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Later flowering is associated with a compressed flowering season and reduced reproductive output in an early season floral resource

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Climate change-induced shifts in flowering phenology can expose plants to novel biotic and abiotic environments, potentially leading to decreased temporal overlap with pollinators and exposure to conditions that negatively affect fruit and seed set. We explored the relationship between flowering phenology and reproductive output in the common shrub pointleaf manzanita *Arctostaphylos pungens* in a lower montane habitat in southeastern Arizona, USA. Contrary to the pattern of progressively earlier flowering observed in many species, long-term records show that *A. pungens* flowering onset is shifting later and the flowering season is being compressed. This species can thus provide unusual insight into the effects of altered phenology. To determine the consequences of among- and within-plant variation in flowering time, we documented individual flowering schedules and followed the fates of flowers on over 50 plants throughout two seasons (2012 and 2013). We also measured visitation rates by potential pollinators in 2012, as well as both fruit mass and seeds per fruit of flowers produced at different times. Fruit set was positively related to visitation rate but declined with later dates of flower production in both years. Total fruit production per plant was positively influenced by flowering duration, which declined with later flowering onset, as did fruit mass. Individual flowering schedules were consistent between years, suggesting that plants that begin flowering late have lower reproductive output each year. These patterns suggest that if pointleaf manzanita flowering continues to shift later, its flowering season may continue to become shorter, compressing floral resource availability for pollinators and leading to reduced reproductive output. These results reveal the negative effects of delayed phenology on reproductive output in a long-lived plant. They highlight the value of using natural variation in flowering time, in combination with long-term data, to anticipate the consequences of phenological shifts.

The flowering phenologies of many plant species are changing in association with changing climatic conditions (Bradley et al. 1999, Abu-Asab et al. 2001, Fitter and Fitter 2002, Miller-Rushing and Primack 2008). In temperate climates, a pattern reported worldwide is for flowering onset to shift earlier in concert with warmer springtime temperatures (Fitter and Fitter 2002, Miller-Rushing and Primack 2008, Chambers et al. 2013). The magnitude and even the direction of shifts in flowering time can, however, vary among species in the same community (Bradley et al. 1999, Miller-Rushing and Primack 2008, CaraDonna et al. 2014) and along elevational gradients (Crimmins et al. 2010). There is some evidence that the phenologies of pollinating insects are shifting with climate change, as well (Roy and Sparks 2000, Gordo and Sanz 2006, Doi et al. 2008, Burkle et al. 2013). Together, these observational data have generated concern that phenological shifts occurring at different rates could disrupt plant–pollinator interactions by causing mismatches in the timing of flowering and pollinator availability (Memmott et al. 2007, reviewed by Hegland et al. 2009).

Increasingly, research on climate change-driven phenological shifts in the context of pollination has focused on the consequences of such shifts for plant reproductive success (Kudo et al. 2004, Rafferty and Ives 2012, Kudo and Ida 2013). Shifts in the timing of life history events can expose species to novel abiotic and biotic environments, and these components can interact to determine reproductive output. The flowers of plants that bloom very early can, for example, be more vulnerable to damaging frosts (Inouye 2008), as well as reduced pollinator availability (Kudo and Ida 2013), whereas plants that bloom late can be vulnerable to desiccation (Giménez-Benavides et al. 2007). Measures of how reproductive output varies with flowering phenology yield useful information about potential temporal mismatches in the context of both the biotic and abiotic environment.

To develop a predictive understanding of the potential reproductive consequences of a long-term shift in flowering onset, we took advantage of existing variation in flowering phenology at the population level in one species. Relatively few studies have used natural variation in the timing

of flower production among and within individual plants to project the consequences of sustained, directional shifts in phenology associated with climate change (reviewed by Rafferty et al. 2013). Yet this approach can yield insight into how individuals with different phenologies will be affected by climate change-induced shifts (Forrest and Thomson 2010). It is particularly valuable for studying long-lived species, whose phenologies can be difficult or impossible to manipulate experimentally.

We explored how current, within-population variation in phenology affects reproductive output in pointleaf manzanita *Arctostaphylos pungens*, a long-lived evergreen shrub that grows in isolated mountain ranges termed 'sky islands' in the Sonoran Desert, USA. Pointleaf manzanita is of particular interest because it is the first and, for several weeks, the only resource available to floral visitors in the study area (Richardson and Bronstein 2012). Thus, both the timing of flowering onset and the length of the flowering season should be important determinants of food availability for floral visitors, particularly for known pollinators such as *Osmia ribifloris*, a solitary bee that emerges early in the season, and occasional visitors such as broad-tailed hummingbirds *Selasphorus platycercus* that migrate to the area in the spring (McKinney et al. 2012). Moreover, like a number of plant species in the sky islands (Crimmins et al. 2010), the flowering phenology of pointleaf manzanita has changed significantly in the last three decades, as we document herein. Contrary to the expected pattern, its flowering onset is shifting later, likely in response to later winter rains (Crimmins et al. 2010). Pointleaf manzanita is largely self-incompatible (Richardson and Bronstein 2012) and therefore may be particularly vulnerable to climate change effects that reduce phenological overlap with pollinators. Thus, studying the consequences of delayed flowering in this species allows us to gain new insight into the effects of changed phenology, which is nearly always studied in the context of shifts in one direction, toward earliness. Specifically, we asked 1) what has been the phenological pattern of pointleaf manzanita flowering at the population level over the past three decades? 2) What are the fine-scale temporal patterns of flowering among and within plants over two years? 3) How do those patterns scale up to season length and flowering duration? 4) What are the consequences for rates of flower visitation, and for fruit set, seeds per fruit, and fruit mass? These measures of reproductive output should reflect both pollination success and abiotic conditions. From these patterns, we generated predictions about the consequences of future shifts in flowering phenology in this species.

Material and methods

Study species

Pointleaf manzanita *Arctostaphylos pungens* (Ericaceae) is a long-lived perennial shrub that grows at elevations of about 1200–2500 m in chaparral habitats, including in the sky island mountain ranges of Arizona, USA. Plants can live up to 130–150 years (Harlan 1977), can reach a height of 3 m and produce small pink urn-shaped flowers in racemes, which have on average four concurrently open flowers. Floral bud primordia are formed in the previous year (Harlan 1977). Flowers are open for about three days. They contain 5–10 ovules and 10 stamens, which dehisce pollen via pores in the anthers. The fruits are berries. Flowers are visited by a wide variety of generalist insect species; common floral visitors include 10 species of bees and two species of flies (Richardson and Bronstein 2012).

Long-term data

We used long-term data to determine whether the onset of pointleaf manzanita flowering has progressively changed in the region near our focal population in the Santa Catalina Mountains (part of the Coronado National Forest) in southeastern Arizona. From 1984–2013, the onset and end of flowering of pointleaf manzanita populations from 1935–2211 m on Mt Kimball were documented in a series of regular observations by one of us (CDB). Onset and end of flowering were defined as the date the first individual, fully open flower was seen and the date the last bud or open flower was seen, respectively. On average, observations were made every seven days, with more than 1400 sampling dates in total. The methodology and frequency of observations are described in detail by Crimmins et al. (2013).

Study site

The focal population (32°20′N, 110°43′W), located at about 1500 m elevation on Mt Lemmon, is about 16 km from the long-term study populations on Mt Kimball in the same mountain range. It is situated on all aspects and the apex of a hill and comprises about 200 individual plants in a 4200 m^2 area of scrub grassland and oak woodland. Although the Mt Lemmon and Mt Kimball populations differ in elevation, both sites are found well within the typical elevational range of the species, and we have no reason to expect divergent phenological responses. First, the (higher) population on Mt Kimball has a predominantly southern exposure and is found in shallow soils on a substrate of gneiss and mica schist. Temperatures are likely colder in winter than at the (lower) Mt Lemmon site, but the exposure and slope help to mitigate against sustained cold temperatures. Second, although precipitation is likely greater at the higher elevation site, the shallow soil depth and substrate prevent water storage. Thus, plants at both sites probably experience a similar range of climate conditions that are known to influence flowering phenology (Crimmins et al. 2010).

Flowering phenology

Within the study population, we surveyed all pointleaf manzanita plants ($n \approx 200$) weekly, recording when each plant first came into bloom and marking it. From the set of plants newly in bloom each week, we randomly selected plants to include in our focal sample, adding up to 10 plants each week (in some weeks, particularly at the beginning and end of the season, fewer than 10 newly flowering plants were available). We documented the onset and end of flowering (defined in the same ways as for the Mt Kimball site) for each focal plant weekly from January–April of 2012 and 2013. In June we measured the maximum height and width

of all focal plants (n = 52 in 2012 and n = 58 in 2013, with n = 18 common to both years).

Fruit set, fruit mass and seeds per fruit

To track fruit development, we followed the fates of individual flowers on each focal plant by marking the pedicels of all open flowers on up to five tagged racemes per plant with permanent marker. In this manner, all of the open flowers on as many as five new, randomly chosen racemes were added per focal plant per week. The total number of flowers marked per raceme was recorded (and ranged from 1–14). Thus, on average, several new racemes and tens of flowers per plant were added to the sample each week. This method enabled us to determine the number of fruits produced from a standardized sample of inflorescences for each focal plant each week, regardless of the total number of flowers per plant. This method does not necessarily scale with floral display size; however, there were no apparent differences in flowering intensity for plants that started flowering earlier versus later in the season. Because floral bud primordia are formed more than six months in advance of flowering (Harlan 1977), it is unlikely that plants could adjust flowering on shorter time scales.

After all floral buds matured and all of the flowers (both marked and unmarked) on each tagged raceme senesced, we placed small mesh drawstring bags over each marked raceme to protect developing fruits from loss or damage. Once fruits had fully ripened, they were brought to the laboratory where they were dried in an oven at 45°C for one week and then weighed. The seeds within a random subset of fruits from each year were also counted (n = 788 fruits (47%) for 2012 and n = 519 fruits (41%) for 2013).

Flower visitor observation

In 2012, we measured floral visitation rates by insects by conducting 10-min focal observations of plants each week, rotating among unique focal plants in bloom. We observed entire plants (thus, visitation rates are summed over all flowers). On average eleven 10-min observation periods were conducted per week (n = 105 focal observation periods total for 45 plants). We did not distinguish between legitimate and nectar-robbing visits (Richardson and Bronstein 2012); as long as a visitor contacted the corolla, a visit was recorded.

Statistical analyses

To determine if there has been a significant long-term change in the date of flowering onset, end, or season length, we regressed the date of first flowering, date of last flowering, or population-level flowering duration, respectively, against year (1984–2013). No *A. pungens* plants were observed to flower in 2003, likely to due to very dry conditions the previous year, complete data were not available for 2004–2005 because the observer was incapacitated, and *A. pungens* was observed flowering on only one date in 2006 even though observations were made at least twice monthly, again likely due to very limited winter and spring precipitation. Thus, these years were omitted from analyses that required data on the full flowering season. We also used these long-term data to determine the correlation between date of flowering onset at the population level and length of the flowering season. To account for the fact that *A. pungens* began flowering on 1 December in 1986, we used a day of year value of −31.

Using data from our focal population on Mt Lemmon, we correlated the dates of first bloom of individual plants in 2012 versus 2013 to determine if the order of flowering was consistent between years. Otherwise, we performed all analyses of data from 2012 and 2013 separately. We regressed dates of first bloom against plant size (estimated as width × height) and against the flowering duration of individual plants. As described below, we investigated four response variables: fruit set (the proportion of flowers that set fruit), the total number of fruits (from tagged racemes and marked flowers) per plant, individual fruit mass, and the number of seeds per fruit. For each response, we constructed either generalized linear models (GLM), generalized linear mixed models (GLMM), or linear mixed models (LMM). To assess multiple coefficients in the models at the same time, we used likelihood ratio (LR) tests. The models we report are those that LR tests showed fit the data significantly better than did models without the reported combination of predictor variables. All statistical analyses were conducted in R ver. 3.1.1 (< www.r-project.org >).

To investigate variation in fruit set we used GLMMs. Because the number of flowers marked per raceme varied, the response variable, fruit set, was treated as a binomial process with n = the number of flowers and p = the probability of a flower producing fruit. To baseline models with individual plant (factor with 52 and 58 levels for 2012 and 2013, respectively) as a random effect, we introduced the following predictor variables: week (when an individual flower was open), date of first bloom (at the whole plant level), number of co-flowering conspecifics, total plant size (width × height), and visitation rate (2012 only).

We investigated variation in the total number of fruits from marked flowers per plant using GLMs with a negative binomial distribution. We used a goodness-of-fit χ^2-test on the residual deviance to verify that models with this distribution fit the data. To these models, we introduced date of first bloom, flowering duration, and plant size as predictor variables. To further explore the relationship between fruit production and flowering duration, we regressed the total number of fruits per plant against flowering duration of individual plants.

Variation in fruit mass was explored with LMMs with individual plant (factor with 52 and 54 levels for 2012 and 2013, respectively), individual raceme (factor with 43 and 33 levels for 2012 and 2013, respectively), and individual fruit (factor with 12 levels for both 2012 and 2013) as nested random effects. We introduced week and date of first bloom as predictor variables.

Finally, we investigated variation in seeds per fruit with GLMMs with individual plant (factor with 50 and 54 levels for 2012 and 2013, respectively), individual raceme (factor with 41 and 33 levels for 2012 and 2013, respectively), and individual fruit (factor with 12 levels for both 2012 and 2013) as nested random effects. Seeds per fruit was assumed to be Poisson distributed due to the low numbers of seeds

per fruit (1–9). To these models, we introduced fruit mass, week, and date of first bloom.

Results

Flowering phenology

In the last 30 years, the flowering onset of a population of *Arctostaphylos pungens* within 20 km of our study site has shifted progressively later ($R^2 = 0.22$, $F_{1,25} = 6.88$, $p < 0.015$; Fig. 1a). On average, flowering has started 1.6 days later each year since 1984. With later dates of first flowering but no change in the end of flowering ($R^2 = 0.0013$, $F_{1,24} = 0.030$, $p < 0.86$), the length of the flowering season has shortened by an average of 1.3 days per year ($R^2 = 0.15$, $F_{1,24} = 4.30$, $p < 0.049$; Fig. 1b). Correspondingly, there is a significant negative relationship between date of flowering onset and duration of flowering season at the population level ($R^2 = 0.81$, $F_{1,24} = 104.26$, $p < 0.00001$; Fig. 1c).

At our study site, flowering began in mid-January in 2012 and mid-February in 2013; yet, in both years, flowering ceased in early April (Fig. 2). Thus, the flowering season was about 20% shorter in 2013 (55 versus 69 days). Although almost every plant that flowered in 2012 also flowered in 2013, some plants flowered only in 2013. Among plants, the order of flowering onset was consistent between years: the date of flowering for a given plant in 2012 was significantly positively correlated with that in 2013 ($r = 0.45$, $t_{50} = 3.57$,

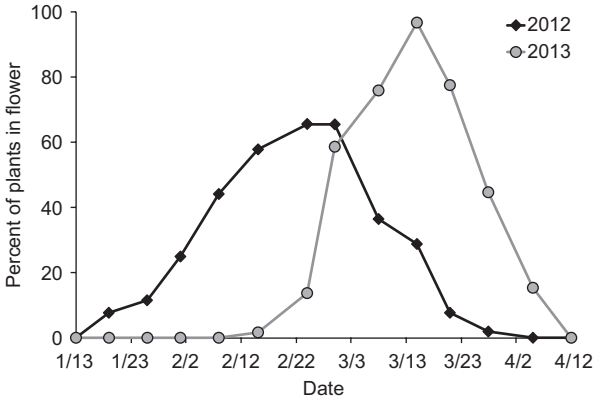

Figure 2. Flowering curves for *Arctostaphylos pungens* study population on Mt Lemmon in 2012 and 2013.

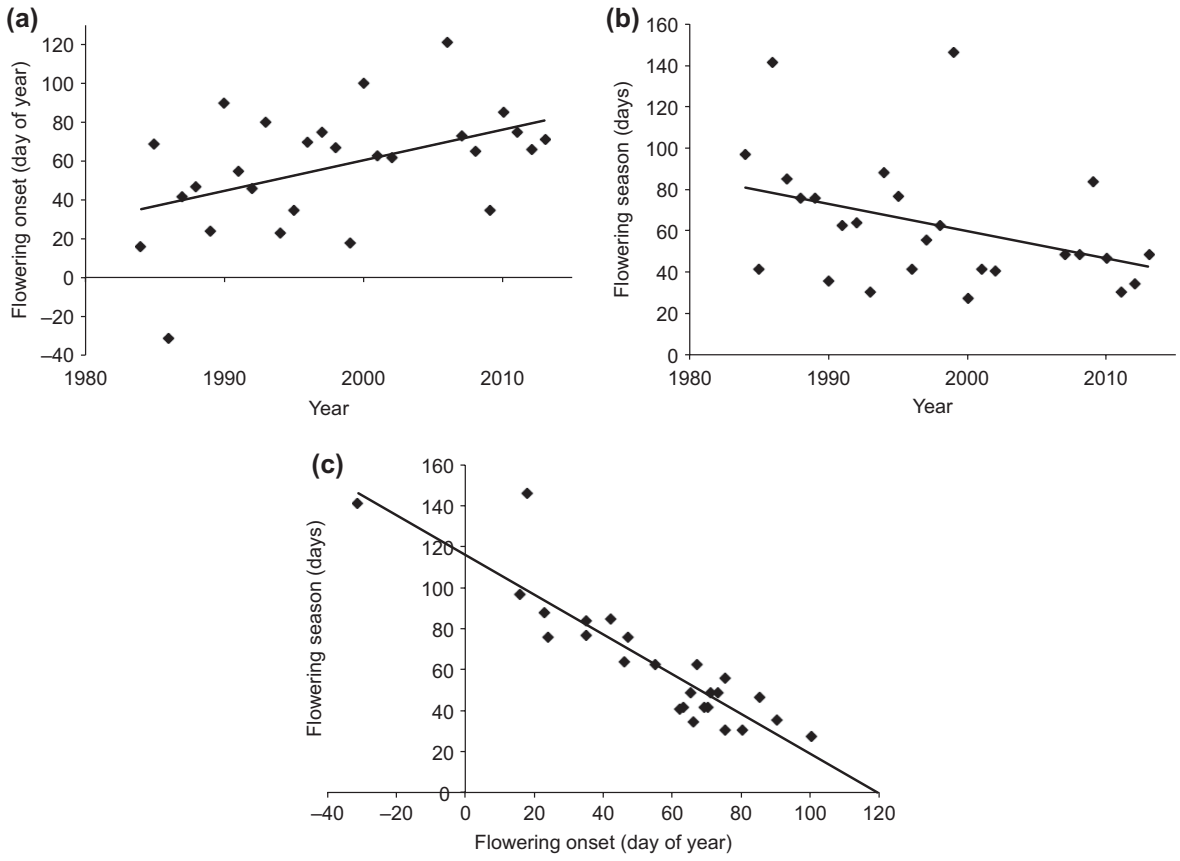

Figure 1. For the *Arctostaphylos pungens* population on Mt Kimball in the Santa Catalina Mountains in Arizona: (a) date of flowering onset regressed against the years 1984–2013 ($R^2 = 0.22$, $n = 27$), (b) length of flowering season regressed against the years 1984–2013 ($R^2 = 0.15$, $n = 26$), and (c) date of flowering onset regressed against the length of the flowering season ($R^2 = 0.81$, $n = 26$). No plants were observed to flower in 2003, complete data were not available for 2004–2005, and *A. pungens* was observed flowering on only one date in 2006 (these years were omitted from analysis, with the exception that 2006 was included in the analysis of flowering onset). A negative day of year was used to represent the year in which *A. pungens* began flowering on 1 December of the previous calendar year.

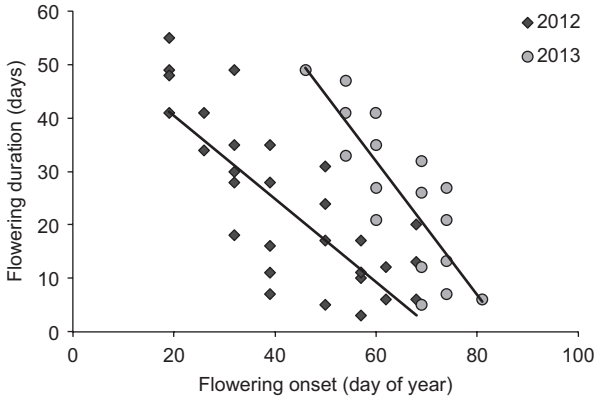

Figure 3. Relationship between flowering onset and flowering duration for focal *Arctostaphylos pungens* plants on Mt Lemmon in 2012 ($r = 0.78$, $n = 52$) and 2013 ($r = 0.83$, $n = 58$).

$p < 0.0008$). Larger plants flowered earlier in both 2012 ($R^2 = 0.15$, $F_{1,50} = 8.50$, $p < 0.005$) and 2013 ($R^2 = 0.32$, $F_{1,56} = 25.99$, $p < 0.00001$).

At the individual plant level, the correlation between flowering onset and duration of flowering mirrored the long-term pattern at the population level: plants that began flowering later had shorter flowering periods in both 2012 ($r = 0.78$, $t_{50} = 8.75$, $p < 0.00001$) and 2013 ($r = 0.83$, $t_{56} = 11.26$, $p < 0.00001$; Fig. 3).

Fruit set, fruit mass and seeds per fruit

Fruit set varied significantly with date of flower anthesis, with fruit set declining as the season progressed in 2012 and 2013 (Table 1, Fig. 4a–b). Thus, plants that flowered later in the season had lower fruit set than did those that flowered earlier. For 2012, the best model for fruit set also included

Table 1. Best-fitting models for fruit set, total fruits per plant, fruit mass, and seeds per fruit of *Arctostaphylos pungens* plants in 2012 and 2013.

Response	Model	Distribution	Year	Effects	Estimate	SE/SD*	*z*/*t***	p	n
Fruit set	GLMM	Binomial	2012	Fixed					
				week	−0.13	0.025	−5.35	<0.00001	852
				no. co-flowering	0.021	0.0047	4.43	<0.00001	852
				visitation rate	0.069	0.019	3.57	0.0004	852
				Random					
				individual plant		0.61			52
			2013	Fixed					
				week	−0.25	0.036	−7.03	<0.00001	875
				no. co-flowering	0.034	0.0039	8.63	<0.00001	875
				Random					
				individual plant		0.63			58
Fruits per plant	GLM	Negative binomial	2012	Fixed					
				flowering duration	0.054	0.0062	8.65	<0.00001	52
			2013	Fixed					
				flowering duration	0.026	0.011	2.28	0.02	58
				date of first bloom	−0.40	0.12	−3.31	0.0009	58
Fruit mass	LMM	Gaussian	2012	Fixed					
				date of first bloom	−0.0081	0.0032	−2.52	0.01	1694
				Random					
				individual plant		0.038			52
				individual raceme		0.012			43
				individual fruit		0.055			12
			2013	Fixed					
				date of first bloom	−0.031	0.0073	−4.24	0.00002	1271
				Random					
				individual plant		0.047			54
				individual raceme		0.051			33
				individual fruit		0.065			12
Seeds per fruit	GLMM	Poisson	2012	Fixed					
				fruit mass	2.61	0.24	11.02	<0.00001	788
				Random					
				individual plant		0.090			50
				individual raceme		0			41
				individual fruit		<0.0001			12
			2013	Fixed					
				fruit mass	1.91	0.19	9.88	<0.00001	519
				Random					
				individual plant		<0.0001			53
				individual raceme		0			33
				individual fruit		0			6

*SE for fixed effects, SD for random effects. **z for GLMM and GLM, t for LMM

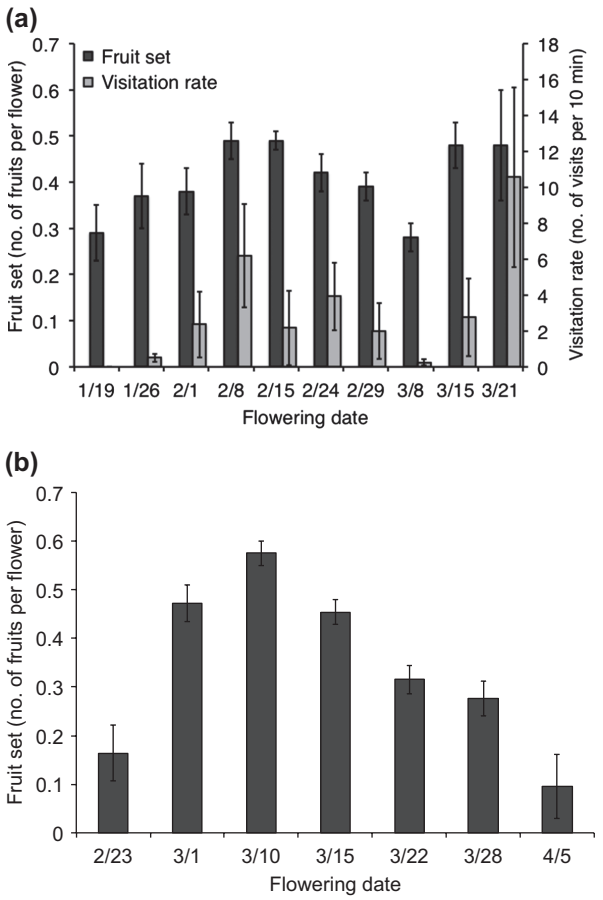

Figure 4. Mean (± SE) fruit set of *Arctostaphylos pungens* flowers according to the date of flower production in (a) 2012, along with mean (± SE) visitation rates (number of visits per 10 min at whole plant level, n = 4–15 observation periods per date), and (b) 2013. In 2012, no visits were observed on 19 January, only three and one focal plants were still flowering on 21 and 28 March, respectively, and none of the marked flowers set fruit on 28 March (visitation data were not collected on that date).

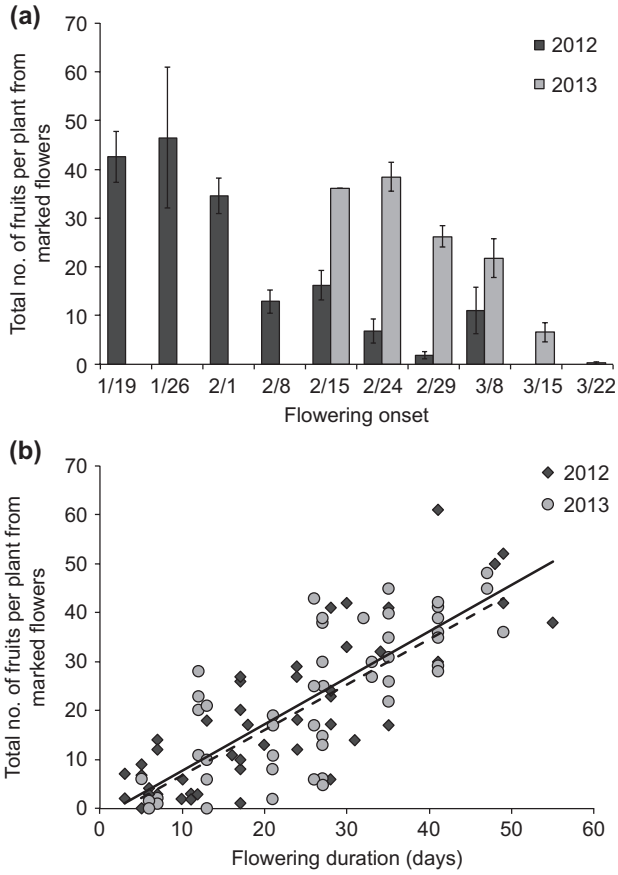

Figure 5. (a) Mean (± SE) total number of fruits produced from marked flowers per *Arctostaphylos pungens* plant that began flowering at different times in 2012 and 2013 (only one plant began flowering on 15 February 2013), and (b) total number of fruits produced from marked flowers according to the flowering duration for each plant in 2012 (solid line: $R^2 = 0.71$, n = 52) and 2013 (dashed line: $R^2 = 0.61$, n = 58).

rate of floral visitation and the number of co-flowering manzanita plants, both of which positively affected fruit set. For 2013, the best model included week and the number of co-flowering conspecifics.

The total number of fruits from marked flowers per plant in 2012 was significantly influenced only by flowering duration, whereas in 2013, both flowering duration and date of first bloom were significant predictors (Table 1, Fig. 5a). That is, the longer the flowering period, the greater the number of fruits plants produced (2012: $R^2 = 0.71$, $F_{1,50} = 123.37$, $p < 0.00001$; 2013: $R^2 = 0.61$, $F_{1,56} = 89.29$, $p < 0.00001$; Fig. 5b), and plants that began flowering later in 2013 produced fewer total fruits. At the population level, fewer fruits were produced (from tagged racemes and marked flowers) in 2013 (n = 1269) than in 2012 (n = 1688).

Among plants, fruit mass declined significantly with later dates of first bloom in both years (Table 1). In addition, seeds per fruit in both years was significantly positively related to fruit mass (Table 1).

Flower visitor observation

As noted above, visitation rate was found to positively influence fruit set in 2012 (Table 1). Visitation rates were quite variable within weeks, however, and were low at the start of manzanita flowering, with no visits observed during the first week. Visitation rates increased near the end of flowering when only a few plants were still in bloom (Fig. 4a).

Discussion

Few studies have investigated the plant reproductive consequences of delayed flowering in the context of climate change, even though delays are a commonly observed phenological pattern among plant species (Abu-Asab et al. 2001, Fitter and Fitter 2002), particularly at middle elevations in the sky island habitats of the American southwest (Crimmins et al. 2010, 2011). Like advanced phenology, delayed phenology is associated with changing climatic cues, especially altered precipitation patterns (Crimmins et al. 2010), which can be a critical trigger of flowering for shrubs in the Sonoran Desert (Bowers and Dimmitt 1994, Bowers 2007). That the reproductive consequences of delayed manzanita flowering

were negative in 2012 and 2013 suggests that phenological shifts can be detrimental regardless of their direction. Indeed, there is evidence that plant species that show advanced phenology and have responded more strongly to changing climate cues are performing better in terms of reproductive and vegetative traits than are plants with delayed phenology (Cleland et al. 2012).

Not only has the onset of flowering in pointleaf manzanita shifted later over the last three decades, but the length of the flowering season has become compressed at the population level. By taking advantage of existing among- and within-plant variation in dates of first bloom and flower production over two seasons, we were able to corroborate the larger-scale pattern of compression, and determine the reproductive consequences of delayed phenology at the individual plant level. Together, these data suggest that a continued trend toward later flowering in pointleaf manzanita will result in shorter flowering periods, fewer fruits produced per plant, and the production of fruits that weigh less and contain fewer seeds. Thus, delayed phenology in pointleaf manzanita appears to negatively affect reproductive output and could result in an absence of floral resources for pollinators.

Evidence for compression of flowering comes from both among- and within-year comparisons. Across years, the later the population as a whole started flowering, the shorter the flowering season (Fig. 1c); furthermore, in any given year, the later individual plants start flowering, the shorter their flowering periods (Fig. 3). At the community level, too, later flowering onset is associated with shorter duration, with sky island species that begin flowering later flowering for less time (Crimmins et al. 2013).

Because total fruit production is positively related to flowering duration in manzanita (Fig. 5b), with delayed flowering onset at the population level across years, we expect shorter flowering seasons and therefore fewer total fruits to be produced. For any given plant, however, the relative date of onset likely matters more than absolute date: relatively early flowering plants in 2013 produced almost as many fruits as the earliest flowering plants in 2012, even though flowering at the population level was delayed in 2013 relative to 2012 (Fig. 5a). This finding suggests that biotic variables, such as synchrony with conspecifics, dictate fruit production more than do abiotic conditions. The trend of increased fruit set with greater numbers of co-flowering conspecifics further supports the importance of outcross pollination in this largely self-incompatible species (Richardson and Bronstein 2012), as does the positive effect of visitation rate on fruit set. Again, among plants within a year, individuals that begin flowering relatively late are likely not only to flower for less time and produce fewer fruits but also to produce lighter fruits with fewer seeds. If populations are seed-limited, depressed seed output could interrupt manzanita recruitment.

Much attention has been focused on the potential for shifts in flowering time to lead to temporal mismatches with pollinators (reviewed by Hegland et al. 2009, Bartomeus et al. 2011, 2013). We did not find strong evidence of a mismatch between flowering onset and floral visits by insects, which might have been expected on the pollinator side if early season visitors are now emerging or arriving before manzanita begins to flower. If this were case, however, we might expect high visitation at the start of flowering, rather than the relatively low rates we documented (Fig. 4a). In fact, peak visitation rates seemed to match 2012 peak flowering fairly closely, with the increased rates near the end of flowering (21 March) reflecting the fact that visitors were concentrated on the only three plants still in bloom.

Less consideration in the literature has been given to the possible consequences of compressed flowering seasons for plant–pollinator interactions. The delay in and compression of flowering in 2013 relative to 2012 might be due to the fact that little precipitation fell in November 2012, and temperatures in early January and most of February were below normal in 2013. Below average temperatures in February and well below freezing temperatures in early March might also partly explain why fewer fruits were produced at the population level in 2013, as emergence of pollinators might have been delayed. The greater number of plants initiating flowering in 2013 might have been due to significant precipitation in December 2012 and February 2013. At the extreme, plants may fail to flower under future climate change, which is expected to bring drier conditions to southwestern North America (Seager et al. 2007). The two years in which manzanita was observed to flower not at all or on only one date, 2003 and 2006, were characterized by below-normal winter precipitation and were preceded by below-normal monsoon precipitation. A reduced time span of flower availability, particularly in an important early season floral resource such as pointleaf manzanita, could reduce food availability for, and negatively affect, pollinators. In turn, reduced fruit and seed production associated with later flowering could negatively affect both manzanita recruitment and animals dependent on these resources.

Further study of the implications of delayed phenology is needed, particularly for flowering plants and pollinators and particularly in the southwestern United States and other regions where this pattern is common. The results presented here indicate that such shifts could have large consequences for the annual reproductive output of a winter-flowering shrub. Studying existing phenological variation within populations in this way is a valuable method to reveal the potential consequences of climate change-induced shifts, particularly in long-lived species that are less tractable for experimental manipulations of phenology.

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