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Authors

Gilman, R Tucker
Fabina, Nicholas S
Abbott, Karen C
et al.

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Evolution of plant–pollinator mutualisms in response to climate change

R. Tucker Gilman, Nicholas S. Fabina, Karen C. Abbott and Nicole E. Rafferty

Department of Zoology, University of Wisconsin, Madison, Wisconsin

Abstract

Climate change has the potential to desynchronize the phenologies of interdependent species, with potentially catastrophic effects on mutualist populations. Phenologies can evolve, but the role of evolution in the response of mutualisms to climate change is poorly understood. We developed a model that explicitly considers both the evolution and the population dynamics of a plant–pollinator mutualism under climate change. How the populations evolve, and thus whether the populations and the mutualism persist, depends not only on the rate of climate change but also on the densities and phenologies of other species in the community. Abundant alternative mutualist partners with broad temporal distributions can make a mutualism more robust to climate change, while abundant alternative partners with narrow temporal distributions can make a mutualism less robust. How community composition and the rate of climate change affect the persistence of mutualisms is mediated by two-species Allee thresholds. Understanding these thresholds will help researchers to identify those mutualisms at highest risk owing to climate change.

Introduction

Climate change is altering the phenologies of species worldwide (Parmesan and Yohe 2003; Root et al. 2003; Bertin 2008). For example, the onset of flowering in many Northern Hemisphere temperate plants (Sparks et al. 2000; Abu-Asab et al. 2001; Post et al. 2001; Fitter and Fitter 2002; Primack et al. 2004; Miller-Rushing and Primack 2008) and the first emergence dates of some insects (Roy and Sparks 2000; Gordo and Sanz 2006; Parmesan 2007) have advanced with earlier warming. Because the responses of species to climate change may differ in magnitude and even direction (Fitter and Fitter 2002; Sherry et al. 2007), phenological mismatches between interdependent species are expected (Harrington et al. 1999; Stenseth and Mysterud 2002; Durant et al. 2007; Memmott et al. 2007; Hegland et al. 2009). Asynchrony between host plants and their associated insects has already been observed in some systems (Visser and Holleman 2001; Doi et al. 2008), to the apparent detriment of food-limited herbivores (Visser and Holleman 2001) and pollen-limited plants (Schemske et al. 1978; Kudo et al.

2004). Memmott et al. (2007) argued that such asynchrony may become sufficiently severe to cause local extinctions of some mutualist populations.

In many species, phenological events are triggered by environmental cues that have historically predicted optimal conditions for ensuing life-history stages (Brewer and Platt 1994; Schauber et al. 2002; Harper and Peckarsky 2006). For example, many plants use photoperiod as a flowering cue because it has historically predicted optimal conditions for reproduction (del Pozo et al. 2000; Keller and Korner 2003; Venn and Morgan 2007). Climate change can decouple cues from the conditions that they have historically predicted (Visser et al. 1998; Buse et al. 1999; Both and Visser 2001; Visser and Holleman 2001; Lawrence and Soame 2004), creating strong selection on populations to use different cues or to use the same cues differently (Franke et al. 2006; Moller et al. 2008; Munguia-Rosas et al. 2011). In many species, there is substantial genetic variability in the use of phenological cues (Blanckenhorn and Fairbairn 1995; Vaughton and Ramsey 2001; Kelly et al. 2008; Samis et al. 2008), and such species may have the potential to evolve rapidly in response

to changes in the predictive value of their environments (Burgess et al. 2007; Van Dijk and Hautekeete 2007; Jensen et al. 2008). There is mixed empirical evidence that plant phenology can indeed evolve in response to climate change (Kochmer and Handel 1986; Etterson and Shaw 2001; Burgess et al. 2007; Franks et al. 2007), and there is some evidence that insects can evolve in response to changes in host–plant phenology (van Asch et al. 2007).

Whether a plant–pollinator mutualism can survive climate change will likely depend on how the species' phenologies evolve (Bronstein et al. 2004; Elzinga et al. 2007), but the conditions that promote or oppose the coevolution of phenologies in complex communities with changing environments have received little study (Lavergne et al. 2010). Forrest and Thomson (2009) argued that pollen limitation may prevent the evolution of flowering plant phenology when pollinator foraging is frequency dependent and pollinator phenology is constant, and suggested that this might lead to the extirpation of flowering plant populations under strong selection. If both plant and pollinator phenologies evolve, the set of potential outcomes may be more complicated. Empirical studies of coevolution in plant–pollinator mutualisms require intensive long-term sampling and may be slow, costly, and logistically difficult to conduct. Mathematical models can offer testable predictions to guide empirical research and may help to identify systems of management concern before empirical data become available.

We developed a model that simulates a plant–pollinator mutualism. The phenology of each individual in each population is genetically determined, and the optimal phenologies depend on climate and on species–species interactions. The environment includes alternative hosts available to the focal pollinator and alternative pollinators available to the focal plant. We modeled a climate change event that moves the climatically determined optimal flowering date of the focal plant earlier, and we tracked the evolution of phenology in both the plant and pollinator populations. We asked whether the mutualism persists through climate change and how the phenologies of the mutualist species after climate change depend on the rate of climate change and on the density and temporal distribution of nonfocal species in the community.

Methods

Overview of the focal populations

We modeled a single population of flowering plants and a single population of pollinating insects. The focal plant is pollinated by and provides food resources to the focal pollinator. The focal plant can also be pollinated by background (i.e., nonfocal) pollinators or autogamy, and the focal pollinator can also collect food from alternative resources. The rates of background pollination and autogamy and the density of alternative resources are set by model parameters (Table 1). Depending on the values assigned to these parameters, each focal population can be an obligate mutualist (i.e., unable to persist without its focal partner) or a facultative mutualist (i.e., able to persist without its focal partner) of the other.

Focal populations undergo discrete generations that correspond to years. Empirical evidence suggests that the

Table 1. Parameter values used in simulations.

Parameter	Symbol	Default value
Days modeled per year (i.e., length of the focal plant growing season)	d	60
Date of maximum of flowering rate function before climate change	θ_i	40
Date of maximum of flowering rate function after climate change	θ_f	15
Standard deviation of flowering rate function (days)	σ_θ	15
Maximum flowering rate of focal plant (flowers/plant)	r^*	4
Date of peak alternative resource density	μ_a	40
Standard deviation of alternative resource density function (days)	σ_a	$\sim$
Peak alternative resource density (portion of carrying capacity of focal plant)	A^*	$\sim$
Standard deviation in flowering probability function (days)	σ_{pf}	2
Standard deviation in pollinator foraging function (days)	σ_{pp}	4
Pollinator search rate (maximum portion of patch searched/unit pollinator/day)	s	5.82
Handling time per unit of resource visited (days/unit resource/unit pollinator)	h	0.15
Reward of alternative resource (pollinator offspring/unit resource visited)	ω_a	0.5
Rate of autogamy in unpollinated flowers (days^{-1})	c_s	0 or 0.5
Rate of pollination by nonfocal pollinators (days^{-1})	c_b	0.05
Mortality rate of unpollinated focal flowers (days^{-1})	m_f	1
Maximum duration of any single flower (days)	s_f	1
Segregation variance of focal plant (units genetic value^2)	σ_{gf}^2.	4
Segregation variance of pollinator (units genetic value^2)	σ_{gp}^2.	4

Values of A^* and σ_a are assigned separately to each simulation.

phenologies of wild annual plants may be more strongly affected by climate change than those of their longer-lived congeners (Fitter and Fitter 2002). Univoltine pollinators include some dipterans, lepidopterans, and solitary bees (Pellmyr and Thompson 1992; Peat et al. 2005; Biesmeijer et al. 2006), and there is evidence that univoltine pollinators may be more vulnerable to environmental change than multivoltine species (Biesmeijer et al. 2006). Thus, our use of discrete generations captures cases in which the effect of climate change on focal species is expected to be severe.

The potential flowering season in each year comprises d nonoverlapping time steps that we call 'days.' Each individual focal plant or pollinator is characterized by a single genetic value that governs the days on which it flowers or forages in each year (i.e., its phenology). We ignored demographic stochasticity and tracked the density rather than the number of individuals with each genetic value.

Model environment

The environment experienced by the focal species is described by two functions: a *flowering rate function* and an *alternative resource density function* (Fig. 1). In nature, the day-to-day quality of an environment for plant growth and reproduction depends on climatically determined factors such as temperature, water availability, photoperiod, interspecific competition or facilitation, parasitism, and herbivory rate (Rathcke and Lacey 1985; Jones and Sharitz 1989). The flowering rate function describes the quality of the environment experienced by a focal plant with a particular flowering phenology. Specifically, the flowering rate function governs the expected number of flowers that will be produced by a focal plant seedling with a phenology that flowers on day τ of year t:

$$f(t, \tau) = \begin{bmatrix} r^* e^{-\frac{(\theta_t - \tau)^2}{2\sigma_\theta^2}} & \text{for } 1 \leq \tau \leq d \\ 0 & \text{for } \tau < 1, \tau > d \end{bmatrix} . \quad (1)$$

Here, r^* is the maximum flowering rate of the focal plant and σ_θ determines how strongly the flowering rate depends on the flowering date. Plants that flower before or after the climatically determined optimal flowering date θ_t achieve lower flowering rates (Moss 1971; Chaikiattiyos et al. 1994; Morrison and Stewart 2002). The flowering rate function captures both the effect of climate at the time of flowering and the cumulative effect of climate on focal plant fitness prior to flowering, including any effect of climate on seedling survival. Thus, our model is appropriate if the effect of climate on focal plant fitness is mediated by survival (e.g., Espigares and Peco
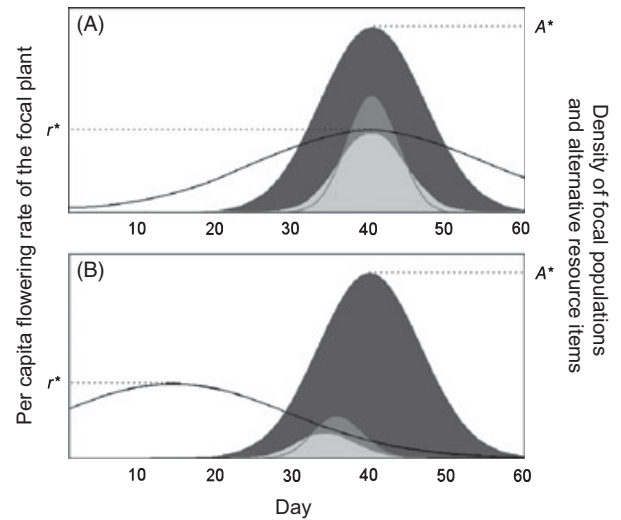

Figure 1 Functions that define the within-year model environment before (A) and after (B) climate change. The flowering rate function (black line) describes the expected number of flowers produced by a focal plant flowering on any given day. The peak annual per capita flowering rate of the focal plant, r^*, occurs on day θ_t (A: $\theta_t = 40$, B: $\theta_t = 15$). The alternative resource density function (dark gray) represents the density of alternative resource items available to the focal pollinator on each day. The peak annual density of the alternative resource, A^*, occurs on day μ_a (A, B: $\mu_a = 40$). The distributions of focal plants (light gray) and focal pollinators (middle gray) are determined by the genetic values of focal plants and pollinators in the system. Parameters are as shown in Table 1, with $c_s = 0$, $A^* = 0.095$, and $\sigma_a = 6.1$. The population state shown in B is from year 76 of the process shown in Fig. 2 I and J and is not evolutionarily stable.

1993; Quintana et al. 2004; Young et al. 2004) or by flowering rate (Morrison and Stewart 2002).

The alternative resource density function describes the density of alternative resources available to the focal pollinator on day τ of each year:

$$A(\tau) = A^* e^{-\frac{(\mu_a - \tau)^2}{2\sigma_a^2}}. \quad (2)$$

A^* represents the maximum density of the alternative resource, achieved on day μ_a, and σ_a describes how strongly alternative resource density depends on date. The dynamics of the alternative resource are not affected by the dynamics of the focal pollinator population. In nature, this might be true if flowering plants in the alternative resource pool are not pollen limited (e.g., some autogamous species (Larson and Barrett 2000) or species with common alternative pollinators (Rymer et al. 2005)), if the focal pollinator does not efficiently pollinate alternative resource flowers (e.g., Lazri and Barrows 1984; Adrienne et al. 1985; Marten-Rodriguez and Fenster 2008), or if the alternative resource is a nonflower item (e.g., dung or carrion (Meeuse and Hatch 1960)).

Population dynamics

We let $P_i(t)$ and $S_i(t)$ represent the density of pollinators and of viable focal plant seeds, respectively, having genetic value i at the beginning of year t. In each year, focal plant seeds germinate and seedlings experience density dependence as a result of competition for resources or space (Mazer and Schick 1991; Webb and Peart 1999; Lambers et al. 2002). The number of focal plant seedlings with genetic value i that survive intraspecific competition in year t follows a Beverton–Holt function:

$$S'_i(t) = \frac{S_i(t)}{1 + (r^* - 1)\sum_j S_j(t)}. \tag{3}$$

Density dependence in the focal pollinator population is due to competition for focal plant flowers and alternative resources as described below.

On each day of each year, a series of biological events occurs in the following order: (i) focal plants flower, (ii) pollinators become active, (iii) pollinators visit flowers, (iv) pollinated flowers seed, (v) pollinators lay eggs, and (vi) flowers die or senesce. We discuss these steps in the order in which they occur.

Focal plants flower

The probability that a focal plant with genetic value i flowers on day τ is described by a Gaussian function centered on day i. The standard deviation, σ_{pf}, captures the variability in flowering dates for focal plants with a given genetic value. We assume that σ_{pf} is a constant property of the focal plant population and that there is no effect of focal plant density on flowering date (but see Mazer and Schick 1991). If a focal plant flowers, the number of flowers produced is governed by the flowering rate function. Thus, the density of focal plant flowers with genetic value i opening for the first time on day τ of year t is

$$F'_i(t,\tau) = \frac{S'_i(t)}{2}\left(\mathrm{erf}\left(\frac{i - \tau + \frac{1}{2}}{\sqrt{2}\sigma_{pf}}\right) - \mathrm{erf}\left(\frac{i - \tau - \frac{1}{2}}{\sqrt{2}\sigma_{pf}}\right)\right)f(t,\tau), \tag{4}$$

where erf represents the Gauss error function. The total density of flowers with genetic value i present on day τ of year t is

$$F_i(t,\tau) = F'_i(t,\tau) + F^\circ_i(t, \tau - 1), \tag{5}$$

where $F^\circ_i(t, \tau - 1)$ is the density of flowers of genetic value i persisting from day τ-1 (see eqn 13). This parameterization assumes that density dependence acts before climate-driven selection on phenology. We examine the opposite case in Appendix S1.

Focal pollinators become active

The probability that a focal pollinator of genetic value i forages on day τ is a Gaussian function with a maximum at day i and a standard deviation σ_{pp} that we assume to be an unchanging property of the population. Thus, the density of pollinators of genetic value i foraging on day τ of year t is

$$P_i(t,\tau) = P_i(t)e^{-\frac{(i-\tau)^2}{2\sigma_{pp}^2}}. \tag{6}$$

Other biologically reasonable foraging probability functions, including platykurtic and leptokurtic distributions and Gaussian distributions with maxima <1, yield results qualitatively similar to those we present here. We measure phenology according to the flowering date for focal plants but the peak activity date for pollinators. Pollinator longevity is captured in σ_{pp}, but flower longevity is modeled explicitly as described below. This allows us to model the biologically reasonable case in which each flower may persist for multiple days but produces seeds only once.

Pollinators visit flowers

We assumed that individual focal pollinators move randomly and visit or ignore focal plant flowers and alternative resource items they encounter in order to maximize their resource uptake. In nature, many pollinators preferentially visit flowers that offer higher rewards (Zimmerman 1988; Goulson 1999), and optimal resource selection provides the limiting case for this behavior. Other pollinators preferentially select more common resource items (Smithson 2001; Forrest and Thomson 2009), and we consider the case of frequency-dependent resource selection in Appendix S2.

When focal plant flowers and alternative resource items are common, an optimally selecting pollinator will visit only the more rewarding resource type. If the more rewarding resource is rare, or when its expected reward has been sufficiently reduced, the pollinator will visit both resources (Charnov 1976). The portion of day τ in year t for which pollinators visit only the more rewarding resource, $\eta(t,\tau)$, depends on the density of and the reward offered by each resource type and on the foraging efficiency of the pollinator. We use Holling (1959) to derive $\eta(t,\tau)$ in Appendix S3:

$$\eta(t,\tau) = \frac{(1 + hsR_1(t,\tau))\ln\left[\frac{hsR_1(t,\tau)\omega_1}{(1+hsR_1(t,\tau))\omega_2}\right]}{P(t,\tau)}, \tag{7}$$

where $R_1(t,\tau)$ is the density of the more rewarding resource type on day τ (i.e., $\sum_i F_i(t,\tau)$.or $A(\tau)$), s is the pollinator search rate, and h is the handling time for focal plant flowers and alternative resource items. The densities

of items of the more and less rewarding resource types visited at least once by focal pollinators on day τ of year t, $V_1(t,\tau)$, and $V_2(t,\tau)$ respectively, are

$$V_1(t,\tau) = R_1(t,\tau)$$
$$\left(1 - e^{-s\left(\frac{\eta(t,\tau)}{1+shR_1(t,\tau)} + \frac{1-\eta(t,\tau)}{1+sh(R_1(t,\tau)+R_2(t,\tau))} \right) \sum_i P_i(t,\tau)} \right) \text{ and}$$

(8a)

$$V_2(t,\tau) = R_2(t,\tau) \left(1 - e^{-s\left(\frac{1-\eta(t,\tau)}{1+sh(R_1(t,\tau)+R_2(t,\tau))} \right) \sum_i P_i(t,\tau)} \right),$$

(8b)

where $R_2(t,\tau)$ is the density of the less rewarding resource. In addition to visitation by focal pollinators, focal plant flowers present on each day are visited by background pollinators with probability c_b.

Pollinated flowers seed

For conceptual simplicity, we assumed that each visited flower is pollinated and each flower not visited is pollinated by autogamy with probability c_s. Each pollinated flower produces one seed. Other rates of seed set can be captured by rescaling model parameters (i.e., r^*, A^*, ω_f, ω_a, and h), and thus, our qualitative results do not depend on assumptions about seed set. We assumed that the spatial distribution of flowers is sufficiently random that pollination on any day is random with respect to the genetic value of flowers present on that day. Thus, the density of focal flowers of genetic value i pollinated on day τ of year t by pollen from flowers of genetic value j is

$$F_{ij}^{\bullet}(t,\tau) =$$
$$\begin{bmatrix} F_i(t,\tau)\left(\frac{\left(V_f(t,\tau)(1-c_b)+c_b\right)F_j(t,\tau)}{F(t,\tau)^2} + c_s\left(1 - \frac{V_f(t,\tau)}{F(t,\tau)}\right) \right) & i = j \\ F_i(t,\tau)\left(\frac{\left(V_f(t,\tau)(1-c_b)+c_b\right)F_j(t,\tau)}{F(t,\tau)^2} \right) & i \neq j \end{bmatrix},$$

(9)

where $V_f(t,\tau)$ is the density of focal plant flowers visited on day τ of year t (i.e., either $V_1(t,\tau)$ or $V_2(t,\tau)$) and $F(t,\tau) = \sum F_i(t,\tau)$.

Genetic ^{i} value is passed from parents to offspring according to a quantitative genetic model (i.e., an infinitesimal alleles model, Fisher 1918; Bulmer 1980). This allows us to simulate evolution in a general and biologically reasonable way while avoiding system-specific assumptions about genetic architecture (Hill 2010). The expected genetic value of the offspring of any pair of focal plants is the interparental mean, and the variance among those offspring is the segregation variance, σ_{gf}^2. Thus, heritability is potentially large but always <1 (Mazer and Schick 1991; Geber and Griffen 2003). For simplicity, we assumed that σ_{gf}^2 is constant. This assumption is valid in the limit of weak selection (Bulmer 1980; Turelli and Barton 1994), but in real climate change events selection is likely to be strong and to vary in time. Mutualisms in simulations using heuristic functions that coupled segregation variance to selection strength showed decreased robustness to climate change, but the qualitative effects of model parameters were unchanged. For the purpose of simulations, we discretized genetic values by day according to expected flowering date. Thus, the density of seeds having genetic value k in year $t + 1$ is

$$S_k(t+1) = \sum_\tau \sum_i \sum_j \frac{F_{ij}^{\bullet}(t,\tau)}{2}\left(erf\left(\frac{\frac{i+j+1}{2} - k}{\sqrt{2}\sigma_{gf}} \right) \right.$$
$$\left. - erf\left(\frac{\frac{i+j-1}{2} - k}{\sqrt{2}\sigma_{gf}} \right) \right).$$

(10)

When populations are large and pollinator movement is sufficiently random, this model is general to monoecious, dioecious, and subdioecious species, including species in which seed set varies among individual plants or among flowers on the same plant.

Pollinators lay eggs

For many species of pollinators, the number of offspring an individual produces increases with the amount of resource that individual collects (Richards 1994; Stone 1995; Atanassov and Shearer 2005; Song et al. 2007). We assumed that pollinators produce eggs in proportion to the resources they collect on each day and that eggs are fertilized at random by another pollinator active on that day. This assumption may be reasonable for pollinators that mate at foraging sites (Villalobos and Shelly 1991; Petersson and Hasselrot 1994; Stone 1995; Fischer and Fiedler 2001; Turlure and Van Dyck 2009). We note, however, that our qualitative results are unchanged if (i) pollinators mate on a day other than that on which they collect resources but mating phenology is fully correlated with foraging phenology or (ii) if pollinators mate at random once or more than once during their active periods without regard to the date on which resources are collected. We scaled units of pollinators so that one unit of pollinators is the number of viable eggs produced with the resources gathered from one unit of focal plant flowers. Thus, the total density of viable eggs produced by all pollinators on day τ of year t is

$$E(t, \tau) = V_f(t, \tau) + \omega_a V_a(t, \tau) \tag{11}$$

where $V_a(t,\tau)$ is the density of alternative resource items visited on day τ of year t and ω_a is the ratio of the reward offered by alternative resource items to that offered by focal plant flowers. Because pollinators compete for limited resources on each day, eqn (11) imposes density dependence on the focal pollinator population. Using the same quantitative genetic model we used for focal plants, the density of pollinators with genetic value k in year $t + 1$ will be

$$P_k(t+1) = \sum_\tau \sum_i \sum_j E(t, \tau) \frac{P_i(t, \tau) P_j(t, \tau)}{P(t, \tau)^2}$$
$$\left(erf\left(\frac{\frac{i+j+1}{2} - k}{\sqrt{2}\sigma_{gp}} \right) - erf\left(\frac{\frac{i+j-1}{2} - k}{\sqrt{2}\sigma_{gp}} \right) \right) \tag{12}$$

where σ_{gp} is the segregation variance in the pollinator population and $P(t, \tau) = \sum_i P_i(t, \tau)$.

Flowers die or senesce.
Flowers visited by pollinators on day τ are removed from the population at the end of day τ. Flowers not visited by pollinators die with probability m_d. Inbreeding depression in seeds of self-pollinated flowers is included implicitly in m_d. Each flower may persist for up to m_s days, after which that flower senesces. Thus, the density of flowers of genetic value i persisting from day τ to day $\tau + 1$ is

$$F_i^\circ(t, \tau) = \sum_{j=1}^{m_s} (1 - m_d)^j F'_i(t, \tau + 1 - j)$$
$$\prod_{k=\tau+1-j}^{\tau} 1 - \frac{(1 - c_s)V_f(t, k) + c_s}{F(t, k)}. \tag{13}$$

We iterated d days to simulate each year and iterated years to simulate population dynamics and the evolution of phenology in the focal populations.

Simulations

We seeded our model with focal plant and pollinator populations, each with an initially uniform distribution of genetic values, and we iterated years until the distribution of genetic values in each population stabilized. This burn-in process ensured that initial population states included all genetic values capable of persisting in the model environment before climate change. Because some genetic values were eliminated during burn-in, the distribution of genetic values in each focal population at the start of simulations was unimodal rather than uniform (Fig. 1A).

Unless otherwise noted, we used the parameter values in Table 1. These values yield an initial state in which focal plant flowering, focal pollinator foraging, and peak alternative resource density are closely synchronized. Synchrony between the focal plant and pollinator populations is requisite for strong mutualism and is the initial condition we wished to study. Because the alternative resource comprises items that the focal pollinator is adapted to exploit, synchrony between the focal pollinator and the alternative resource is reasonable when pollinators are most able to exploit resources that are present during their historical periods of activity (e.g., Cane and Payne 1993; Thiele and Inouye 2007). Competition for pollinators can drive the evolution of allochrony between flowering plant species (Rathcke 1983; Van Dijk and Bijlsma 1994), but is unlikely to do so when pollen limitation is weak and there is no direct reproductive interference (e.g., stigma clogging (Waser 1978)) between species (Devaux and Lande 2009). In nature, many pollinators visit multiple flower species (Haslett 1989; Olesen et al. 2002), and thus, synchrony between focal plant flowering and alternative resource availability is biologically reasonable. Our parameter values resulted in systems with flowering periods and pollinator life spans in the range of those observed in the field (Motten 1986; Inoue et al. 1990; Kakutani et al. 1990; Kato et al. 1990; Okuyama et al. 2004), including those in some early season and montane systems that may be particularly vulnerable to climate change (e.g., Kakutani et al. 1990; Makrodimos et al. 2008). In the initial state, the flowering rate function and the temporal distribution of focal pollinators impose stabilizing selection on focal plant flowering phenology, and the temporal distributions of focal plant flowers and alternative resource items impose stabilizing selection on focal pollinator foraging phenology.

To simulate a climate change event that affects some species differently than others, we moved day θ_t earlier by 25 days relative to other biological events in the system. This imposes directional selection on focal plant flowering phenology. In the absence of evolution, climate change of this magnitude is sufficient to cause the extinction of the focal plant population. This allows us to ask whether evolution can allow focal populations to avoid extinction. Climate change occurred either instantly or incrementally over 45 or 90 years. In nature, some populations of flowering plants experienced phenological shifts of 25 days or more in the 45 years between 1954 and 2000 (Fitter and Fitter 2002; Primack et al. 2004). We iterated the model for 1000 generations after climate change to eliminate transient population states. Our formulation does not imply that biological events other than day θ_t, such as peak alternative resource density or the emergence of pollinators with particular genetic values, are insensitive

to climate change, but rather assumes that all such events experience the same direction and magnitude of change. This allows us to simulate climate change events that exert differing selective pressures on interdependent species while keeping the model simple enough that we can identify the mechanisms that underlie model outcomes.

Our model simulates a complex biological process (i.e., the coevolution of a plant–pollinator mutualism) based on mechanistic formulations of its component parts (e.g., pollinator foraging, pollination, and natural selection). The results of complex simulations can depend on assumptions about the component processes. Although we present only a subset of our results below, we confirmed the generality of our qualitative results under several alternative sets of parameter values and biologically reasonable assumptions (Table 2). Thus, we believe that our results are broadly relevant, even though the components of our simulation model are in some cases quite specific.

Results

Stable states available to the mutualism after climate change

There are seven different evolutionarily stable states that our plant–pollinator mutualism can achieve after climate change (Fig. 2). In two of these states, the focal species phenologies remain closely coupled. In the *early pollinator* state (Fig. 2A,B), focal plant flowering and focal pollinator emergence coincide with day θ_f, the climatically optimal flowering date for the focal plant after climate change. In the *bimodal pollinator* state (Fig. 2C,D), focal

plant flowering coincides with day θ_f. One group of focal pollinators emerges with focal plant flowering and a second emerges with peak alternative resource density on day μ_a. In the *late pollinator* state (Fig. 2E,F), the mutualism persists but synchrony between the focal species is reduced. The focal pollinator continues to emerge near day μ_a. The focal plant is constrained by pollen limitation from evolving to flower on day θ_f, and a reduced population flowers between days θ_f and μ_a. In the final four states (*joint extinction*, *plant extinct*, *pollinator extinct*, and *independent phenologies*, Fig. 2G–N), the mutualism is disrupted. Obligate mutualists are eliminated, and facultative mutualists persist at reduced densities. Although the seven states differ qualitatively, population densities and phenologies during the evolution of each state can be quite similar, particularly in early stages when climate change is ongoing (Fig. 2A–N).

Mechanisms leading to the evolution of different stable states

After climate change in our model, a stable state in which the focal species phenologies are closely coupled is always available. Whether the mutualism attains this state depends on the interaction between three distinct mechanisms: a two-species Allee effect, evolutionary trapping, and competition for pollinators.

Plant–pollinator mutualisms in our model experience two-species Allee thresholds. Climate change imposes selection on the focal plant population and so reduces its density. If the focal plant becomes sufficiently rare, a pollinator population that relies on the focal plant is unable

Table 2. Tests of qualitative results under relaxed model assumptions.

Basic assumption	Alternative assumption	Results
Density-dependent selection owing to competition acts before selection because of climate change in each generation	Selection owing to climate change acts before density-dependent selection in each generation	Appendix S1
Pollinators forage optimally	Pollinator foraging is frequency dependent	Appendix S2
Segregation variances are constant ($\sigma_{gf} = 4$ and $\sigma_{gp} = 4$)	Segregation variances increase, decrease, or change randomly over time	Qualitatively unchanged
	$\sigma_{gf} > < 4$ and/or $\sigma_{gp} > < 4$	Appendix S4
No demographic or environmental stochasticity	Demographic and/or environmental stochasticity is present	Appendix S5
Flowering cues are fixed. Focal plant phenology must evolve to track θ_t	Flowering cues track θ_t. Focal plant phenology must evolve to track focal pollinator foraging	Appendix S5
Focal plant flowering and focal pollinator foraging dates are normally distributed around expected dates	Distributions of focal plant flowering and focal pollinator foraging dates are platykurtic or leptokurtic	Qualitatively unchanged
Pollinators mate at random daily and produce offspring in proportion to resources collected on each day	Pollinators mate at random once and produce offspring in proportion to lifetime resources collected	Qualitatively unchanged
Focal flowers do not replenish rewards after pollination	Focal flowers replenish rewards after pollination	Qualitatively unchanged
Focal flowers are short-lived ($m_f = 1$ or $s_f = 1$)	Focal flowers are longer-lived ($m_f < 1$ and $s_f < 1$)	Qualitatively unchanged

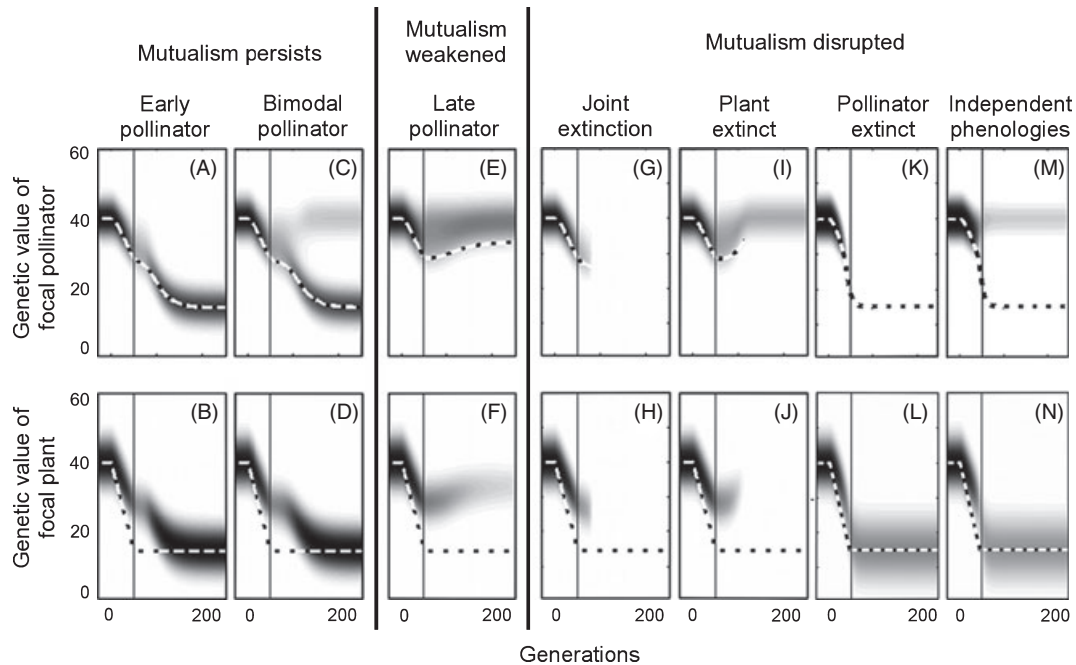Results listed as qualitatively unchanged are not presented graphically.

Figure 2 Evolutionary trajectories of the phenologies of mutualist pollinator (top row) and plant (bottom row) populations in response to climate change resulting in each of seven possible stable states. Darker areas correspond to higher absolute population densities. Dotted lines in the bottom row show day θ_t in each year. Dotted lines in the top row show the date of peak focal flower abundance in each year and end when total focal flower density drops below 10^{-4}. Climate change begins in year zero, and the vertical line in each panel shows the year in which the climate stops changing. Parameter values are as shown in Table 1, except A, B: $A^* = 0.053$, $\sigma_a = 6.5$, $c_s = 0$; C, D: $A^* = 0.1$, $\sigma_a = 6.5$, $c_s = 0$; E, F: $A^* = 0.1$, $\sigma_a = 6.1$, $c_s = 0$; G, H: $A^* = 0.048$, $\sigma_a = 5.9$, $c_s = 0$; I,J: $A^* = 0.095$, $\sigma_a = 6.1$, $c_s = 0$; K, L: $A^* = 0.02$, $\sigma_a = 8.8$, $c_s = 0.5$, $s = 2.98$, $h = 0.29$; and M,N: $A^* = 0.12$, $\sigma_a = 4.7$, $c_s = 0.5$, $s = 2.98$, $h = 0.29$.

to achieve a positive growth rate. A reduced density of pollinators in the next generation reduces the pollination rate and thus reduces the population growth rate of the focal plant. If both populations become sufficiently low, the positive impact of each species on the other becomes negligible, and the mutualism is decoupled. Obligate mutualists proceed to extinction, and facultative mutualists evolve phenologies that allow them to use alternative partners. Our model uncovers two factors that mediate this Allee effect. First, the rate of climate change controls the strength of selection experienced by the focal plant. When climate change is faster, selection is stronger and the focal plant population is more severely reduced. The effect of reduced density is augmented by the lag that develops between the evolving focal plant and pollinator phenologies, which further reduces the per capita interaction rate between the focal populations. Thus, rapid climate change is more likely than slow climate change to disrupt mutualisms (Fig. 3: compare among A–C and among D–F). Second, the presence of a dense alternative resource with a wide temporal distribution can subsidize the focal pollinator population as it evolves, preventing the mutualism from crossing its Allee threshold. Mutualisms are more likely to survive climate change when such

resources are present (Fig. 3A,B,D,E: compare top right to bottom left in each panel).

While a dense alternative resource with a wide temporal distribution can make a mutualism more robust to climate change, a dense alternative resource with a narrow temporal distribution can make a mutualism less robust (Figs 3C,F and 4: lower right in each panel). Because the focal pollinator experiences selection to emerge with dense and temporally narrowly distributed resources, such a resource can become an evolutionary trap (sensu Ferrière et al. 2004) that prevents the pollinator from evolving an earlier emergence phenology as focal plant flowering moves earlier. Interestingly, this can happen even if the focal pollinator population cannot persist on the alternative resource alone. The pollinator experiences weak selection to emerge near the peak in alternative resource density even when the benefit it receives from the alternative resource is small. This increases the lag between focal plant flowering and pollinator emergence during climate change. As the focal plant phenology moves earlier (Fig. 3F), or as its population density decreases (Fig. 4: zone JE₁), the mutualism is disrupted and the focal pollinator goes extinct. In this way, a dense alternative resource can induce evolutionary suicide
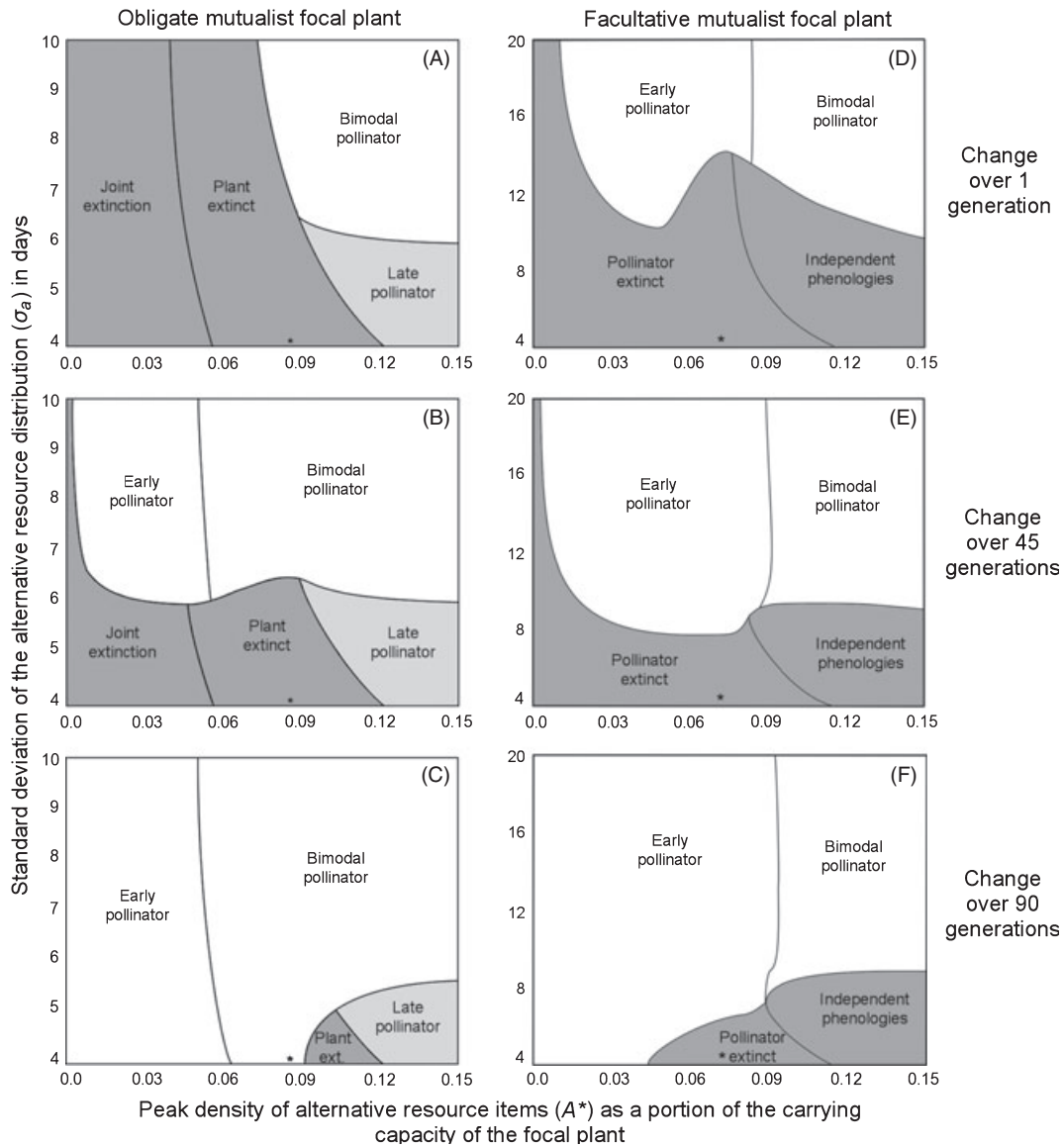
Figure 3 Evolutionarily stable states after climate change in systems with different densities and temporal distributions of alternative resources. The x axes represent the density of the alternative resource available to the focal pollinator, and asterisks indicate the peak daily density of focal plant flowers in the stable state prior to climate change. The y axes show the length of time that the alternative resource was available each year, with longer periods of availability at the top. Simulated climate change events of magnitude 25 days occurred over 1 (A,D), 45 (B,E), or 90 (C,F) years. In dark gray regions, the mutualism was disrupted, and in white regions, the mutualism persisted. In light gray regions, the mutualism persisted but synchrony between the focal species phenologies was reduced. In A–C, the focal plant was an obligate mutualist ($c_s = 0$), and in D–F, the focal plant was a facultative mutualist ($c_s = 0.5$, $s = 2.98$, $h = 0.29$). Other parameters are as in Table 1.

(sensu Dieckmann and Ferrière 2004) when a less dense alternative resource would be a weaker attractor and would allow the mutualism to persist.

Finally, direct competition from the alternative resource for pollinator visits can make a mutualism less robust to climate change. Alternative resources compete with focal plant flowers for pollination. If the subsidy from the alternative resource to the focal pollinator popu-

lation is large, the alternative resource allows the focal pollinator to maintain a higher population density. Thus, the diffuse effect of the alternative resource on the focal plant population can be positive, and the alternative resource can be an apparent facilitator (sensu Davidson 1980) of the focal plant (Moragues and Traveset 2005; Ghazoul 2006). In contrast, if the reward offered by the alternative resource is small, its subsidy to the focal
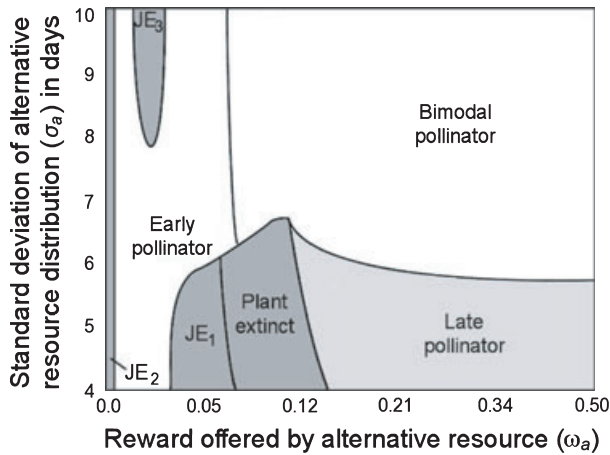
Figure 4 Evolutionarily stable states after climate change in systems with different alternative resource rewards and temporal distributions. The x axis represents the reward offered to the focal pollinator by each alternative resource item. The y axis shows the length of time that the alternative resources were available each year, with longer periods of availability at the top. Climate change events of magnitude 25 days occurred over 45 years. In dark gray regions, the mutualism was disrupted; in white regions, the mutualism persisted; and in light gray regions, the mutualism persisted but synchrony between the focal species phenologies was reduced. The label JE indicates zones of joint extinction. Parameters were $c_s = 0.1$, $c_b = 0$, and $A^* = 0.5$, with other parameters as reported in Table 1.

pollinator is small. Optimally foraging pollinators do not visit alternative resources with small rewards when focal plant flowers are common, but do visit them when focal plant flowers are rare. This means that alternative resources with low rewards compete most intensely with the focal plant when the focal plant population has been pushed close to its Allee threshold, and can sometimes push the focal plant across that threshold (Fig. 4: zone JE_3). An alternative resource with a lower reward (that offers less competition) or a higher reward (that offers a greater subsidy) would allow the mutualism to persist.

Discussion

Evolution can sometimes allow a population to persist through a disturbance when the same population would be destined for extinction in the absence of evolution, a phenomenon called evolutionary rescue (Gomulkiewicz and Holt 1995). We show that whether evolution can rescue a mutualism from climate change depends on the rate of climate change and on the density and temporal distribution of other species in the community. In some cases, this result is intuitive. For example, it has often been argued that facultative mutualists should be more robust to disturbances than obligate mutualists (Bronstein et al. 2004), and we found that over large parts of parameter

space focal pollinators were indeed more likely to persist when they had abundant alternative food resources (Fig. 3B,E). In other cases, the result is more surprising, as when the presence of an alternative resource induces evolutionary suicide in a pollinator population (Fig. 3C).

We focused on the evolution of phenology, but in nature, other plant and pollinator traits also evolve. If focal species persist at reduced densities after climate change (e.g., the late pollinator or independent phenologies states), the focal plant may evolve increased autogamy (Darwin 1876; Jain 1976; Lloyd 1979; Schoen et al. 1996; Knight et al. 2005) or greater flower longevity (Ashman and Schoen 1994), and both species may evolve increased ability to interact with alternative partners (Waser et al. 1996; Armbruster and Baldwin 1998). Nonetheless, the reduced-density states we predict may be pivotal, as populations that persist at reduced densities will be vulnerable to extinction owing to disturbances or demographic stochasticity (MacArthur and Wilson 1967; Ludwig 1976; Ewens et al. 1987; Lande 1993) before they have fully adapted to their novel biotic and abiotic environments. In contrast, allochrony and disruptive selection, as in the bimodal pollinator state, are expected to promote speciation (Crosby 1970; Gavrilets and Vose 2007). Thus, climate change might sometimes lead to the generation rather than to the loss of species.

To keep our model simple enough that we could unambiguously interpret the results, we made several assumptions. First, we assumed that there were no demographic stochasticity and no environmental stochasticity in the model parameters (e.g., r^*, θ_t, s). In nature, interactions between environmental stochasticity and climate change have been implicated in the extinction of some specialist herbivore populations (Singer and Parmesan 2010) and are likely also to be important for mutualist populations. If environmental parameters vary by year, populations in our model are more vulnerable to extinction (Appendix S5). An unfavorable year can push a mutualism that would otherwise survive climate change across its two-species Allee threshold, setting one or both populations on a trajectory toward extinction. Mutualisms that cross Allee thresholds often decline rapidly, and favorable years less frequently rescue otherwise doomed populations. In contrast, when environmental parameter values vary by day within each year, stochasticity can protect populations from extinction. In this case, focal species cannot evolve phenologies that specialize on narrow and predictable ranges of highly favorable days. The distribution of phenologies in each population becomes wider, and climate change is less likely to fully desynchronize the mutualism. Because demographic stochasticity makes it harder for favored genetic values to permanently exclude less favored genetic values, it also widens

the distributions of phenologies in the focal species, and its effects are similar to those of day-to-day environmental stochasticity. Nonetheless, neither between-year nor within-year stochasticity changes our qualitative results or the mechanisms that drive them.

Second, we assumed that the rates of pollination by background pollinators and autogamy were constant within years. Because our results were similar whether background pollination was low (Fig. 3A–C) or high (Fig. 3D–F), the magnitude of background pollination is unlikely to be the main driver of the patterns we report. However, in nature, rates of pollinator visitation (Elzinga et al. 2007) and autogamy (Kameyama and Kudo 2009) vary temporally, and such variation can create additional evolutionary attractors for focal plant phenology. Our model captures the limiting case in which the evolution of focal plant phenology is not constrained by temporal heterogeneity in background pollination rate. When variation is present, the evolution of flowering time may be more constrained, and the rate of evolution less uniform, than in our model.

Finally, we assumed that climate change alters the climatically optimal flowering date for the focal plant but does not affect the timing of peak alternative resource density or of the cues that trigger focal plant flowering and focal pollinator foraging. Our model is equally valid if climate change affects these latter events, as long as it affects them all in the same way. Thus, it provides a framework for examining the case in which climate change affects one species differently than it affects all other species in a community, which is the simplest version of the question we wished to study. The mechanisms we identified are likely to underlie evolutionary processes in more realistic communities where climate change has different magnitudes and directions of effect on each focal and nonfocal species (Fitter and Fitter 2002; Primack et al. 2004; Sherry et al. 2007). Our model serves as a foundation for models of these more complicated communities.

The assumption that climate change does not directly affect the date of focal plant flowering means that any change in focal plant flowering phenology must evolve. This implies that focal plant flowering phenology is not plastic with respect to climatically optimal flowering conditions (DeWitt and Scheiner 2004). In nature, flowering phenology can be plastic with respect to an array of environmental variables (Tarasjev 1997; Simons and Johnston 2000; Williams et al. 2008). To capture the opposite extreme from that presented in Fig. 3, we modeled the case in which focal plant flowering cues change with θ_t, and any change in flowering phenology relative to θ_t (e.g., later flowering to obtain higher pollination rates) must evolve. Because focal plants flower closer to their climatically optimal date in this case, the density of flowers is higher and the mutualism is less likely to fall below its two-species Allee threshold. Thus, the mutualism is more robust to the same rate and magnitude of climate change. Nonetheless, the qualitative effects of the alternative resource density and distribution and of the rate of climate change are the same as those we present in Fig. 3 (Appendix S5).

Because the evolutionary trajectories leading to qualitatively different stable states can be similar (Fig. 2), researchers may not be able to predict the fate of a given mutualism based on population densities, temporal distributions, or even interaction frequencies between focal populations during a climate change event. Rather, researchers will need to know whether an evolving mutualism is close to its two-species Allee threshold. Manipulations that vary the densities and measure the population growth rates of both mutualist partners could be used to estimate two-species Allee thresholds, but may be difficult to conduct in the field. A number of studies have demonstrated Allee effects in flowering plant populations (e.g., Kunin 1993; Forsyth 2003; Knight 2003), but these are believed to result primarily from density-dependent foraging by pollinators. While other theoretical studies have predicted two-species Allee thresholds (Amarasekare 2004; Morgan et al. 2005), we know of no study that has attempted to quantify or even demonstrate their existence in nature. If Allee thresholds cannot be estimated, a first step may be to determine whether a mutualism is obligate or facultative for a given population. It will be not sufficient to know whether the focal plant has alternative pollinators or the focal pollinator has alternative food resources (Kay and Schemske 2004; Herrera 2005). Rather, researchers must determine whether each focal population can persist in the absence of the other (Johnson and Steiner 2000).

Focal species will be most able to evolve new phenologies in response to climate change if they can obtain mutualist partners outside of the current flowering or foraging periods. Studies that compare seed set in flowering plant populations with experimentally advanced, delayed, and control flowering periods can tell us whether focal plants are likely to achieve adequate pollination rates as their phenologies change. Rafferty and Ives (2011) presented evidence that flowering plants that receive fewer pollinator visits when their flowering time is advanced have experienced less change in phenology over the past 70 years than plants that receive ample visits from early pollinators. Studies of this sort can help to identify populations in which evolutionary response to climate change may be constrained by pollen limitation. Similar studies that measure resource collection by pollinators with advanced or delayed foraging dates could help to identify

pollinator populations for which evolution is constrained by resource abundance.

Much remains to be learned about how communities will evolve in response to climate change. Our results point to the importance of species interactions in mediating when and how populations can adapt to changing abiotic conditions. As system-specific data on the genetics of phenology and on species interaction rates at the community level become available, more detailed mechanistic models may help researchers and practitioners to more precisely identify mutualisms at risk owing to climate change.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Evolution of a plant-pollinator mutualism when selection due to climate change acts before density dependence.

Appendix S2. Evolution of a plant-pollinator mutualism in response to climate change when pollinator foraging is frequency dependent.

Appendix S3. Derivation of $\eta(t,\tau)$, the time on day τ of year t for which an optimally foraging pollinator will visit only the more rewarding of two resources.

Appendix S4. Effects of segregation variance in the focal plant and pollinator populations.

Appendix S5. Supplementary figures.

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