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

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Summary

1. Mechanisms by which climatic factors drive reproductive investment and phenology in masting species are not completely understood. Climatic conditions may act as a proximate cue, stimulating the onset of reproduction and indirectly increasing fitness through benefits associated with synchronous reproduction among individuals. Alternatively, climatic conditions may directly influence individual-level allocation to reproduction and reproductive success through effects occurring independently of synchronous reproduction. We previously showed that masting in a ponderosa pine (*Pinus ponderosa*) population was strongly influenced by spring mean temperature 2 years before seed cone maturation (T_{i-2}). However, recent work shows that the difference in temperature between previous growing seasons (ΔT) is more predictive of reproductive investment in long-lived tree species.

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

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

4. *Synthesis.* We demonstrate that a single climatic factor provides fitness benefits to individuals directly, by weakening reproductive trade-offs, and indirectly through the benefits associated with synchrony and masting. This suggests a mechanism for the origin and maintenance of masting: individuals initially respond to climatic cues that directly enhance reproduction (e.g. lower reproductive costs through weakened trade-offs) and this dynamic, expressed across multiple individuals, reinforces these benefits through the economies of scale associated with synchrony and masting.

Key-words: economies of scale, *Pinus ponderosa*, plant population and community dynamics, reproductive trade-offs, resource limitation, seed cone production, ΔT model

Introduction

Masting is a reproductive strategy defined as the episodic production of large, synchronous seed crops by a plant population (Silvertown 1980; Kelly 1994). Several fitness advantages have been associated with masting that entail economies of scale such as seed predator satiation (Janzen

1971; Kelly *et al.* 2000; Fletcher *et al.* 2010), improved seed dispersal (Norton & Kelly 1988; Kelly 1994) and increased pollination efficiency (Kelly, Hart & Allen 2001; Kon *et al.* 2005a; Rapp, McIntire & Crone 2013; Moreira *et al.* 2014), all of which have been invoked to explain the occurrence and maintenance of this reproductive phenomenon.

The reproductive dynamics of masting species are strongly influenced by climatic conditions previous to or during the initiation of reproduction, which influence allocation to

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reproduction and the degree of synchrony in seed production (Schauber *et al.* 2002; Kon *et al.* 2005b; Kelly *et al.* 2008; Smaill *et al.* 2011; Roland, Schmidt & Johnstone 2014). For example, high seed production is frequently linked to warm temperatures during the previous growing season (e.g. Schauber *et al.* 2002; Selås *et al.* 2002; Kelly *et al.* 2008; Masaki *et al.* 2008). In addition, other studies have found that drought in the early summer has positive effects on flowering the following year (e.g. Piovesan & Adams 2001; Krebs *et al.* 2012).

The mechanisms by which climatic factors drive reproductive patterns in masting species are not fully understood, but several non-mutually exclusive scenarios are commonly considered. First, climatic conditions may act as proximate cues that directly stimulate the onset of reproduction and reproductive phenology (Kelly & Sork 2002; Kelly *et al.* 2013). Under this scenario, the fitness advantage of individual plants responding similarly (in amount and timing) originates from the economies of scale associated with population-level reproductive synchrony (Norton & Kelly 1988; Kelly 1994). Nevertheless, it is difficult to explain the evolution of a reproductive response to a cue that provides no direct, individual-level benefit (Koenig *et al.* 2015). Secondly, other authors argue that climatic factors shape reproductive patterns at the individual level and that any benefit of masting associated with economies of scale arises secondarily. Climatic factors may directly alter resource availability (Koenig *et al.* 1996, 2015; Richardson *et al.* 2005; Pearse, Koenig & Knops 2014) such that there are individual-level fitness advantages of responding to climatic factors (Pearse, Koenig & Knops 2014; Koenig *et al.* 2015). For example, seasonality in precipitation or temperature has been shown to influence plant nitrogen and carbon availability (Allen & Platt 1990; Richardson *et al.* 2005; Smaill *et al.* 2011), as well as soil moisture (Abrahamson & Layne 2003; Richardson *et al.* 2005), which may in turn influence within-plant resource allocation patterns (Barringer, Koenig & Knops 2013; Pearse, Koenig & Knops 2014). As a consequence of such effects on resource availability, climatic conditions may strengthen or weaken trade-offs between current and past reproduction; such effects may be particularly strong in the case of masting species due to resource depletion during large reproductive events (Sala *et al.* 2012). Finally, so-called pollen coupling has been proposed to underlie masting in the absence of climatic drivers (see reviews by Miyazaki 2013; Crone & Rapp 2014), where interannual variation is driven by reproduction trade-offs among years, and synchrony occurs because outcross pollen limitation renders asynchronous reproduction unsuccessful.

A recent analysis of long-term data sets of 15 species across five plant families proposed a new predictive model to explain how climatic conditions modulate reproductive investment and phenology in masting species (Kelly *et al.* 2013). Specifically, for 12 of the 15 species studied, a model using the difference in temperature from one previous growing season to the next (ΔT model hereafter) as a predictor of reproductive investment better predicted (i.e. smaller Akaike information criterion and higher correlation coefficient) seed production relative to a model including the temperature from a single previous growing season as predictor (Kelly *et al.* 2013). The authors offered

several reasons for why the ΔT model exhibited a better fit relative to the model based upon a temperature from a single previous season. First, a model based on temperature from a single previous season is not capable of explaining why two previous consecutive warm years rarely cause two consecutive years of high seed production (i.e. climatic effects of previous consecutive years are not additive). Secondly, the ΔT model predicts that long-term plant reproductive responses are not influenced by gradual increases in mean temperature (such as those produced by climate change) but rather by averaging effects of climatic conditions across multiple growing seasons. This would also explain why the frequency of high seed years (i.e. mast years) remains relatively constant over large periods of time (Kelly *et al.* 2013). However, not all studies have been supportive of this model's predictions. For example, Koenig & Knops (2014) showed that acorn production of three out of four oak species was correlated with spring and summer temperature and precipitation, but not with differences between previous growing seasons for each of these climatic variables. Accordingly, further tests are needed to determine the general applicability of the ΔT model, as well as to identify the climatic drivers that best predict reproduction in long-lived species and the mechanisms underlying such effects.

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

Here, we sought to determine which climatic factors drive synchronous reproduction in *P. ponderosa* by comparing different competing models and address whether responses to such climatic factors provide direct, individual-level reproductive benefits independent of those previously shown to occur through synchrony (Mooney, Linhart & Snyder 2011; Linhart *et al.* 2014; Moreira *et al.* 2014). First, we compared four candidate models that predict mature seed cone production in *P. ponderosa* based upon different climatic factors: (i) a model using as predictor the difference between spring mean temperature 2 and 3 years before cone maturation (ΔT model, i.e. $T_{i-2} - T_{i-3}$) (Kelly *et al.* 2013), (ii) a model using as predictor the mean temperature 2 years before cone maturation (i.e. T_{i-2} ; Mooney, Linhart & Snyder 2011), (iii) a model using as predictor the temperature 3 years before seed cone maturation (T_{i-3}) and (iv) a model using as predictor the individual effects of spring temperature 2 years and spring temperature 3 years before cone maturation (2T model hereafter, i.e. T_{i-2} and T_{i-3}) (Kelly *et al.* 2013). Secondly, after determining which temperature predictor best explained seed cone production

(based upon results from the above models), we tested for a potential mechanism by which such climatic variables could provide a direct reproductive advantage not associated with the economies of scale from synchronized reproduction. Specifically, we tested whether temperature influenced within-plant resource allocation patterns via reproductive trade-offs. In so doing, this study identifies the climatic factors influencing reproductive investment and phenology in a long-lived plant and proposes a mechanism by which masting originates and is maintained.

Material and methods

PINE SPECIES, STUDY AREA AND DATA COLLECTION

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

We carried out a long-term (31 years) field survey during which we monitored the reproduction of 217 individuals from a ponderosa pine population distributed over a 2-ha area on the south-facing slope of Boulder Canyon, at an elevation of 1740 m in the Front Range of the Rocky Mountains (near the town of Boulder, Colorado, 40°00'48" N, 105°18'12" W; Linhart & Mitton 1985; Mooney, Linhart & Snyder 2011). To reduce among-tree variation in abiotic factors strictly associated with fine-scale environmental conditions at each tree location, we selected the experimental trees from an area with a uniform slope, soils, sun and wind exposure. At the beginning of this study, the age of the studied trees ranged from ca. 40 to over 280 years based upon trunk cores taken at 30–50 cm above ground level. We also measured the basal diameter of each tree at the beginning of this study.

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

STATISTICAL ANALYSES

Comparison of climatic predictors of ponderosa pine reproduction

In a previous study using the same population, we related mean monthly precipitation and temperature to mature seed cone production (Mooney, Linhart & Snyder 2011). We found that increased mature

seed cone production was associated with decreases in spring temperature (mean of May, June, July) 2 years before, increases in summer precipitation (mean of July, August, September) 2 years before and increases in winter temperature (mean of December, January, February) during the previous year (Mooney, Linhart & Snyder 2011). To achieve normality of residuals in our models, seed cone data were log-transformed for the present analyses. After log-transforming, spring temperature 2 years before was the only significant predictor of mature seed cone production. Additionally, because pollen and ovule meiosis corresponded with spring temperature 2 years before seed cone maturation (Mooney, Linhart & Snyder 2011), the effect of this climatic factor would likely be the best predictor of reproductive investment. For both these reasons, in the present study, we only tested models that included predictors based upon spring temperatures (calculated as the mean of May, June and July monthly means; Mooney, Linhart & Snyder 2011).

We compared four candidate models using log-transformed seed cone data at the population level (Kelly *et al.* 2013; Pearse, Koenig & Knops 2014). First, we assessed the predictive power of the T_{i-2} model, where increased mature seed cone production was previously shown to be associated with decreases in spring (May–July) temperature 2 years before at the studied ponderosa pine population (Mooney, Linhart & Snyder 2011). Secondly, we sought to compare the T_{i-2} model with a model based on the difference in temperature between T_{i-2} and the year preceding the initiation of reproduction ($T_{i-2} - T_{i-3}$), that is the ΔT model. Finally, for the sake of thoroughness, we ran two additional models, one including both T_{i-2} and T_{i-3} (2T model) and the other including T_{i-3} alone (T_{i-3} model) (Pearse, Koenig & Knops 2014). The four candidate models were compared using the Pearson r correlation coefficient and the corrected Akaike information criterion (AIC_c) (see Krebs *et al.* 2012; Kelly *et al.* 2013; Pearse, Koenig & Knops 2014). The AIC_c is a measure of the relative fit of a statistical model based upon the observed data. The model with the smallest AIC_c has the best fit because it minimizes the information loss (Burnham & Anderson 2002; Murtaugh 2014). In addition, this information criterion penalizes the model based upon the number of parameters included (Burnham & Anderson 2002; Murtaugh 2014).

Mechanism of climatic effects on reproduction

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

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

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

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

Results

A total of 194 052 seed cones were produced at the site over the 31 years of study for a site-wide average of 6064 ± 1410 cones per year (mean \pm SE). Seed cone production varied extensively among the 217 trees, ranging from 0 to 26 040 seed cones produced throughout the 31 years sampled.

MODELS OF CLIMATIC PREDICTORS OF SEED CONE PRODUCTION IN PONDEROSA PINE

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

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

Predictors	AIC _c	r	P
T_{i-2}	95.4	-0.605	<0.001
T_{i-3}	108.5	0.081	0.664
ΔT	108.9	-0.517	0.002
2T (T_{i-2} , T_{i-3})	96.0	-0.615	0.001

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

TEMPERATURE AS A DRIVER OF SEED CONE PRODUCTION IN PONDEROSA PINE

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

Discussion

OVERVIEW

Our past research with the same *P. ponderosa* population demonstrated reproductive benefits of masting through both

Fig. 1. Climatic predictors of seed cone production. Relationships between log-transformed seed cone production in *Pinus ponderosa* and (a) spring temperature (May–July) from 2 years before seed production (T_{i-2}) and (b) the difference in mean spring temperature 2 and 3 years before mature seed production (ΔT). Each point represents a year ($N = 31$). Pearson's r correlation coefficients and P -values are shown.

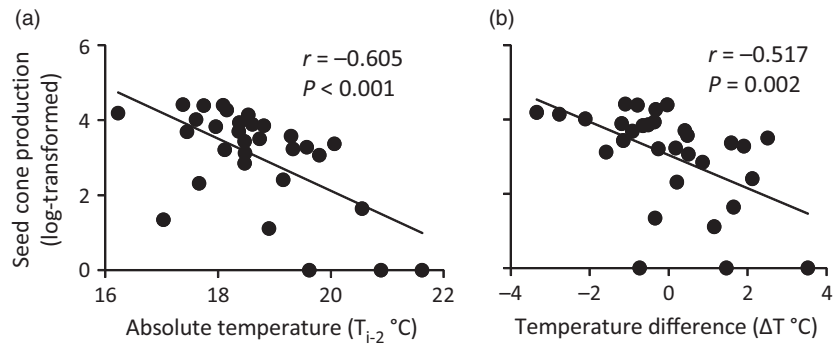


Table 2. Results from models linking mature seed cone production (N_i) and resource limitation in *Pinus ponderosa*. (a) Regression model testing for a relationship between current mature seed cone production and mature seed cone production during the previous year (N_{i-1}), that is test of reproductive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

	(a) $N_i = N_{i-1} + D$			(b) $N_i = N_{i-1} + D + T_{i-2} + N_{i-1} \times T_{i-2}$		
	β (SE)	F -value (d.f.)	P	β (SE)	F -value (d.f.)	P
N_{i-1}	-0.0943 (0.0123)	58.55 (1,5866)	<0.001	0.6075 (0.1372)	19.60 (1,5864)	<0.001
Diameter (D)	0.3119 (0.0273)	130.58 (1,5866)	<0.001	0.3084 (0.0270)	130.68 (1,5864)	<0.001
T_{i-2}	–	–	–	-14.699 (0.818)	322.87 (1,5864)	<0.001
$N_{i-1} \times T_{i-2}$	–	–	–	-0.0369 (0.0072)	26.22 (1,5864)	<0.001

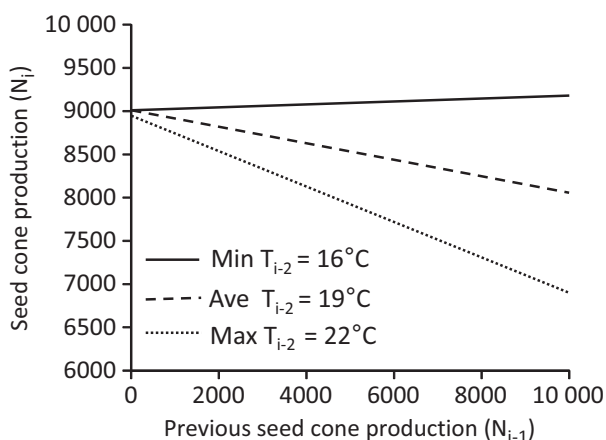


Fig. 2. Model predictions for the relationship between current seed cone production (N_i) and past seed cone production (N_{i-1}) at spring temperatures (mean of May, June and July 2 years before seed production; T_{i-2}) representing the maximum, minimum and averaged temperatures observed for the studied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

predator satiation and pollination efficiency (Linhart *et al.* 2014; Moreira *et al.* 2014). In the present work, we further show that the same climatic conditions that drive mast seeding exert direct effects on individuals by influencing the strength of trade-offs between current and past reproduction. This suggests that individual-level responses to climatic factors have the potential to influence interannual patterns in plant reproduction in the absence of the collective benefits associated

with mast seeding. Together, these findings suggest a potential mechanism that explains the origin and maintenance of mast seeding: individuals initially respond to climatic cues that directly enhance reproduction (e.g. lower reproductive costs through weakened trade-offs) and this dynamic, expressed across multiple individuals, reinforces these benefits through the economies of scale associated with synchrony and mast seeding.

MODELS OF CLIMATIC PREDICTORS OF SEED CONE PRODUCTION

Our findings run counter to the proposition by Kelly *et al.* (2013) that the ΔT model is superior for predicting seed production than other climatic variables. They concluded that the ΔT model was more robust to the introduction of additional data, as well as insensitive to increases in global mean temperature. However, to date, only three studies spanning 20 mast seeding species across six families have tested the relative fit of this model, and their findings provide mixed support (Kelly *et al.* 2013; Koenig & Knops 2014; Pearce, Koenig & Knops 2014). For example, the study by Kelly *et al.* (2013) was generally supportive as they found that the ΔT model had a better fit in predicting seed production for 12 of 15 studied plant species (see Table 2 in Kelly *et al.* 2013). However, Koenig & Knops (2014) found that temperature and precipitation during the previous spring and summer were strongly linked to acorn production by four oak species (*Quercus*

spp.), whereas a ΔT model failed to predict acorn production for three of these species. Similarly, Koenig *et al.* (2015) documented that temperatures during the spring flowering period (but not temperature difference) in *Quercus lobata* altered the patterns of synchrony and temporal variability in acorn production. Finally, Pearse, Koenig & Knops (2014) found that the ΔT model explained only a slightly higher proportion of acorn production by *Q. lobata* than a model that included April temperature alone (i.e. similar R^2 and P -values).

Two factors may explain why our findings for ponderosa pine (and several other studies) have failed to support the ΔT model: specifically, (i) differences in environmental heterogeneity and in the steepness of the environmental gradients among species' distribution ranges (e.g. alpine grasslands and lowland forests in Kelly *et al.* 2013 vs. montane forests in our case) and (ii) differences in species life-forms and longevity (herbs and small trees in Kelly *et al.* 2013 vs. a long-lived, large tree). Both factors may result in species-to-species variability in the effects of temperature on reproductive investment and phenology. In this context, pines (and oaks) are long-lived species that occupy a wide range of edaphic and climatic conditions, spanning from temperate to tropical regions of the world and from sea level to high elevations (Richardson 1998). Therefore, it is likely that long-lived tree species with broad distributions (as opposed to short-lived herbs with narrower distributions) will exhibit a greater range of responses to temperature variation and will be better adapted to assimilate temperature data over long periods of time (as opposed to biannual cycles as proposed by the ΔT model) and adjust their reproduction accordingly.

DRIVERS OF SEED CONE PRODUCTION IN PONDEROSA PINE

The responses of co-occurring individuals to a single climatic cue may provide fitness advantages to individuals through the economies of scale associated with synchrony (Silvertown 1980; Kelly 1994). Our past studies of this population demonstrate synchrony in response to cues that indirectly and positively affect individual fitness through both predator satiation (Linhart *et al.* 2014) and increased pollination efficiency (Moreira *et al.* 2014). Such fitness benefits from synchrony are suggestive of natural selection for response to a common cue, but it is difficult to explain the evolution of a reproductive response to a cue that provides no direct, individual-level benefit (Koenig *et al.* 2015).

For *P. ponderosa*, cool spring temperatures 2 years before seed cone maturation reduced the strength of the trade-off between past and current reproduction (Fig. 2), thus providing a direct reproductive benefit for individuals responding to this cue. Our finding of reproductive trade-offs is similar to that reported for other long-lived tree species (Sork, Bramble & Sexton 1993; Koenig *et al.* 1994; Crone, Miller & Sala 2009). The prevailing interpretation of such patterns has been that the production of a large seed crop depletes substantial amounts of stored resources, resulting in allocation constraints

during subsequent reproductive events (e.g. Crone, Miller & Sala 2009; Sala *et al.* 2012; Han *et al.* 2014). Accordingly, Kelly (1994) proposed that individual variation in seed output in masting species might largely depend on how heavily each plant invests resources during masting events, the so-called depletion coefficient. If this depletion coefficient is high, plant reserves would be depleted and the plants would not subsequently reproduce again for some time.

An alternative mechanism proposed to explain masting behaviour independently of climatic cues is given by the 'pollen coupling hypothesis'. This hypothesis describes how endogenous resource dynamics linked to pollen limitation can drive masting in the absence of climate drivers (see reviews by Miyazaki 2013; Crone & Rapp 2014). This hypothesis assumes density-dependent pollination, a high cost of producing seed as compared to pollen and ovules, and reproductive trade-offs among years (Isagi *et al.* 1997). During years of low reproduction, seed set of reproducing individuals is low and stored resources are not depleted, promoting future reproductive investment. In contrast, during years of higher reproduction, seed set is high and stored resources are depleted, thus reducing future reproductive investment. Accordingly, over time individuals are eventually entrained into synchronous and variable reproduction (i.e. masting) in the absence of any climatic cues. In our ponderosa pine population, we demonstrated two of the conditions necessary for pollen coupling to function: pollen limitation (Moreira *et al.* 2014) and a negative correlation between past and current reproduction (current study). Accordingly, while this study was not aimed at testing this hypothesis, we acknowledge that other mechanisms not associated with climatic cues might also be at work and explain masting events in this population.

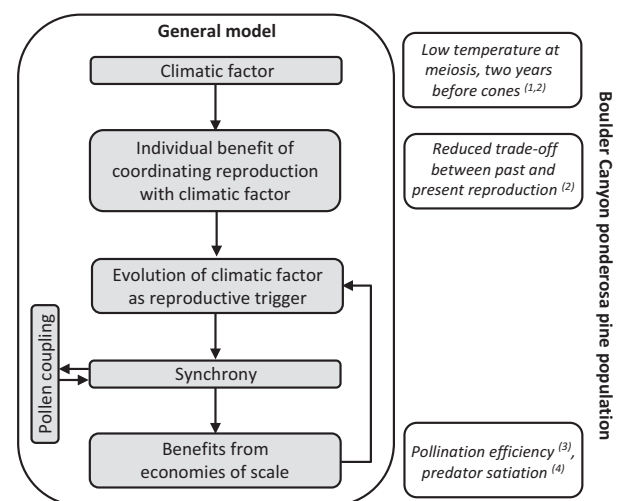


Fig. 3. Diagram representing proposed links between individual- and population-level responses to climatic factors for the studied ponderosa pine population. Pollen coupling was included as it has been proposed to underlie masting in the absence of climatic drivers, where interannual variation is driven by reproductive trade-offs among years, and synchrony occurs because outcross pollen limitation renders asynchronous reproduction unsuccessful. ⁽¹⁾ Mooney, Linhart & Snyder (2011); ⁽²⁾ this study; ⁽³⁾ Moreira *et al.* (2014); ⁽⁴⁾ Linhart *et al.* (2014).

We propose a model for the ecological and evolutionary origins of masting based upon our findings for ponderosa pine (Fig. 3). First, there is selection to time reproduction in response to a climatic factor providing a direct fitness benefit to the individual (i.e. selection for initiating reproduction during cool springs reduces reproductive trade-offs and thus minimizes the costs of reproduction). Such responses, when expressed across multiple individuals, result in synchrony. This synchrony may in turn be enhanced through two complementary mechanisms, one evolutionary and one ecological. First, selection for response to the climatic cue may be strengthened by the indirect fitness benefits associated with synchrony and economies of scale (e.g. pollination efficiency, predator satiation). Secondly, in the absence of any additional selection, synchrony may be strengthened through the ecological dynamics of pollen coupling. Finally, these mechanisms might complement each other through feedbacks, where pollen coupling leverages a small evolutionary response into population-level synchrony, which could in turn reinforce selection. It is important to note, however, that the interpretation of our results within an evolutionary context should be made with caution as we measured the reproductive response to a climate cue on annual scales and throughout a portion of this species lifetime. In this sense, it is difficult to demonstrate that a particular pattern of reproduction in a long-lived species leads to greater lifetime fitness (i.e. cumulative seed cone production over the lifetime of an individual).

FUTURE DIRECTIONS

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

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Data accessibility

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

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