Timing is Everything: An Overview of Phenological Changes to Plants and Their Pollinators

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ABSTRACT: Plant-pollinator interactions are a critical component of a healthy plant community and a healthy ecosystem. However, these interactions are at risk due to many factors, including potential phenological mismatches that may disrupt the timing of successful pollination. Environmental variables influence both when plants flower and when insects pollinate, and if those variables change, so might the timing of each species. If those changes do not track each other, plants and pollinators may not be active at the same time, potentially causing substantial problems to both groups. Yet, there is little consensus thus far about how the timing of plants and pollinators has been changing and how that might ultimately influence this important ecological interaction. Here, we review the evidence for phenological shifts in both species and find that there is evidence of change, but that it is extremely species-specific with some species advancing their activities, some delaying, and some staying about the same. We also provide some management guidelines to help promote healthy plant-pollinator relationships in light of the potential variability in phenological shifts and the other threats these species face in natural areas.

Index terms: mutualism, phenological shifts, pollinator conservation, pollinator management

INTRODUCTION

Plant-pollinator mutualisms are among the best known and most important ecological interactions. Approximately 75% of flowering plants engage in some sort of plant-pollinator interaction (National Research Council 2007), and those interactions play a critical role in the reproduction of the plants being pollinated and the larger plant community (Kearns et al. 1998). The economic benefits of insect pollinators have been well documented in agricultural systems as many of the world's crop species depend on animal pollinators either partially or completely (Losey and Vaughan 2006; Klein et al. 2007; Gallai et al. 2009). However, plant-pollinator relationships are also critical to the health and sustainability of natural areas. Besides the genetic and reproductive benefits plants receive from pollination (Kearns et al. 1998; Harmon et al. 2011), animal pollinators play less obvious, though often imperative, roles in maintaining plant diversity and conservation (e.g., Travers et al. 2011) and as critical parts of the food webs that sustain insects, fish, and wildlife (Black et al. 2011; Gilgert and Vaughan 2011). While harder to quantify, these ecological services are also incredibly valuable (Losey and Vaughan 2006; Gilgert and Vaughan 2011). Despite their importance, plant-pollinator interactions are facing serious threats, and it is becoming increasingly important to understand these mutualistic species and the pressures they face so that we may best design scientific investigations and management strategies to ensure their long-term sustainability.

Over 200,000 animal species may act as plant pollinators (Buchmann and Nabhan 1996), and the dangers they face are seemingly just as diverse. The iconic honey bee (*Apis mellifera*), for example, faces challenges from a variety of sources that may be contributing to its decline as part of colony collapse disorder (Watanabe 1994). Other bees have specific habitat requirements that are often in short supply (Gilgert and Vaughan 2011). Moreover, land-use change and other anthropogenic disturbances are substantial disruptions to all pollinators (Black et al. 2011; Gilgert and Vaughan 2011), which includes bees, moths, butterflies and the other groups of insect that can help pollinate plants (Harmon et al. 2011).

More recently, concerns have arisen about a very different type of threat, specifically that the timing of when plants and pollinators are active and receptive to pollination may be changing and could ultimately become mismatched so that they can no longer interact effectively (Sparks and Menzel 2002; Memmott et al. 2007; Hegland et al. 2009; Solga 2012; Wolkovich et al. 2012). For successful plant-pollinator interactions, this timing is crucial: plants need to be in flower at the same time as their pollinators are active or both organisms will likely suffer. Phenology is the area of study that investigates the timing of such life cycle events and how they respond to the changing seasons or climatic conditions (Forrest and Miller-Rushing 2010). The phenology of both plants and their insect pollinators can be regulated by a variety of environmental cues, including photoperiod, temperature, and precipitation (reviewed in

Solga 2012). Recent evidence of changes in temperature, precipitation, and other potential phenological cues (IPCC 2007) increases the concern that the timing of plants and pollinators may also be changing and that these changes could lead to mismatches that threaten plant-pollinator interactions.

Our overall objectives are to review the threat that changing phenologies may present to plant-pollinator interactions and to provide some ideas as to what conservation or management actions can be implemented to help conserve pollinators and ensure successful pollination. We first evaluate the evidence for changes in the timing of flowering plants and then insect pollinators individually. If a mismatch is going to develop, there needs to be change by individuals in at least one of these groups. We then integrate changes to both plants and pollinators together, primarily by reviewing specific case-studies. Finally, we discuss management considerations that could help strengthen the health of plant-pollinator interactions as they face environmentally-induced phenological changes as well as other potential threats.

EVIDENCE FOR CHANGE IN FLOWERING PHENOLOGY

Our first goal is to understand the current evidence for changes in flowering phenology over time. It is usually difficult to quantify such long-term ecological changes, but fortunately there have been opportunities to continue or re-establish data on first flowering dates for some plant communities. Past observations made by naturalists like Aldo Leopold and his daughter Anna in Wisconsin over a 61 year period (Bradley et al. 1999), and author Henry David Thoreau in Massachusetts during the mid-nineteenth century (Miller-Rushing and Primack 2008; Willis et al. 2008), among others, have given us valuable records of first flowering dates and the ability to determine how flowering phenology has changed across plant species in particular locations. Observations of first flowering date give us a good sense of phenological change and it is the best and longest data we have available; but since it only addresses when things start and not how long flowering happens, it is only a partial picture of phenological changes.

A recent meta-analysis (Wolkovich et al. 2012) has used a very large database of observational measurements to show that there is an overall advancement in the timing of both flowering and leafing in plants. This paper does an exceptional job of demonstrating that across all of the observational data they could find there is an overall significant advancement in the phenology of plants in response to changing temperature. These results mean that we would expect that most plants are flowering earlier than they have in the past; however, this overall effect doesn't address the species-to-species variation we might find. The overall trend may be advancement by a given amount, but how many of the plants in a given community are changing by that same, average amount? How many are flowering even earlier? How many might not be responding or may even be delaying the timing of their flowering? By looking at the distribution of species responses we can get a sense of how each plant in a broader group are changing their first flowering dates and get a first response to some of these additional, complementary questions to the established overall effect.

To characterize the distribution of changes to plant species, we reviewed six studies that quantify the change in first flowering date for multiple plants in a given location (Bradley et al. 1999; Abu-Asab et al. 2001; Fitter and Fitter 2002; Cook et al. 2008; Bai et al. 2011; Dunnell and Travers 2011; Table 1). Our criteria for choosing data sets include that they have at least 10 plant species within the same area, that they cover at least a 10 year stretch of time, and that they report the change in individual flowering plant species over time. We wanted

Table 1. Characteristics of the six studies used to identify changes in flowering phenology across plant species in a given location (Figure 1) and the four studies used to identify changes in insect pollinator phenology (Table 2).

Phenology Articles	Species	Duration	Analysis	Location & Latitude
Flowering Plants				
Fitter and Fitter 2002	385	1954-2000	Subtraction	Oxfordshire, UK; 51.8°N
Dunnell &Travers 2011	178	1910-2010	Subtraction	MN & ND, USA; 46.9°N
Abu-Asab et al. 2001	100	1970-1999	Regression	Washington DC, USA; 38.9°N
Bai et al. 2011	48	1963-2007	Regression	Beijing, China; 39.9°N
Bradley et al. 1999	55	1936-1998	Regression	WI, USA; 43.5°N
Cook et al. 2008	19	1928-2002	Regression	NY, USA; 41.8°N
Insect Pollinators				
Roy & Sparks 2000	35	1976-1998	Regression	British Isles, UK; 54°N
Forister & Shapiro 2003	23	1972-2002	Regression	CA, USA; 38.6°N
Stefanescu et al. 2003	19	1988-2002	Regression	El Cortalet, Spain; 42.2°N
Bartomeus et al. 2011	10	1880-2010	Regression	Northeast USA; 36-50°N

to focus our study on plants relevant to animal pollination, so we were able to exclude some obvious wind-pollinated plant communities. However for the studies we did use, we did not further evaluate the relative importance of animal-pollinated out-crossing for each plant species.

To facilitate comparing data across studies, we calculated frequency distributions of the observed changes in flowering phenology (in days) within each community (as in Fitter and Fitter 2002). Because our main purpose was to get an overview of these qualitative distribution patterns across species and studies, we treated all published information the same; however, there is a great deal of variation among species and studies, with authors finding some patterns to be statistically significant and others not. To calculate our graph of changes in days, we performed different transformations depending on the published analysis. Studies that took the average first flowering date for a past time period and then found the difference with an average date for a more recent period needed no transformation; however, in one study (Dunnell and Travers 2011), we used their data to calculate the recent average flowering date and subtracted the reported average from the older period. Other studies used linear regression to look at first flowering date over time and reported the slope of that analysis. To put the data in the same format, we multiplied those reported slopes with the total number of years in the study to arrive at an overall change in flowering (in days) over the entire study as predicted by regression analysis. It is completely possible that the transformations we performed induced biases; however, with the data we have, we cannot differentiate potential biases from our transformation from potential biases of the data itself since it was collected and reported in different ways or from other potential differences among the studies themselves. Therefore, we make only rough qualitative comparisons across studies and do not try to make formal statistical analyses of the data.

The result is six histograms that demonstrate the distribution of changes in flowering phenology across 738 plant species in six geographical locations (Figure 1). The individual distributions for each study provide an interesting picture of how many species within a given area have changed in their flowering dates by a given amount.

In trying to compare results across studies, it can be difficult to make strong inferences without accurately accounting for the length of time of the study, the actual changes in temperature and other environmental cues within each site, as well as additional characteristics of both the sites and the plants themselves (for a discussion and thorough example of dealing with these issues, see Wolkovich et al. 2012). However, we wanted to provide crude estimates of what happened across these different distributions, so we provide some descriptive statistics of species response in relation to changes within or beyond five days. Five days is somewhat arbitrary and can be more or less meaningful depending on the length of the study or the amount of temperature change a given study site has observed. However we found a characteristic divide in our data that makes five days a useful measure of comparison.

Across all studies, almost half (48.5%) of the species flowered within five days of their historical flowering dates, indicating little or no evidence of a phenological change over the observed time period. A similar proportion (41.4%) flowered earlier in the season (> 5d earlier) and the remaining 10.0% began flowering later in the season (> 5d later). Two studies had notably greater proportions of species that flowered more than five days early (65.1% – Abu-Asab et al. 2001; 75.0% – Bai et al. 2011), and one study had relatively more species that delayed flowering by greater than five days after using our standardization method (26.5% – Dunnell and Travers 2011). These results are consistent with other studies investigating individual plant species or small communities that have reported similar patterns in flower timing in response to recent environmental change (Inouye et al. 2003; Crimmins et al. 2010; Gordo and Sanz 2010; Lesica and Kittelson 2010; Crimmins et al. 2011).

EVIDENCE FOR CHANGE IN INSECT POLLINATOR PHENOLOGY

Similarly, we reviewed the literature to determine the evidence for changing phenology in potential insect pollinators.

Unfortunately, compared to plants, there have been fewer data sets for groups of insects that span a decade or more. However, using the criteria above, we identified three studies on butterflies (Roy and Sparks 2000; Forister and Shapiro 2003; Stefanescu et al. 2003) and one on wild bees (Bartomeus et al. 2011) (Table 1). Only the bee study was done in the context of pollination, so we cannot say for certain that all these species are important pollinators. All four studies looked at the adult insects' date of first appearance with the first three using observations from monitoring efforts and the fourth relying on first museum specimens collected within each year. Data were transformed as above, but given the relatively small number of species observed, we could not use the fine-scaled distributions as we did with plants. Instead we made our distributions extremely course by combining the information into three broad, somewhat arbitrary categories: (1) phenological advances (> 5 days earlier); (2) little to no change (± 5 days); or (3) phenological delays (> 5 days later). Again, our primary goal is to view the distribution of species-specific responses, especially within studies as opposed to making quantitative statistical inferences. The results from Stefanescu et al. (2003) are slightly different in that species showing a non-significant change in first appearance are placed in the "little to no change" category.

As we saw for first flowering dates in plants, the way the first flight of insects changed over time was highly variable (Table 2), with the relative proportion of species in our three arbitrary categories in approximately the same ratio for insects (44.0% > 5d earlier; 48.8% little to no change; 7.1% > 5d later) as it was for plants. Two of the four studies (Stefanescu et al. 2003; Bartomeus et al. 2011) had greater proportions of their species with a large phenological advance. However, in the case of Bartomeus et al. (2011), this was likely an artifact of our reporting predicted days changed over their very long study period as opposed to the more accurate slope values reported in the study.

EVIDENCE FOR CHANGE IN PLANT-POLLINATOR PHENOLOGY

While the previous studies looked at either plants or pollinators individually, few stud-
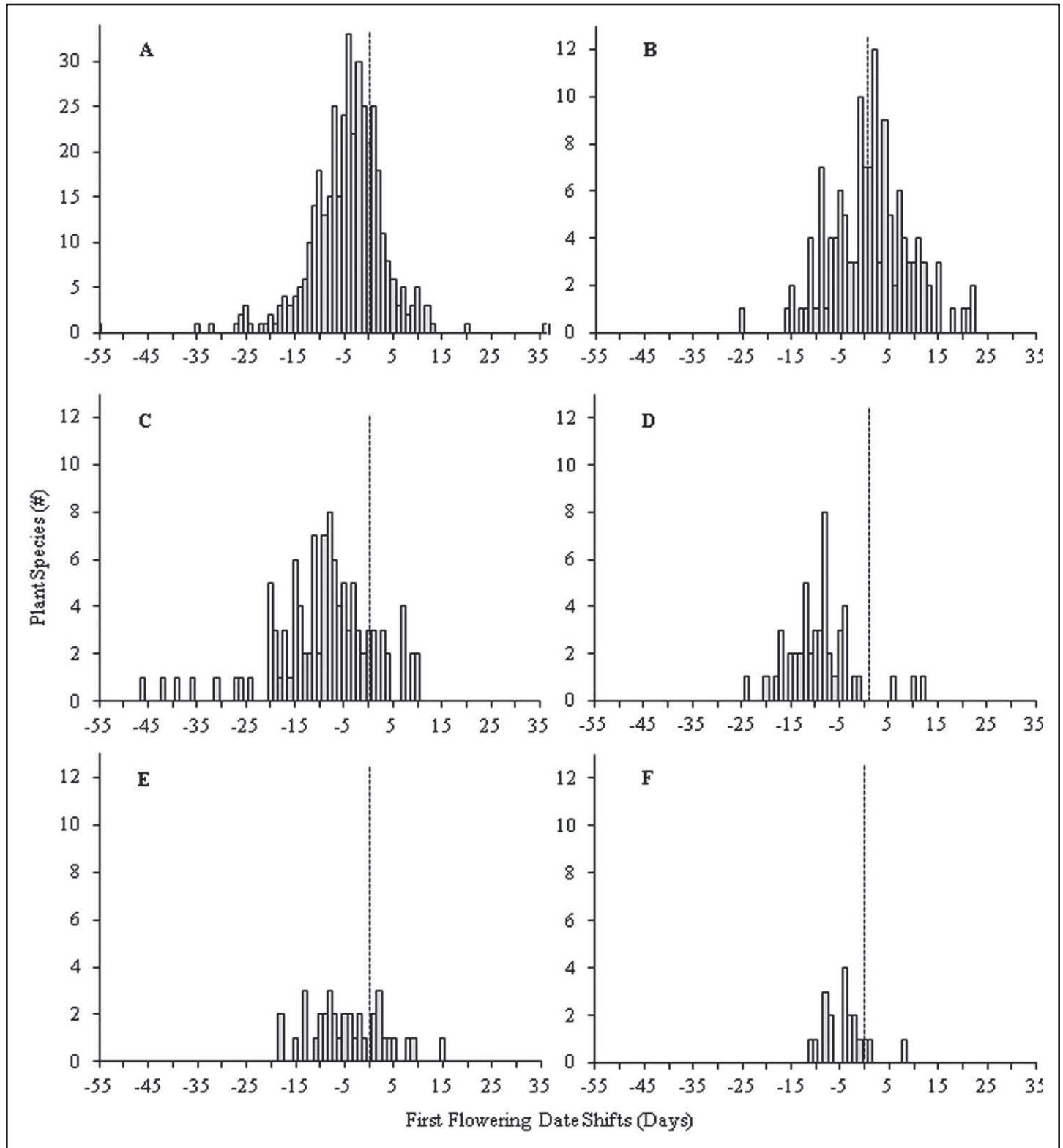
Figure 1. The distribution of phenological changes in first flowering dates for plant species with the dashed line at 0 represents no change, negative numbers representing earlier flowering dates, and positive numbers representing later following dates for studies conducted in (A) Oxfordshire, U.K., (B) Minnesota and North Dakota, U.S.A., (C) Washington, D.C., U.S.A., (D) Beijing, China, (E) Wisconsin, U.S.A., and (F) New York, U.S.A.

Table 2. Change in potential insect pollinators over time. The number is the number of species found within that category (calculations used to standardize reported data found in text) and the percentage is the percentage of species within a given study found in each category.

	Phenological Advances (>5 days earlier)	Little to No Change (±5 days)	Phenological Delays (> 5 days later)
Roy & Sparks 2000	12 species	23 species	0 species (0%)
Forister & Shapiro 2003	5 species	12 species	6 species (26%)
Stefanescu et al. 2003	11 species	5 species	0 species (0%)
Bartomeus et al. 2011	9 species	1 species	0 species (0%)

ies thus far have looked for changes in pollinators and plants simultaneously. An exception is Bartomeus et al. (2011), where museum specimens were used to identify changes in first capture (as an estimate of first flight) in a community of generalist bees in the northeastern United States, and these changes were compared to published data for plants that are pollinated by these generalist bees in the same area. Overall, they concluded that these pollinators and their plants were changing at about the same rate.

Further evidence is provided from case studies of particular plants and pollinators. For example, an out-crossing plant, yan hu suo (*Corydalis ambigua*), suffered from low seed-set when it advanced its flowering date due to warmer spring temperatures; but its primary pollinator, bumblebee queens, did not advance their emergence date (Kudo et al. 2004). Likewise, the solitary bee pollinator of yellow star-of-Bethlehem (*Gagea lutea*) was not available for pollination when this plant advanced its bloom times (Kudo et al. 2004). In a similar case, the glacier lily (*Erythronium grandiflorum*) experienced pollination limitation early in its bloom period due to unavailability of bumblebee queens to pollinate its flowers (Thomson 2010).

At other times, pollinators might demonstrate plasticity in their phenology so that they can keep pace with a changing host plant and thereby avoid a mismatch. The mutualism between pollinating flies and their host plants, *Adonis ramose* and *Anemone flaccid,* at an alpine site did not show any mismatch due to earlier spring season arrival dates, which may indicate that this pollinator is responding to the same cues, or that it has been able to quickly adapt to its plants' emergence (Kudo et al. 2004).

Under certain conditions, a mismatch may actually not be detrimental. *Hoplitis fulgida,* a solitary bee, completely missed the flowering period of its host legume, *Lathyrus*, during one season at several alpine sites (Forrest and Thomson 2011). Even though a complete decoupling between these two species occurred, this generalist pollinator was able to use other local flowering resources that were available, and *Lathyrus* avoided pollination limitation because of frequent pollination by other visiting insects (Forrest and Thomson 2011).

Just as we highlighted the variation that can occur among different species, there is good reason to expect additional variation in plant-pollinator phenology within species. For example, geographic location influences how the arrival of a hummingbird and the availability of its early-season nectar resources have changed over time (McKinney et al. 2012). At the southern edge of the hummingbird's breeding range, neither arrival nor first flowering dates have changed. However, at the northern edge, first flowering has become increasingly earlier, resulting in a shorter overlap between flower and hummingbird.

MANAGEMENT CONSIDERATIONS

To safeguard plant-pollinator mutualisms and other interactions within ecosystems, conservation measures must be implement-ed to counteract current threats, including those from a changing environment. Challenges exist for managers who are balancing conservation efforts with limited funding, time, and often the availability of suitable habitat. We first discuss general practices that can enhance the overall health of the plant-pollinator relationship and then highlight practices relevant to changing phenology in particular.

Just like other animal species, insect pollinators require certain habitat conditions and resources to thrive and reproduce. Management efforts targeting pollinator conservation typically emphasize protecting and enhancing existing pollinator habitat through a variety of best management practices. For example, pollinators require a variety of resources to use as sites for building their nests or laying their eggs, and these resource needs should be incorporated into pollinator conservation plans (Mader et al. 2011). Most native bees either nest in the ground or use cavities in dead wood for nests (Vaughan and Black 2007); ground nesting bees require open areas of ground that have the appropriate soil texture that enables bees to tunnel to build their nests, whereas certain cavity nesting bees require old dead trees to excavate for nests. Wood block nests provided by humans are used by some nesting bees and can provide a ready material in areas such as grasslands that may otherwise be devoid of trees, shrubs, or dead wood resources. Butterflies, on the other hand, require specific host plants on which to lay their eggs, as once the larvae emerge from eggs they will require plant leaves to provide them with vital food resources.

Habitat management practices such as mowing, haying, grazing, prescribed fire, and pesticide application can directly and indirectly affect pollinators and should, therefore, be appropriately timed (Black et al. 2011; Cane 2011). Mortality induced from direct exposure to management practices is perhaps easier to mitigate though proper timing than indirect exposure. Mowing, haying, and grazing of plants can potentially harm pollinators while depriving them of food (Noordijk et al. 2009). Improper timing of prescribed fire may also negatively affect ground nesting

bees, especially solitary bees, because the heat can reach shallower nesting species (Potts et al. 2003). Cavity nesting bees, depending on how closely their nests are located to the ground surface, can also be damaged by fire (Cane 2011). Pollinators are also known to be vulnerable to pesticides in their habitat (National Research Council 2007). Butterflies in various stages of development can be directly affected by receiving pesticide spray meant for insect pests of plants (Russell and Schultz 2010). Developing bees are particularly sensitive to pesticides contained in pollen that is deposited in their nests (Kearns and Inouye 1997).

Management practices can also indirectly affect pollinators if not coordinated with plant-pollinator life cycles. For example, untimely mowing, haying, or grazing may remove plants that provide vital oviposition sites for butterflies and nesting sites for bees (Vaughan and Black 2007; Black et al. 2011). Heavy livestock stocking rates can cause compaction of the soil, making it difficult for ground nesting bees to excavate their nests (Kearns and Inouye 1997). Overwintering or oviposition sites for butterflies can be threatened if fire occurs during the immature stages of their lifecycle (Swengel 2001; Cane and Neff 2011). Prescribed fire should also be avoided when plants are in susceptible growth stages or blooming; however, proper frequency and timing can supply an eruption of forbs the following spring (Kearns and Inouye 1997; Potts et al. 2003) or expose bare ground for excavating by ground nesting bees (Campbell et al. 2007).

To overcome mismatches that may occur due to changing environmental conditions, managers can create a buffer to safeguard pollinators against potential limitations in floral resources within their habitats. Pollinators require an abundance and diversity of floral resources spanning the entire duration of their respective life cycles (Potts et al. 2009; Dicks et al. 2010). Pollinators, especially bees, depend on nectar and pollen resources for their energy needs and to nourish their offspring, whereas most butterflies require nectar as adults but use specific host plants as plant-eating juvenile

caterpillars (Kearns and Inouye 1997). To provide for a variety of pollinator species and life cycle requirements, a succession of blooming resources spanning the entire growing season can be implemented (Vaughan and Black 2006; USDA 2008). Pollinator species vary in different regions of the country and their life cycles span fairly short time periods, many times only a few weeks. For pollinator habitats to flourish, be sustainable, and provide for the needs of a wide assortment of pollinators, an array of plant species needs to be promoted so that the needs of all specialist and generalist pollinators are met. Ultimately, a well-timed heterogeneous floral bloom that is available to pollinators throughout the growing season will likely provide the diversity of pollen and nectar resources required for them to not only prosper, but also to face future habitat alterations that environmental change may generate.

CONCLUSION

Although there is evidence that some plants and pollinators are undergoing phenological changes, there is a great deal of species-specific variation in how things have changed over the last 50–100 years. Future efforts to understand this variation (e.g., Altermatt 2010; Diamond et al. 2011) and its implications will help us make better predictions and more refined conservation policies. In the meantime, the evidence reviewed here implies that phenological change has at least the potential to disrupt plant and pollinator species, thereby threatening their interactions and the health of the ecosystems they reside in. Therefore, it is imperative that we develop management strategies to counteract current and future threats to preserve the ecosystem diversity and function that comes from healthy pollination interactions.

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