhart *et al.* 2014) while the coefficient of variation of  $T_{i-2}$  was 0.06.

304

## 305 **Temperature as a driver of seed cone production in ponderosa pine**

306 In accordance with the expectation of reproductive trade-offs, we found that the current  
307 year's mature seed cone production ( $N_i$ ) was negatively affected by the production of  
308 mature seed cones during the previous year ( $N_{i-1}$ ) (Table 2a). Moreover, we found a  
309 significant interaction between seed cone production in the previous year and  $T_{i-2}$  on  
310 current seed cone production (Table 2b), showing that the observed reproductive trade-  
311 off was contingent upon the spring temperature two years before seed cone maturation.  
312 A negative value for the interaction parameter was observed (interaction between  $T_{i-2}$   
313 and  $N_{i-1}$ ; Table 2b), which indicates that as  $T_{i-2}$  increases, the relationship between  
314 current seed cone production and past seed cone production becomes more negative (i.e.  
315 stronger trade-off between seed cone production in  $N_{i-1}$  and  $N_i$ ), or alternatively, that as  
316  $T_{i-2}$  decreases the relationship becomes less negative (Fig. 2). This demonstrates that  
317 cool spring temperatures two years previous to mature seed cone production are not  
318 only positively associated with masting (and the benefits obtained due to the economies  
319 of scale from synchrony; Moreira *et al.* 2014; Linhart *et al.* 2014), but are also  
320 associated with an independent, direct positive effect on reproduction by decreasing the  
321 strength of individual-level trade-offs between current and past reproduction (Fig. 2).

322

## 323 **DISCUSSION**

### 324 Overview

325 Our past research with the same *P. ponderosa* population demonstrated reproductive  
326 benefits of masting through both predator satiation and pollination efficiency (Linhart *et*  
327 *al.* 2014; Moreira *et al.* 2014). In the present work, we further show that the same  
328 climatic conditions that drive masting exert direct effects on individuals by influencing  
329 the strength of trade-offs between current and past reproduction. This suggests that

330 individual-level responses to climatic factors have the potential to influence inter-annual  
331 patterns in plant reproduction in the absence of the collective benefits associated with  
332 masting. Together, these findings suggest a potential mechanism that explains the origin  
333 and maintenance of masting: individuals initially respond to climatic cues that directly  
334 enhance reproduction (e.g. lower reproductive costs through weakened trade-offs) and  
335 this dynamic, expressed across multiple individuals, reinforces these benefits through  
336 the economies of scale associated with synchrony and masting.

337

### 338 Models of climatic predictors of seed cone production

339 Our findings run counter to the proposition by Kelly *et al.* (2013) that the  $\Delta T$  model is  
340 superior for predicting seed production than other climatic variables. They concluded  
341 that the  $\Delta T$  model was more robust to the introduction of additional data, as well as  
342 insensitive to increases in global mean temperature. However, to date only three studies  
343 spanning 20 masting species across six families have tested the relative fit of this model,  
344 and their findings provide mixed support (Kelly *et al.* 2013; Koenig & Knops 2014;  
345 Pearse, Koenig & Knops 2014). For example, a study by Kelly *et al.* (2013) was  
346 generally supportive as they found that the  $\Delta T$  model had a better fit in predicting seed  
347 production for 12 of 15 studied plant species (see Table 2 in Kelly *et al.* 2013).  
348 However, Koenig & Knops (2014) found that temperature and precipitation during the  
349 previous spring and summer were strongly linked to acorn production by four oak  
350 species (*Quercus* spp.), whereas a  $\Delta T$  model failed to predict acorn production for three  
351 of these species. Similarly, Koenig *et al.* (2015) documented that temperatures during  
352 the spring flowering period (but not temperature difference) in *Quercus lobata* altered  
353 the patterns of synchrony and temporal variability in acorn production. Finally, Pearse,  
354 Koenig & Knops (2014) found that the  $\Delta T$  model explained only a slightly higher

355 proportion of acorn production by *Q. lobata* than a model that included April  
356 temperature alone (i.e. similar  $R^2$  and P-values).

357         Two factors may explain why our findings for ponderosa pine (and several other  
358 studies) have failed to support the  $\Delta T$  model. Specifically, (i) differences in  
359 environmental heterogeneity and in the steepness of the environmental gradients among  
360 species' distribution ranges (e.g. alpine grasslands and lowland forests in Kelly *et al.*  
361 2013 vs. montane forests in our case), and (ii) differences in species life forms and  
362 longevity (herbs and small trees in Kelly *et al.* 2013 vs. a long-lived, large tree). Both  
363 factors may result in species-to-species variability in the effects of temperature on  
364 reproductive investment and phenology. In this context, pines (and oaks) are long-lived  
365 species that occupy a wide range of edaphic and climatic conditions, spanning from  
366 temperate to tropical regions of the world and from sea level to high elevations  
367 (Richardson 1998). Therefore, it is likely that long-lived tree species with broad  
368 distributions (as opposed to short-lived herbs with narrower distributions) will exhibit a  
369 greater range of responses to temperature variation and will be better adapted to  
370 assimilate temperature data over long periods of time (as opposed to biannual cycles as  
371 proposed by the  $\Delta T$  model), and adjust their reproduction accordingly.

372

### 373 Drivers of seed cone production in ponderosa pine

374 The responses of co-occurring individuals to a single climatic cue may provide fitness  
375 advantages to individuals through the economies of scale associated with synchrony  
376 (Silvertown 1980; Kelly 1994). Our past studies of this population demonstrate  
377 synchrony in response to cues that indirectly and positively affect individual fitness  
378 through both predator satiation (Linhart *et al.* 2014) and increased pollination efficiency  
379 (Moreira *et al.* 2014). Such fitness benefits from synchrony are suggestive of natural

380 selection for response to a common cue, but it is difficult to explain the evolution of a  
381 reproductive response to a cue that provides no direct, individual level benefit (Koenig  
382 *et al.* 2015).

383         For *P. ponderosa*, cool spring temperatures two years before seed cone  
384 maturation reduced the strength of the trade-off between past and current reproduction  
385 (Fig. 2), thus providing a direct reproductive benefit for individuals responding to this  
386 cue. Our finding of reproductive trade-offs is similar to that reported for other long-  
387 lived tree species (Sork, Bramble & Sexton 1993; Koenig *et al.* 1994; Crone, Miller &  
388 Sala 2009). The prevailing interpretation of such patterns has been that the production  
389 of a large seed crop depletes substantial amounts of stored resources, resulting in  
390 allocation constraints during subsequent reproductive events (e.g. Crone, Miller & Sala  
391 2009; Sala *et al.* 2012; Han *et al.* 2014). Accordingly, Kelly (1994) proposed that  
392 individual variation in seed output in masting species might largely depend on how  
393 heavily each plant invests resources during masting events, the so-called “depletion  
394 coefficient”. If this depletion coefficient is high, plant reserves would be depleted and  
395 would not subsequently reproduce again for some time.

396         An alternative mechanism proposed to explain masting behaviour independently  
397 of climatic cues is given by the “pollen coupling hypothesis”. This hypothesis describes  
398 how endogenous resource dynamics linked to pollen limitation can drive masting in the  
399 absence of climate drivers (see reviews by Miyazaki 2013; Crone & Rapp 2014). This  
400 hypothesis assumes density-dependent pollination, a high cost of producing seed as  
401 compared to pollen and ovules, and reproductive trade-offs among years (Isagi *et al.*  
402 1997). During years of low reproduction, seed set of reproducing individuals is low and  
403 stored resources are not depleted, promoting future reproductive investment. In contrast,  
404 during years of higher reproduction, seed set is high and stored resources are depleted,

405 thus reducing future reproductive investment. Accordingly, over time individuals are  
406 eventually entrained into synchronous and variable reproduction (i.e. masting) in the  
407 absence of any climatic cues. In our ponderosa pine population, we demonstrated two of  
408 the conditions necessary for pollen coupling to function: pollen limitation (Moreira *et*  
409 *al.* 2014) and a negative correlation between past and current reproduction (current  
410 study). Accordingly, while this study was not aimed at testing this hypothesis, we  
411 acknowledge that other mechanisms not associated with climatic cues might also be at  
412 work and explain masting events in this population.

413         We propose a model for the ecological and evolutionary origins of masting  
414 based upon our findings for ponderosa pine (Fig. 3). First, there is selection to time  
415 reproduction in response to a climatic factor providing a direct fitness benefit to the  
416 individual (i.e. selection for initiating reproduction during cool springs reduces  
417 reproductive trade-offs and thus minimizes the costs of reproduction). Such responses,  
418 when expressed across multiple individuals, result in synchrony. This synchrony may in  
419 turn be enhanced through two complementary mechanisms, one evolutionary and one  
420 ecological. First, selection for response to the climatic cue may be strengthened by the  
421 indirect fitness benefits associated with synchrony and economies of scale (e.g.  
422 pollination efficiency, predator satiation). And second, in the absence of any additional  
423 selection, synchrony may be strengthened through the ecological dynamics of pollen  
424 coupling (see above). Finally, these mechanisms might complement each other through  
425 feedbacks, where pollen coupling leverages a small evolutionary response into  
426 population-level synchrony, which could in turn reinforce selection. It is important to  
427 note, however, that the interpretation of our results within an evolutionary context  
428 should be made with caution as we measured the reproductive response to a climate cue  
429 on annual scales and throughout a portion of this species lifetime. In this sense, it is

430 difficult to demonstrate that a particular pattern of reproduction in a long-lived species  
431 leads to greater life-time fitness (i.e. cumulative seed cone production over the life-time  
432 of an individual).

433

#### 434 Future directions

435 Because climatic variables correlated with seed cone production can dramatically vary  
436 from site to site (e.g. Mooney, Linhart & Snyder 2011; Koenig & Knops 2014), the  
437 observed effects of climate on trade-offs between past and current reproduction may  
438 therefore be contingent upon site-specific conditions (e.g. plant species, environmental  
439 heterogeneity). Based on this, a combination of long-term data sets (such as that in this  
440 study) collected at multiple sites is needed for more tree species in order to determine  
441 the relative importance of different climatic drivers influencing plant reproductive  
442 investment and phenology, as well as to assess the general mechanisms underlying such  
443 effects. In addition, our results call for further studies and analyses that separate direct,  
444 individual-level effects of climate on reproductive investment, from indirect,  
445 population-level effects via synchrony. In doing so, we will be able to establish a link  
446 between individual-level dynamics (e.g. via trade-offs as in this study) and population-  
447 level dynamics via synchrony. Furthermore, by addressing specific plant traits underlying  
448 these individual-level responses as well as selection upon such traits we will be able to  
449 understand the mechanisms determining the evolution of masting. Finally, we call for  
450 comparative studies across habitat types, plant growth forms, and life histories in order  
451 to shed light into the relative influence of exogenous (abiotic factors) and endogenous  
452 (resource allocation patterns) processes driving long-term patterns of reproductive  
453 investment and phenology.

454

455 **ACKNOWLEDGEMENTS**

456 We gratefully acknowledge more than 60 people who participated in collecting data in  
457 the field. Comments and suggestions by three anonymous reviewers helped to improve  
458 the manuscript. This research was supported by National Science Foundation grants  
459 BMS 75-14050, DEB 78-16798, BSR 8918478, and BSR 912065 to YBL and DEB  
460 1120794 and DEB 1354734 to KAM, and by the Ramon y Cajal Research Programme  
461 (RYC-2013-13230) to XM. LAR was funded by a GAANN fellowship and a  
462 UCMEXUS-CONACyT scholarship.

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464 **Data accessibility**

465 Data are available in the Dryad Digital Repository, doi: 10.5061/dryad.h29r7 (Moreira  
466 *et al.* 2015). Data will be publicly available 12 months after publication.

467

468 **References**

- 469 Abrahamson, W.G. & Layne, J.N. (2003) Long-term patterns of acorn production for  
470 five oak species in xeric Florida uplands. *Ecology*, **84**, 2476-2492.
- 471 Almqvist, C., Jansson, G. & Sonesson, J. (2001) Genotypic correlations between early  
472 cone-set and height growth in *Picea abies* clonal trial. *Forest Genetics*, **8**, 197-  
473 204.
- 474 Allen, R.B. & Platt, K.H. (1990) Annual seedfall variation in *Nothofagus solandri*  
475 (Fagaceae), Canterbury, New Zealand. *Oikos*, **57**, 199-206.
- 476 Barringer, B.C., Koenig, W.D. & Knops, J.M.H. (2013) Interrelationships among life-  
477 history traits in three California oaks. *Oecologia*, **171**, 129-139.

478 Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a*  
479 *practical information-theoretic approach*. Springer Science+Business Media  
480 Inc., New York, USA.

481 Crone, E.E., Miller, E. & Sala, A. (2009) How do plants know when other plants are  
482 flowering? Resource depletion, pollen limitation and mast-seeding in a perennial  
483 wildflower. *Ecology Letters*, **12**, 1119-1126.

484 Crone, E.E. & Rapp, J.M. (2014) Resource depletion, pollen coupling, and the ecology  
485 of mast seeding. *Annals of the New York Academy of Sciences*, **1322**, 21-34.

486 El-Kassaby, Y.A. & Cook, C. (1994) Female reproductive energy and reproductive  
487 success in a Douglas-fir seed orchard and its impact on genetic diversity. *Silvae*  
488 *Genetica*, **43**, 243-246.

489 Fletcher, Q.E., Boutin, S., Lane, J.E., LaMontagne, J.M., McAdam, A.G., Krebs, C.J. &  
490 Humphries, M.M. (2010) The functional response of a hoarding seed predator to  
491 mast seeding. *Ecology*, **91**, 2673-2683.

492 Han, Q., Kabeya, D., Iio, A., Inagaki, Y. & Kakubari, Y. (2014) Nitrogen storage  
493 dynamics are affected by masting events in *Fagus crenata*. *Oecologia*, **174**, 679-  
494 687.

495 Isagi, Y., Sugimura, K., Sumida, A. & Ito, H. (1997) How does masting happen and  
496 synchronize? *Journal of Theoretical Biology*, **187**, 231-239.

497 Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and*  
498 *Systematics* **2**, 465-492.

499 Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology and*  
500 *Evolution*, **9**, 465-470.

501 Kelly, D., Geldenhuis, A., James, A., Holland, E.P., Plank, M.J., Brockie, R.E., Cowan,  
502 P.E., Harper, G.A., Lee, W.G., Maitland, M.J., Mark, A.F., Mills, J.A., Wilson,

503 P.R. & Byrom, A.E. (2013) Of mast and mean: differential-temperature cue  
504 makes mast seeding insensitive to climate change. *Ecology Letters*, **16**, 90-98.

505 Kelly, D., Harrison, A.L., Lee, W.G., Payton, I.J., Wilson, P.R. & Schaubert, E.M.  
506 (2000) Predator satiation and extreme mast seeding in 11 species of *Chionochloa*  
507 (Poaceae). *Oikos*, **90**, 477-488.

508 Kelly, D., Hart, D.E. & Allen, R.B. (2001) Evaluating the wind pollination benefits of  
509 mast seeding. *Ecology*, **82**, 117-126.

510 Kelly, D. & Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where?  
511 *Annual Review of Ecology and Systematics*, **33**, 427-447.

512 Kelly, D., Turnbull, M.H., Pharis, R.P. & Sarfati, M.S. (2008) Mast seeding, predator  
513 satiation, and temperature cues in *Chionochloa* (Poaceae). *Population Ecology*,  
514 **50**, 343-355.

515 Koenig, W.D. & Knops, J.M.H. (2014) Environmental correlates of acorn production by  
516 four species of Minnesota oaks. *Population Ecology*, **56**, 63-71.

517 Koenig, W.D., Knops, J.M.H., Carmen, W.J. & Pearse, I.S. (2015) What drives  
518 masting? The phenological synchrony hypothesis. *Ecology*, **96**, 184-192.

519 Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T. & Mumme, R.L. (1996)  
520 Acorn production by oaks in central coastal California: influence of weather at  
521 three levels. *Canadian Journal of Forest Research*, **26**, 1677-1683.

522 Koenig, W.D., Mumme, R.L., Carmen, W.J. & Stanback, M.T. (1994) Acorn  
523 production by oaks in central coastal California: variation within and among  
524 years. *Ecology*, **75**, 99-109

525 Kon, H., Noda, T., Terazawa, K., Koyama, H. & Yasaka, M. (2005a) Evolutionary  
526 advantages of mast seeding in *Fagus crenata*. *Journal of Ecology*, **93**, 1148-  
527 1155.

- 528 Kon, H., Noda, T., Terazawa, K., Koyama, H. & Yasaka, M. (2005b) Proximate factors  
529 causing mast seeding in *Fagus crenata*: the effects of resource level and weather  
530 cues. *Canadian Journal of Botany*, **83**, 1402-1409.
- 531 Krebs, C.J., Boutin, S. & Boonstra, R. (2001) Ecosystem dynamics of the boreal forest.  
532 The Kluane project. Oxford University Press, New York, NY.
- 533 Krebs, C.J., LaMontagne, J.M., Kenney, A.J. & Boutin, S. (2012) Climatic determinants  
534 of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany*,  
535 **90**, 113-119.
- 536 Linhart, Y.B. & Mitton, J.B. (1985) Relationships among reproduction, growth rates,  
537 and protein heterozygosity in ponderosa pine. *American Journal of Botany*, **72**,  
538 181-184.
- 539 Linhart, Y.B., Moreira, X., Snyder, M.A. & Mooney, K.A. (2014) Variability in seed  
540 cone production and functional response of seed predators to seed cone  
541 availability: support for the predator satiation hypothesis. *Journal of Ecology*  
542 **102**, 576-583.
- 543 Masaki, T., Oka, T., Osumi, K. & Suzuki, W. (2008) Geographical variation in climatic  
544 cues for mast seeding of *Fagus crenata*. *Population Ecology*, **50**, 357-366.
- 545 Miyazaki, Y. (2013) Dynamics of internal carbon resources during masting behavior in  
546 trees. *Ecological Research*, **28**, 143-150.
- 547 Mooney, K.A., Linhart, Y.B. & Snyder, M.A. (2011) Masting in ponderosa pine:  
548 comparisons of pollen and seed over space and time. *Oecologia*, **165**, 651-661.
- 549 Moreira, X., Abdala-Roberts, L., Linhart, Y.B. & Mooney, K.A. (2014) Masting  
550 promotes individual- and population-level reproduction by increasing pollination  
551 efficiency. *Ecology*, **95**, 801-807.
- 552 Murtaugh, P.A. (2014) In defense of P values. *Ecology*, **95**, 611-617.

553 Norton, D.A. & Kelly, D. (1988) Mast seeding over 33 years by *Dacrydium*  
554 *cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of  
555 economies of scale. *Functional Ecology*, **2**, 399-408.

556 Pearse, I.S., Koenig, W.D. & Knops, J.M.H. (2014) Cues versus proximate drivers:  
557 testing the mechanism behind masting behavior. *Oikos*, **123**, 179-184.

558 Piovesan, G. & Adams, J.M. (2001) Masting behaviour in beech: linking reproduction  
559 and climatic variation. *Canadian Journal of Botany*, **79**, 1039-1047.

560 Rapp, J.M., McIntire, E.J.B. & Crone, E.E. (2013) Sex allocation, pollen limitation and  
561 masting in whitebark pine. *Journal of Ecology*, **101**, 1345–1352.

562 Richardson, D.M. (1998) *Ecology and biogeography of Pinus*. Cambridge University  
563 Press, Cambridge.

564 Richardson, S.J., Allen, R.B., Whitehead, D., Carswell, F.E., Ruscoe, W.A. & Platt,  
565 K.H. (2005) Climate and net carbon availability determine temporal patterns of  
566 seed production by *Nothofagus*. *Ecology*, **86**, 972-981.

567 Roland, C.A., Schmidt, J.H. & Johnstone, J.F. (2014) Climate sensitivity of  
568 reproduction in a mast-seeding boreal conifer across its distributional range from  
569 lowland to treeline forests. *Oecologia*, **174**, 665-677.

570 Sala, A., Hopping, K., McIntire, E.J.B., Delzon, S. & Crone, E.E. (2012) Masting in  
571 whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*,  
572 **196**, 189-199.

573 Santos-del-Blanco, L. & Climent, J. (2014) Costs of female reproduction in a conifer  
574 tree: a whole-tree level assessment. *Journal of Ecology*, **102**, 1310-1317.

575 Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., Payton, I.J.,  
576 Wilson, P.R., Cowan, P.E. & Brockie, R.E. (2002) Masting by eighteen New

577 Zealand plant species: the role of temperature as a synchronizing cue. *Ecology*,  
578 **83**, 1214-1225.

579 Selås, V., Piovesan, G., Adams, J.M. & Bernabei, M. (2002) Climatic factors  
580 controlling reproduction and growth of Norway spruce in southern Norway.  
581 *Canadian Journal of Forest Research*, **32**, 217-225.

582 Silvertown, J.W. (1980) The evolutionary ecology of mast-seeding in trees. *Biological*  
583 *Journal of the Linnean Society*, **14**, 235-250.

584 Smaill, S.J., Clinton, P.W., Allen, R.B. & Davis, M.R. (2011) Climate cues and  
585 resources interact to determine seed production by a masting species. *Journal of*  
586 *Ecology* **99**, 870-877.

587 Sork, V.L., Bramble, J. & Sexton, O. (1993) Ecology of mast-fruiting in three species of  
588 North American deciduous oaks. *Ecology*, **74**, 528-541.

589 Zasada, J.C. & Viereck, L.A. (1970) White spruce cone and seed production in interior  
590 Alaska, 1957-68. Pacific Northwest Forest and Range Experiment Station,  
591 Portland, OR.

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602 **Table 1.** Climatic predictors of mature seed cone production in *Pinus ponderosa*. Four  
 603 candidate models were evaluated:  $T_{i-2}$  model (spring mean temperature two years before  
 604 mature seed cone production),  $T_{i-3}$  model (spring mean temperature three years before  
 605 mature seed cone production),  $\Delta T$  model (change in spring mean temperature from  
 606 three to two years before seed production,  $T_{i-2} - T_{i-3}$ ), and 2T model (individual effects  
 607 of spring mean temperature three and two years before seed production). Corrected  
 608 Akaike information criterion ( $AIC_c$ ), Pearson  $r$  correlation coefficients, and  $P$ -values are  
 609 shown. Significant predictors ( $P < 0.05$ ) are typed in bold.

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Predictors	$AIC_c$	$r$	$P$
$T_{i-2}$	95.4	-0.605	<b>&lt;0.001</b>
$T_{i-3}$	108.5	0.081	0.664
$\Delta T$	108.9	-0.517	<b>0.002</b>
2T ( $T_{i-2}$ , $T_{i-3}$ )	96.0	-0.615	<b>0.001</b>

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623 **Table 2.** Results from models linking mature seed cone production ( $N_i$ ) and resource  
624 limitation in *Pinus ponderosa*. (a) Regression model testing for a relationship between  
625 current mature seed cone production and mature seed cone production during the  
626 previous year ( $N_{i-1}$ ), i.e. test of reproductive trade-off. (b) Linear mixed model testing  
627 for the effects of mature seed cone production during the previous year ( $N_{i-1}$ ), spring  
628 mean temperature two years before seed cone maturation ( $T_{i-2}$ ), and the interaction  
629 between  $N_{i-1}$  and  $T_{i-2}$  (i.e. effect of temperature on the trade-off). Statistical analyses of  
630 both mechanistic models were performed at the individual tree level using a mixed  
631 model with tree as a random factor and tree basal diameter at the beginning of this study  
632 (D) as a covariate. The slope estimator ( $\beta$ ) with the standard error (inside brackets), F-  
633 values with the degrees of freedom (inside brackets), and *P*-values are shown.  
634 Significant predictors ( $P < 0.05$ ) are typed in bold.

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	a) $N_i = N_{i-1} + D$			b) $N_i = N_{i-1} + D + T_{i-2} + N_{i-1} \times T_{i-2}$		
	$\beta$ (s.e.)	F-value (df)	<i>P</i>	$\beta$ (s.e.)	F-value (df)	<i>P</i>
$N_{i-1}$	-0.0943 (0.0123)	58.55 (1, 5866)	<b>&lt;0.001</b>	0.6075 (0.1372)	19.60 (1,5864)	<b>&lt;0.001</b>
Diameter (D)	0.3119 (0.0273)	130.58 (1,5866)	<b>&lt;0.001</b>	0.3084 (0.0270)	130.68 (1,5864)	<b>&lt;0.001</b>
$T_{i-2}$	-	-	-	-14.699 (0.818)	322.87 (1,5864)	<b>&lt;0.001</b>
$N_{i-1} \times T_{i-2}$	-	-	-	-0.0369 (0.0072)	26.22 (1,5864)	<b>&lt;0.001</b>

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639 **FIGURE LEGENDS**

640

641 **Figure 1. Climatic predictors of seed cone production.** Relationships between log-  
642 transformed seed cone production in *Pinus ponderosa* and (a) spring temperature (May-  
643 July) from two years before seed production ( $T_{i-2}$ ) and (b) the difference in mean spring  
644 temperature two and three years before mature seed production ( $\Delta T$ ). Each point  
645 represents a year ( $N = 31$ ). Pearson  $r$  correlation coefficients and  $P$ -values are shown.

646

647 **Figure 2.** Model predictions for the relationship between current seed cone production  
648 ( $N_i$ ) and past seed cone production ( $N_{i-1}$ ) at spring temperatures (mean of May, June and  
649 July two years before seed production;  $T_{i-2}$ ) representing the maximum, minimum, and  
650 averaged temperatures observed for the studied population of ponderosa pine.

651

652 **Figure 3.** Diagram representing proposed links between individual- and population-  
653 level responses to climatic factors for the studied ponderosa pine population. Pollen  
654 coupling was included as it has been proposed to underlie masting in the absence of  
655 climatic drivers, where inter-annual variation is driven by reproductive trade-offs  
656 among years, and synchrony occurs because out-cross pollen limitation renders  
657 asynchronous reproduction unsuccessful. <sup>(1)</sup> Mooney *et al.* 2011; <sup>(2)</sup> this study; <sup>(3)</sup>  
658 Moreira *et al.* 2014; <sup>(4)</sup> Linhart *et al.* 2014.

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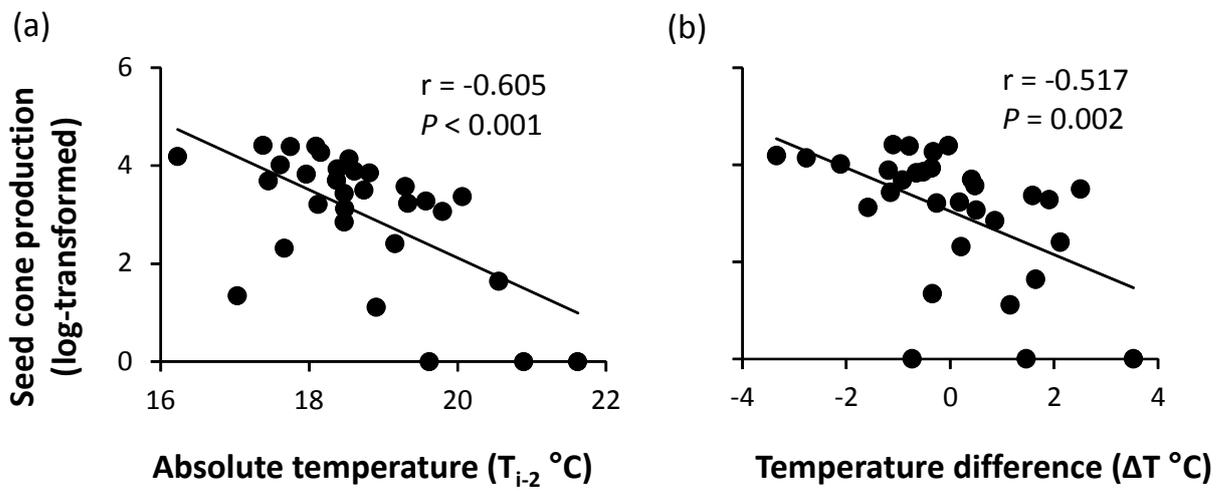
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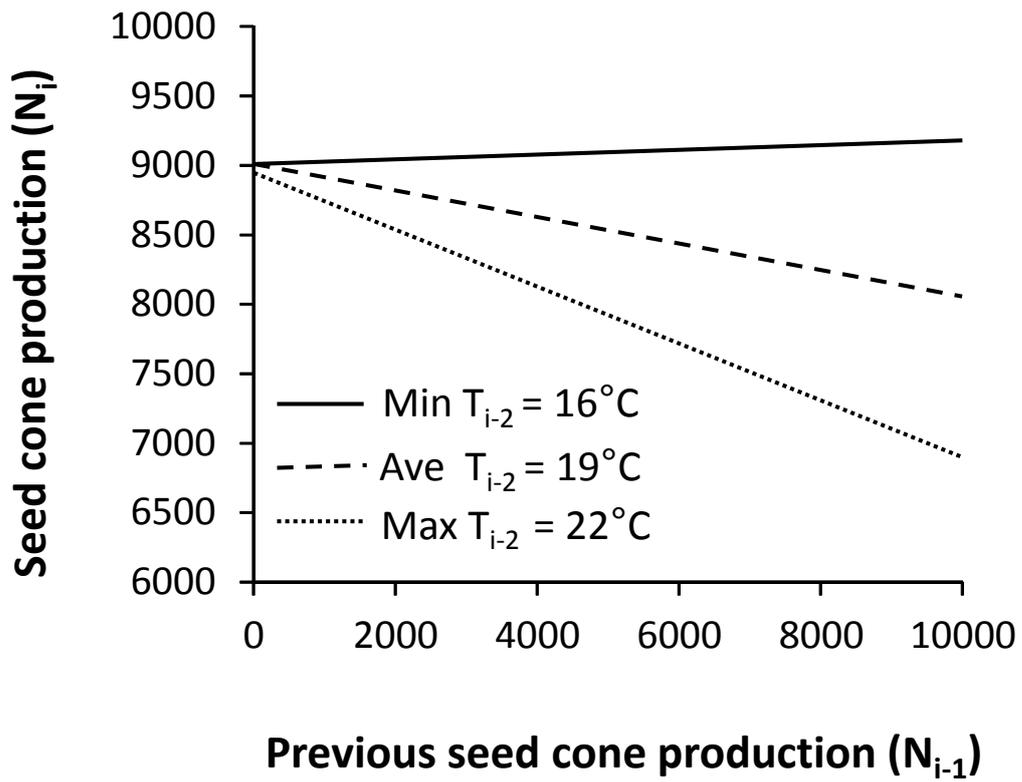
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**Figure 1.** Moreira et al.

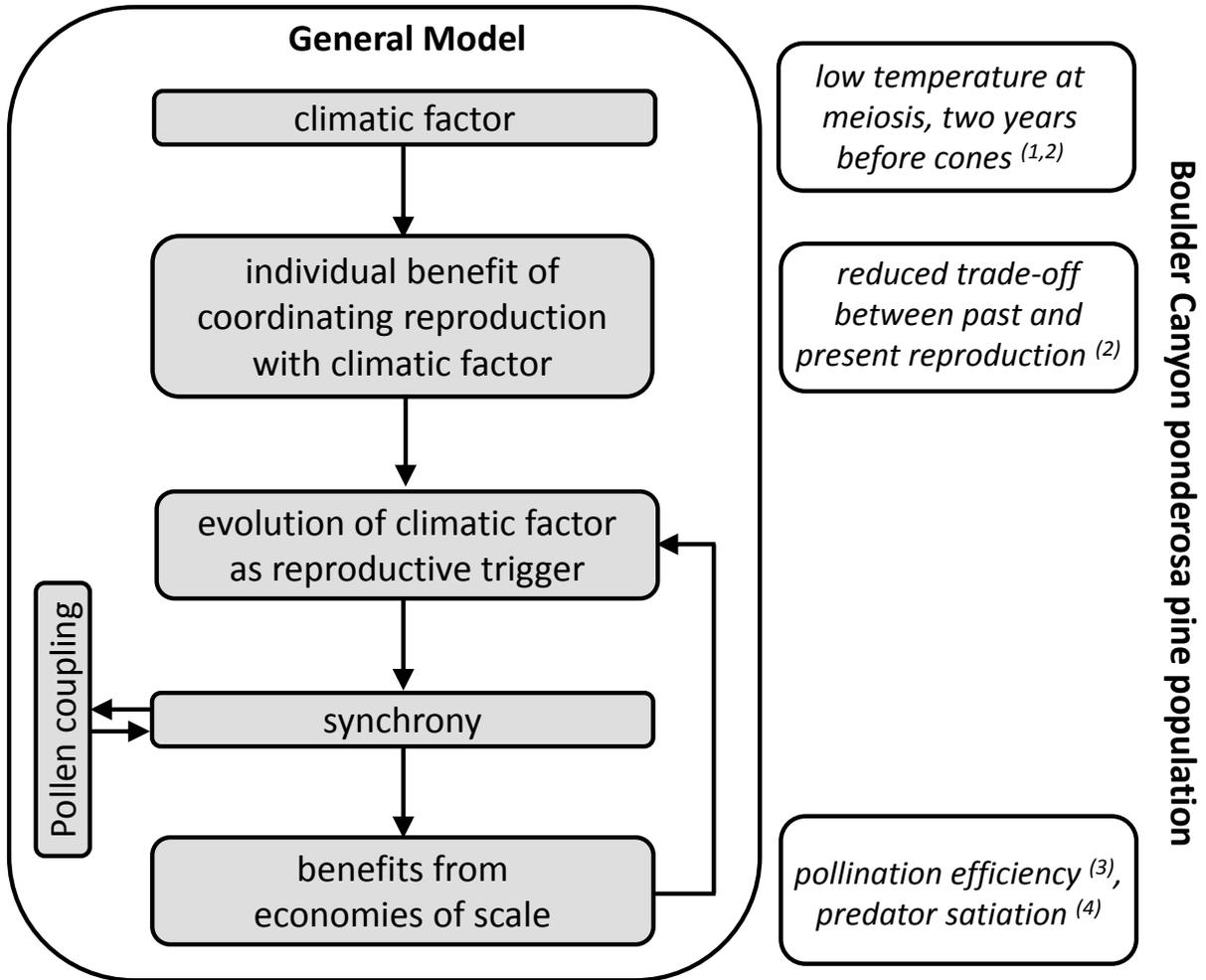
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Figure 2. Moreira et al

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**Figure 3.** Moreira et al