

TIMING IS EVERYTHING: HOW ENVIRONMENTAL CHANGE MAY DISRUPT THE
TIMING OF PLANT-POLLINATOR INTERACTIONS

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ABSTRACT

Ecosystems are experiencing environmental change brought about by warming temperatures, altered precipitation, and increasing atmospheric CO₂, among other factors. These changes could alter interspecies' relationships, including those between plants and pollinators. One important change may be to the timing of when flowers bloom and when pollinators are active. Environmental cues drive the phenology of many flowers and insect pollinators, so an alteration in timing for either species could jeopardize the plant-pollinator relationship. Previous studies indicate that many plant species have changed flowering dates in response to an environmental cue, but the response is species specific. Some pollinators may not be "keeping pace" with flowers, leaving this mutualism at risk. Since not all plants and pollinators are responding equally to change it is important to develop a better understanding of how environmental change may influence vulnerable species in this mutualism and the possible implications to the function and diversity of ecosystems.

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CHAPTER 1. INTRODUCTION

1.1. Why is Environmental Change Important?

The physical conditions found within the environment are crucial factors in shaping the diversity of life, including the interactions that occur between species (Tylianakis et al. 2008; Hegland et al. 2009; Yang and Rudolf 2010). Living species depend on the environment around them to provide essential elements such as suitable light, temperatures, moisture, and nutrients which are required in appropriate quantities for species to survive, grow, and reproduce. For example, all plants are reliant on the sun's light in order to photosynthesize, whereby they fix CO₂ and store energy in the form of simple sugars (Raven et al. 2005). Insects are another example; temperature directly affects insects by influencing how fast they develop, where they can live, and how many individuals there are in a population (Bale et al. 2002).

The predictability of these essential factors to be available in the right place, time, and amount determines individual species' performance and inevitably the structure and functioning of the ecosystems where they reside. One simple example of this connection between ecosystem structure and abiotic factors is found in the large ecosystem categorizations called biomes. Biomes are regions categorized according to the dominant plant and animal species that have adapted their life cycles to the specific environmental conditions of that region (Smith and Smith 2006). For instance, the different grassland biomes across North America are dominated by grasses and forbs that are adapted to the specific precipitation regimes that exist across the continent. The representative vegetation changes across a declining moisture gradient from east to west as observed in the tallgrass prairies of the Midwest, the tall and mixed-grass prairies of the Great Plains, and the shortgrass prairies in the southwest (Smith and Smith 2006). Another example is found within the world's desert biomes. Within the desert the plant and animal

species that thrive are those that possess traits making them resistant to heat and drought, such as plants or animals that time their activity to the cooler or moister periods of the day or season (Hopkins and Hüner 2004; Smith and Smith 2006).

The Earth is one immense dynamic system, with environmental conditions that regularly vary across time and space. Some environmental changes are extremely regular and species have developed adaptations to respond to these changes. For example, insects in temperate habitats endure periods of inhospitable conditions by entering diapause at a predetermined stage in their development (Gullan and Cranston 2010). Similarly, certain mammals such as woodchucks (*Marmota monax*) survive through seasons of limited food and harsh weather by entering a period of hibernation whereby they lower their metabolic rate and body temperature as a means to save energy (Ferron 1996). The energy stores they use for hibernation are drawn from fat reserves stored during the previous summer and fall. Plants also have mechanisms that aid them in survival during the harsh environmental conditions of winter or drought. As days shorten and temperatures drop, autumnal leaf senescence occurs where leaves change color as they stop photosynthesizing and nutrients recycle back into the plant to be stored (Smart 1994). Leaf senescence can also occur when a leaf ages or is no longer in a position to be beneficial to a plant, such as a lower positioned leaf that is shaded from the sun. Senescence in this case allows for nutrients to be taken from older leaves and transported to newer, young leaves that have more optimum light exposure (Smart 1994).

Through the geologic study of the Earth we have learned that environmental conditions have previously gone through dramatic changes and that this has occurred multiple times throughout Earth's history (Crowley 1990; Pagani et al. 2006; Currano et al. 2008). Modifications of Earth's temperatures, precipitation, and CO₂ levels, have been the major

underlying factors prompting these changes (IPCC 2007). For example, in the Cenozoic Era during the Paleocene and Eocene epochs, disruption of normal atmospheric CO₂ levels and rapid warming occurred and this abiotic change altered interactions between insects and plants resulting in increased insect herbivory (Curano et al. 2008). Likewise, during the Pleistocene epoch, climate swings occurred due to the advancement and retreat of glacial ice sheets across the northern continents of the globe (Smith and Smith 2006). On the one hand glacial advancement resulted in colder climates typified by a decline in species' richness. On the other hand, glacial retreats brought warmer conditions which aided in increasing species' diversity (Pearson 2011). Consequently, as a result of extreme swings in environmental conditions, species have not always been able to "keep up" or adapt which has resulted in massive extinctions. Our evidence for extinctions triggered by ineffective adaptation to environmental conditions is the fossil record of numerous plant and animal species that no longer reside within our ecosystems (Pearson 2011).

In more recent years it has been argued that our environment is again going through some dramatic changes, this time at a more accelerated rate than ever before (IPCC 2007). These changes have the potential to interfere with individual species (Bradley et al. 1999; Post and Stenseth 1999; Gordo and Sanz 2005; Visser and Both 2005; Bale and Hayward 2010), the interactions between species (Tylianakis et al. 2008; Hegland et al. 2009; Yang and Rudolf 2010), and the normal structure and functioning of entire ecosystems (Brown et al. 1997; Miller-Rushing and Primack 2008; Tylianakis et al. 2008). Therefore if we want to conserve species' interactions and the functioning of ecosystems we must ascertain the response they might have to changes in their environment, in case these changes occur.

1.1.1. Examples of the consequence of environmental change

There is a diversity of intriguing examples that illustrate the importance of environmental changes on species, their interactions, and the ecosystems where they interact. The American robin (*Turdus migratorius*) for example, is a migratory bird species that relies on environmental conditions within its summer and winter ranges to determine when it migrates. Changes to environmental factors such as temperature can disrupt the migratory timing of this species. In the case of American robins whose summer range includes the Rocky Mountains, earlier arrival of spring in their winter ranges has prompted them to migrate earlier, arriving at their summer ranges prior to snowmelt, resulting in delayed nest construction and egg laying (Stenseth and Mysterud 2002). The gap existing between robin arrival date at its summer range and date of first open bare ground may pose an additional threat to this species if food resources vital for breeding and reproduction are not available due to snow cover (Inouye et al. 2000).

Changing environmental conditions not only effect individual species, but also species interactions, as not all species respond equally to changes in their environment. This uneven response to change can lead to a loss of synchrony between trophic levels which can affect both species' fitness. A well studied example of this is the oak (*Quercus robur*) (plant nomenclature as per USDA PLANTS database) and winter moth (*Operophtera brumata*) (insect nomenclature as per Entomological Society of America) interaction in the Netherlands (Buse and Good 1996; Visser and Hollerman 2001). Insect larvae depend on young vegetation to supply nutrients for their developmental needs. Winter moth larvae rely on proper timing with oak tree bud burst in the spring for that very reason. Both the winter moth and the oak have advanced their life cycle phenologies in recent years as a result of earlier arrival of spring, however the winter moth has advanced its phenology further than the trees, causing moth eggs to hatch too early. This

mismatching between these two species has led to decreased food resources for winter moth larvae and consequently smaller females with reduced egg loads (Buse et al. 1998). With the prediction of climates trending warmer in the coming years, we may see more of a problem with the synchrony between winter moth and oak phenologies eventually resulting in winter moth's very survival being in jeopardy.

Environmental changes can have deep reaching effects on entire ecosystems just as they can have on species and their interactions. Ecosystems are dynamic and the interactions within them can change at various points in time depending on the environmental conditions and circumstances. Sometimes an environmental change can directly affect a particular species thereby positioning it in the role of directly or indirectly affecting the wellbeing of other species and the future stability of an ecosystem. Such is the case with the Chihuahuan Desert ecosystem in Arizona. Changes in precipitation in this area since the late 1970s have caused a dramatic shift in the distribution of plant and animal species inhabiting this region (Brown et al. 1997). This area was typified by warm season C₄ grasses and shrubs, but with the onset of increased precipitation in the 70s, this area has transformed into a C₃ shrub dominated region. Two abundant species of rodents, the banner-tailed kangaroo rat (*Dipodomys spectabilis*) and the silky-pocket mouse (*Perognathus flavus*), responded with recent population declines due to the increase in precipitation and changes in local vegetation. These species typically reside in drier grasslands or desert habitats and are known to be seed-eaters that store their provisions underground. With increased precipitation, the moister soil conditions may have been unsuitable for seed storage or the proliferation of shrub species may have represented a decline in the quality of habitat or food resources these species require (Brown et al. 1997). With a decline in these rodent species, other species in the ecosystem also suffered repercussions, such as the

Mojave rattlesnake (*Crotalus scutulatus*) and the burrowing owl (*Athene cunicularia*). The Mojave rattlesnake was directly impacted as it requires these rodents as a food resource. Both the Mojave rattlesnake and the burrowing owl use rodent burrows for nesting. This is just one example of how a single environmental change can have consequences for numerous species, their ability to interact, and thus the overall structure and function of a particular ecosystem.

1.1.2. What is environmental change?

As demonstrated above, reliable environmental conditions support species, species' interactions, and the ecosystems they live in, so changes to one or more of these conditions can lead to dramatic consequences. The field of ecology has confirmed that numerous biotic and abiotic factors can influence species, and theoretically a change in any of these factors could constitute an environmental change. In practice, however, there are certain factors that have received more attention than others because they themselves have been found to be dramatically changing; they have had a significant effect on particular species, or both. Table 1 reports some of the more common environmental changes that have recently received attention. Since the focus of this paper is on plant-pollinator interactions, I will describe the broad category of environmental changes that have been shown to influence either plants or pollinators.

The introduction of exotic or non-native species into a community is a biotic factor that has resulted in great changes to ecosystems and numerous species within them (Travaset and Richardson 2006; Lopezaraiza-Mikel et al. 2007; Wilke and Irwin 2010). Humans have accidentally, or in some cases knowingly, aided in the transport of exotic plant and animal species to new ranges where they may be free from former competitors and predators, and are therefore able to thrive (Blossey et al. 2001; Schweiger et al. 2010). Some of the most

Table 1. Examples of environmental change factors that are altering plants, pollinators, or plant-pollinator interactions.

Environmental Change Factors	Driver of Change	Literature
Biotic Factors-	<ul style="list-style-type: none"> ○ Biotic Invasion 	<ul style="list-style-type: none"> ○ Wilke & Irwin 2010 (plants); Lopezaraiza-Mikel et al. 2007 (plants & pollinators)
Anthropogenic Factors-	<ul style="list-style-type: none"> ○ Land Use Change ○ Pesticide Use 	<ul style="list-style-type: none"> ○ Winfree et al. 2009 (bees); Kearns et al. 1998 (plants & pollinators) ○ Brittain et al. 2010 (pollinators)
Abiotic Factors-	<ul style="list-style-type: none"> ○ Nitrogen Deposition ○ Atmospheric CO₂ Increase ○ Temperature Increase ○ Precipitation Pattern Alteration 	<ul style="list-style-type: none"> ○ Bobbink et al. 2010 (plants); Zavaleta et al. 2003 (plants) ○ Springer & Ward 2007 (plants); Long et al. 2004 (plants) ○ Hegland et al. 2009 (plants & pollinators); Miller-Rushing & Primack 2008 (plants) ○ Crimmins et al. 2011 (plants); Danforth 1999 (pollinators)

destructive examples of this are exotic plant species that possess the ability to outcompete native plants already established in the community (Schweiger et al. 2010). Such is the case of purple loosestrife (*Lythrum salicaria*), a non-native plant from Eurasia that has invaded North American wetland habitats, thereby altering the structure, function, and productivity of these areas (Blossey et al. 2001). In general, novel plant species establishing in a community can have a negative effect on resident plant species' population dynamics (Wilke and Irwin 2010) by competing for space and resources resulting in decreased diversity. This can lead to changes in existing

networks between resident plants and other species (Lopezaraiza-Mikel et al. 2007) such as birds, mammals, amphibians, and insects (Blossey et al. 2001).

Direct anthropogenic actions can also be considered environmental factors leading to modifications or degradation of ecosystems and the species that reside within them. For example, land-use change has historically, and is currently, a major environmental factor in the destruction of prairies and wildland areas (Kearns et al. 1998; Cane and Tepidino 2001). In paving the way for urban development and intensification of agriculture, natural habitats have undergone changes resulting in loss and fragmentation (Grixti et al. 2009). Urbanization and agricultural practices have fragmented habitats and isolated species, leading to destruction of plant and animal biodiversity (Kearns et al. 1998; Cane 2001; Ahrne et al. 2009; Winfree et al. 2009; Brittain et al. 2010).

Another direct anthropogenic action with ecological repercussions is the use of pesticides in agricultural and urban land management. In recent times, agriculture has amplified its use of pesticides along with other energy inputs in an effort to boost productivity of crops cultivated to feed our growing world population (Kevan et al. 1997). Although pesticides enhance yields of vital food crops for human and livestock needs, they can alter ecosystem functioning and ultimately effect animal species functioning and interactions (Alston et al. 2007; Brittain and Potts 2011). For instance, in an effort to reduce insect and other environmental pests, pesticides have had unintended consequences on other insect species (Brittain et al. 2010). Many of our crops require pollinators in order to set their fruit or seed, therefore, if pollinators are negatively affected by pesticide use (Alston et al. 2007; Kevan et al. 1997), we are not only jeopardizing their existence, but also our own wellbeing (Kearns et al. 1998; Kwaiser et al. 2008; Brittain et

al. 2010). By negatively effecting insect species we also threaten the species higher up on the food chain that feed on these insects (Kendall and Smith 2003).

The final category of environmental changes is related to atmospheric abiotic factors that species are experiencing within their ecosystems. Again, there are a large number of abiotic factors that can affect ecosystems which could be discussed, but I will limit my discussion to those that follow. To begin with, nitrogen deposition from anthropogenic sources and actions has caused changes in ecosystem plant functioning and interactions, thereby stimulating novel interspecies competition and threatening existing plant biodiversity (Bobbink et al. 2010; Zavaleta et al. 2003). Anthropogenic nitrogen deposition occurs through the burning of fossil fuels for energy, and from fertilizer and manure emissions from agricultural fields, among others (Smith and Smith 2006; Bobbink et al. 2010). Eventually all nitrogen emitted into the atmosphere is deposited in terrestrial or aquatic ecosystems, many of which are normally nitrogen limited. In a forest ecosystem, understory forbs and other plants are typically shielded from atmospheric nitrogen deposition effects due to the tree canopy. When nitrogen levels were experimentally increased in a forest ecosystem, interspecific competition was altered. Nitrogen-efficient understory forbs decreased in diversity while an increased dominance of a few nitrophilic plant species replaced them, decreasing biodiversity of plant species in the forest overall (Gilliam 2006). In a similar example, the California grasslands, an area that is normally nitrogen-limited, has undergone an invasion by exotic grass species that are quickly dominating and replacing the native grasses and forbs normally seen. Due to increasing nitrogen deposition from air pollution, native plants are unable to compete with incoming exotics and biodiversity is declining (Weiss 1999). With changes to dominant plant species and alteration of community

structure, animal species will likely feel effects of this change in limited resources available to them.

Several other atmospheric abiotic factors important to bring to light are ozone and ultraviolet radiation. Ozone is a greenhouse gas found within the lower atmosphere that has been acknowledged as an air pollutant (Leisner and Ainsworth 2012). It has been found to be a potent oxidant which can cause a reduction in photosynthesis in certain plants (USEPA 2012; Feng et al. 2008), effectively altering their ability to compete in their habitat (Booker et al. 2009). Ozone exposure at high levels has resulted in respiratory problems in humans, although at present no deleterious effects have been reported in other animals, as studies in this area are lacking (Lovett et al. 2009).

Another abiotic factor, UV radiation, is that portion of the light spectrum emitted from the sun that can provide such beneficial effects as stimulating the skin to produce vitamin D or harmful effects such as decreased photosynthesis in some crop plants (Van et al. 1976; Caldwell and Flint 1994). Increases in the levels of UV-B radiation reaching the Earth's surface has been faulted on depletion of the ozone layer in the stratosphere (Runeckles and Krupa 1994; Caldwell and Flint 1994) potentially leading to effects on humans, animals, and plant species. In humans and animals the effects of solar radiation can be felt in those areas exposed to the sun, mainly the eyes and skin, resulting in cataracts, sunburn, and aging of the skin (Longstreth et al. 1995). In plants, increased UV-B radiation can lead to alterations in plant processes. For example, in a greenhouse experiment on pea (*Pisum L.*), collard (*Brassica*), cabbage (*Brassica oleracea L.*), soybean (*Glycine max L. Merr.*), and oat (*Avena L.*), enhanced UV-B radiation led to reduction in CO₂ uptake ultimately effecting photosynthesis in these plants (Van et al. 1976). Similar results were seen in UV-B radiation studies performed on high latitude tundra and arctic plant

species (Caldwell et al. 1998). In contrast, a temperate latitude conifer species, loblolly pine (*Pinus taeda* L.), showed a decrease in seedlings' biomass, but not necessarily a corresponding decrease in photosynthesis (Caldwell et al. 1998). In some cases it has been argued that in the past unreasonable levels of UV-B radiation have been used in greenhouse and growth chamber experiments affecting scientific results (Caldwell and Flint 1994). Not many studies on the UV-B radiation effects on animals have been undertaken, but it is speculated that they would be very unlikely to feel the effects of elevated UV-B radiation as they would instinctively avoid prolonged sun exposure (Caldwell et al. 1998). Although not particularly affected by UV-B radiation, plant litter decomposition rates are affected by UV-A radiation causing an increase in decomposition and enhanced emission of CO₂ gas into the atmosphere (Ballare et al. 2011).

Select abiotic environmental factors have received more attention recently by science, governments, and the media, in part because they are thought to be more of a threat to humans and natural systems. The three main abiotic factors receiving extra attention recently are warming temperatures, changing precipitation patterns, and rising atmospheric CO₂ levels. Modifications to these environmental factors have been implicated in inducing extraordinary changes in climate conditions worldwide (IPCC 2007). These environmental factors are not only causing changes at the global level, but causing environmental modifications within natural ecosystems, essentially affecting animal species, their interactions, and ultimately ecosystem functioning (Parmesan and Yohe 2003; Parmesan 2006). For the purposes of this paper, I will focus my attention on the environmental changes caused by altered temperatures, precipitation patterns, and atmospheric CO₂ levels. Specifically I will be looking at how these changing abiotic factors may be disrupting the interactions between species, focusing specifically on the

relationship between plants and pollinators. I will begin with an overview of the environmental factors of temperature, precipitation, and atmospheric CO₂ and how they are becoming altered.

Change in our ecosystems is occurring due to altered abiotic factors such as increasing temperatures. Global temperature increases of 0.2°C per decade have been recorded with future warming trends projected to be another 0.1°C to 0.2°C over the next two decades (IPCC 2007). These warming trends are not expected to be evenly distributed across the globe, but may vary from one continent and region to another (Schwartz et al. 2006). Countries in the middle and higher latitudes are expected to see more of a change in temperatures than those closer to the equator within the tropics and subtropics (IPCC 2007). Increases in temperatures have been associated with shifts in the timing of seasons and lengthening of growing seasons (Menzel and Fabian 1999; Dunnell and Travers 2011), having the potential to alter the processes within ecosystems (Menzel et al. 2006; Dunnell and Travers 2011).

Environmental change is expected to not only cause warming of temperatures globally, but to also effect precipitation events and patterns. In certain areas heavy precipitation events have become more commonplace in recent years along with increasing atmospheric water vapor resulting from the warming effects of climate change (IPCC 2007). Precipitation events and patterns are not predicted to be evenly distributed worldwide, but again will vary by region in intensity of occurrences (IPCC 2007). Global precipitation, excluding Antarctica, has increased by 9mm over the 20th century (New et al. 2001) while regions of Africa, Amazonia, and South America are showing a decrease in precipitation (IPCC 2007). Over the past century in the United States there has been an increased frequency of days of precipitation with increased intensity of precipitation events (Karl and Knight, 1998). Rainfall intensification in some regions of the globe could mean a wealth of water for ecosystems, stimulating a boost in primary

plant productivity leading to increased abundance and diversity of species. Increases in the frequency, extent, or duration of precipitation events can also directly impact the functioning of ecosystems causing decreased plant productivity due to area flooding. On the contrary, warmer climates such as the tropics and subtropics have been experiencing longer and more intense drought periods over larger regions since the 1970s (IPCC 2007). Decreases in rainfall amounts or extended periods of drought have the potential to cause loss of species and biodiversity as organisms struggle to survive in parched habitats.

Rising concentrations of CO₂ and other greenhouse gases in the atmosphere have been linked to global changes in our ecosystems (Bazazz 1990). Elevated atmospheric CO₂ levels are already affecting rangeland and agricultural ecosystems by modifying plant growth and developmental processes (Izaurre et al. 2011; Springer and Ward 2007; Long et al. 2004). CO₂ levels are increasing primarily due to two human imposed actions, deforestation and the combustion of fossil fuels. Pre-industrial levels of carbon dioxide were determined to be approximately 280ppm, while recently they have risen to 384 ppm (Levetin and Van de Water 2008). Yearly CO₂ concentration growth rates have been increasing faster in the last decade (1995-2005) than at any other time since atmospheric measurements have been recorded (IPCC 2007). Greenhouse gas emissions, which include CO₂ have increased by 70% between 1970 and 2004 (IPCC 2007). If these emissions continue to rise at the same or increased rates we will witness more intense climate changes in the 21st century than we have in the recent past (IPCC 2007) which will affect our natural ecosystems and the species that reside within them.

1.2. Introduction to Plant-Animal Pollination

There are a multitude of plant species across the Earth, most requiring some mode of pollination. The method of pollination each plant species uses depends upon the environment in

which it lives, its biology, and its life history. Various types of pollination occur such as self-pollination and cross-pollination, as well as the use of multiple pollen vectors. Many flowering plants use animal pollinators as vectors to transport their pollen more efficiently from plant to plant. In this case there is usually a mutualism involved, so the animal vector also benefits from the interaction. Whatever the process or the vector utilized, each method is designed to ensure pollination is a successful endeavor for the plant. In subsequent sections below I will discuss some of the basic types of pollination, the various vectors involved, the diversity of animal pollinators, and the ways in which plants attract and induce animal pollinators to work for them.

1.2.1. Pollination is key to a plant's reproduction

Pollination is a fundamental and essential process in flowering plants' life cycles in a majority of our terrestrial ecosystems. The movement of pollen is just one of the crucial steps in a plant's reproduction that ultimately leads to seed set or fruit production. Pollen is essentially the male gamete of a flower and contains genetic information, thus the movement of pollen allows for the combination of genetic information between two plants of the same species (National Research Council 2007). A flower that does not receive adequate pollen will not produce quality seed or fruit. If seed or fruit has questionable viability, a plant's future success in the community is at risk. It is through the movement of this genetic information that plant generations continue and biodiversity of plant species thrives (Ehrlich and Ehrlich 1992).

1.2.2. Differences in pollination among plants

While not all plants use pollen, plants that produce seeds and fruits fall under the category of angiosperms and gymnosperms, and they reproduce by transferring pollen from the male to female part of flowers using a variety of methods (Raven et al. 2005). A number of plants are self-pollinating, meaning that they can be pollinated with pollen from the same flower

or from flowers of the same plant (Mader et al. 2011). In self-pollinating species, the variety of genetic information passed on to succeeding generations is very limited, many times leading to inbreeding (Mader et al. 2011). Inbreeding can result in lower plant genetic diversity and decreased health, thus predisposing it to stressors (Keller and Waller 2002) such as disease, parasites, and increased herbivory (Ridley et al. 2011). On the other hand, certain plants require cross-pollination or outcrossing with a conspecific plant to achieve their reproductive goals, making the whole process a bit more complex (Mader et al. 2011). In cross-pollination, pollen from the anther of one plant is transported to the stigma of another plant within the same species in order for sexual reproduction to occur. Cross-pollinating plants have various methods they employ to ensure that they become pollinated. In those species that have perfect flowers (male and female parts in the same flower), many times a self-incompatibility mechanism is in place where the ovary will not allow fertilization by pollen of the same plant, such as in the tomato (*Solanum*) and avocado (*Persea*) (Leopold et al. 1975). In other plants, male and female parts may mature at different times obliging the plant to cross pollinate with a different plant. Examples of this are seen in fireweed (*Epilobium*), century plant (*Agave*), and members of the Aster family (Compositae) (Kaufman et al. 1983). In cross-pollinating plants with imperfect flowers, a monoecious condition can exist where both male and female flowers although separate, are on one plant as is the case with corn (*Zea*), squash (*Cucurbita*), or garden cucumbers (*Cucumis*) (Kaufman et al. 1983). A dioecious condition can also exist where one plant contains only male or female flowers, making it necessary for pollen to be transported from one plant to another as in goat's beard (*Aruncus*) and willow (*Salix*) (Kaufman et al. 1983). Ultimately cross-pollination is the most desired condition as it offers the best strategy for plant survival and is the process by which plant species' genetic diversity and overall vigor is

increased (Raven et al. 2005). Through enhanced plant genetic diversity and vigor, ecosystems will be able to develop or maintain biodiversity of species, which may help enable them to withstand impacts from changing environmental conditions.

1.2.2.1. Pollen vectors. Just as there are various methods of pollination leading to reproduction, there are also different ways that pollen is physically transferred between plants. These methods can vary according to the environment and needs of each plant species. A small number of flowering plants use water as an abiotic vector to transport their pollen or sperm cells. Aquatic plants and mosses are good examples of this method (Raven et al. 2005). Other plants such as grasses and pine trees utilize the wind as a means to transfer pollen (Buchmann and Nabhan 1996; Proctor et al. 1996). Typical wind-pollinated plants do not need to waste energy in attracting animal pollinators, so they produce flowers that are small to absent, generate no odor, display little to no coloration, and offer no floral rewards in nectar (Dafni 1992; Proctor et al. 1996). As wind-pollination is not the most efficient method of pollen moving from one plant to another, these plants generally produce copious amounts of pollen to increase the chances of pollen reaching the appropriate target species (Proctor et al. 1996). Although large amounts of pollen are produced in wind-pollinated plants, the disadvantage is that a majority of that pollen does not travel very far from the source plant, which can potentially lead to decreased genetic diversity (Proctor et al. 1996).

In approximately 75% of flowering plant species, animal pollinators interact with plant hosts to become a biotic transfer agent for the movement of pollen (Mader et al. 2011). During pollinator foraging visits, pollen grains containing male gametes become attached to a pollinator's body and are carried and subsequently deposited on the stigma or female part of a plant, facilitating its sexual reproduction. As mentioned earlier, pollinators are essential players

in plant pollination through outcrossing because they assist in dispersing plant genetic material to neighboring plants of the same species (Campbell et al. 1997) thereby increasing genetic diversity. Additionally, pollinators facilitate plants in expanding their conventional ranges by helping them colonize novel areas not easily accessible to plant species.

1.2.2.2. Floral attractants to animals. Plants requiring animal pollinators work to gain their attention and “lure them in” by providing an attractant in the form of showy flowers, fragrant odors, and adequate food rewards (Kevan and Baker 1983), however the exact type of lure depends on the plant species and what pollinator it is trying to attract. Showy floral resources, scents, and rewards are energetically expensive for a plant to produce so plants attempt to attract the greatest variety of efficient and reliable pollinators by providing them with the quality and tasty resources they desire (Kevan and Baker 1983). Animal pollinators are initially lured to their host plants according to specific flower characteristics such as size, color, odor, or shape, and these features determine the kind of pollinator that will likely visit (Buchmann and Nabhan 1996). Once a pollinator visits a flower it’s the quality of the flower’s nectar or pollen rewards that will keep it coming back for more (Kevan and Baker 1983). Bees tend to be attracted to flowers that are blue and yellow colored, with either open or deep shaped flowers that coincide to the length of their respective mouthparts (Proctor et al. 1996). Nocturnal moths that pollinate at dusk or during the night, prefer white or pale colored flowers that emit a sweet scent (Raven et al. 2005). Butterflies are attracted to some of the same flowers as their bee counterparts, but can also feed on flowers possessing long corollas due to the length of their mouthparts or proboscis (Buchmann and Nabhan 1996). Flies are drawn to open bowl-shaped flowers that they can rest and warm their bodies on (Elberling and Olesen 1999) and that release an odor that is fruity or resembles the odor of dung (Proctor et al. 1996). Pollinators are ultimately searching for rewards

that are worthy of their foraging efforts. Pollinators spend much of their time and energy foraging so they are in search of nectar with high sugar content to fuel their bodies and pollen that contains a high percentage of protein for their own metabolic purposes and to nourish their offspring. Floral plants that are able to provide these resources to their pollinators are the ones that will be successful in their reproductive endeavors.

1.2.2.3. Pollinator players in this interaction. As reviewed recently for rangeland systems (Harmon et al. 2011), there are a variety of pollinators both large and small that provide vital pollination services to plants in natural ecosystems and agricultural settings. A number of these pollinators are vertebrates such as the Mexican long-nosed bat (*Leptonycteris nivalis*), a pollinator of the agave or century plant (*Agave*), and the Ruby-throated hummingbird (*Archilochus colubris*), a generalist pollinator of a number of native prairie plants commonly found throughout the Midwest (USDA 2012). Even lizards, rodents, and lemurs make up a percentage of this vertebrate group that seek out flower resources to consume the sweet nectar offered inside (Buchmann and Nabhan 1996). Vertebrates, while important pollinators in their own right, only comprise a small fraction of the number of pollinators that are part of plant-pollinator mutualisms (USDA 2005). By far the most abundant and diverse of all pollinators are the insects (Cane and Tepedino 2001; Winfree et al. 2009). Bees and butterflies are considered to be the most efficient and well-studied of all pollinators, therefore for the purposes of this paper I will direct my attention to these species.

The honey bee (*Apis mellifera*) is the insect pollinator that is familiar to most people as these imports from Europe are commonly employed as a managed pollinator for agricultural crops (Kremen et al. 2002) and raised for the honey and beeswax they can provide. Although domesticated honey bees are used widely, they are not as efficient as some other insects in

pollinating certain crops and many native plants (Kearns and Inouye 1997). Despite their importance to humans, honey bees are also just one type of bee species important for pollination. Unlike the honey bee, bumblebees (*Bombus*) are very proficient at their job using buzz pollination to vibrate the anthers of flowers liberating the pollen grains within the sacs (Goulson 2003). Additionally, solitary bees such as the alkali bee (*Nomia melanderi*), a native pollinator of lotus (*Nelumbo* Adans.) and locoweed (*Oxytropis* DC.) in the western United States, is a very efficient pollinator, able to effectively pollinate up to 2,000 of these flowers daily (Buchmann and Nabhan 1996). Conversely, honey bees have an aversion to tripping the specialized pollination mechanism in lotus and locoweed and many times will pierce the base of the flower to rob the nectar inside, thereby side-stepping pollination (Kearns and Inouye 1997).

Butterflies are also commonplace pollinators in native ecosystems. For instance, the California Bay Checkerspot butterfly (*Euphydryas editha bayensis*), a native species and known to be endangered, thrives in native range habitats of the California annual grasslands (Weiss 1999). Monarch butterflies (*Danaus plexippus*), easily recognizable by their eye-catching coloration and size, are an enormously popular breed in the public's eye, being the focus of many studies and monitoring programs and having the designation of state insect or butterfly for many of our states across the nation (Commission for Environmental Cooperation 2008). What adds to their popularity is their uniqueness in being migratory travelers that trek hundreds of miles across numerous states and provinces on their fall and spring journeys. Of the two migrations of Monarchs that occur within North America, the western Rocky Mountain migration extends as far north as British Columbia, Washington, and Oregon in the spring (Commission for Environmental Cooperation 2008), and as far south as California and Mexico in the winter. The Monarch's nomadic inclinations are in an effort to find milkweed, the only plant on which their

growing larvae feed. Adult Monarchs are more generalist in their diet so they are able to feed on a wide variety of plant nectars.

Closely related to butterflies and within the order Lepidoptera, moths also make important contributions as pollinators. For example the yucca moth (*Tegeticula* and *Pronuba*), originating in the southwestern United States, possesses a specialized relationship with the yucca plant (*Yucca*), as one species cannot survive without the presence of the other (Pellmyr et al. 1996; National Research Council 2007). The yucca moth deposits her eggs within the yucca flower where the larvae that hatch out can obtain nourishment from the flower's seeds and develop in a safe place free from predators. Subsequently, during this process the yucca moth efficiently pollinates the yucca plant ensuring its continued existence as well.

There is a vast diversity of pollinators in ecosystems, and although many do not receive the attention given to bees and butterflies, they can nonetheless be important pollinators to certain plants. For example, beetles are known to be important pollinators, having over 30 species that perform pollination services, native poppies in natural areas being one example (Schneider and Nichols 1984). Flies as pollinators have been found in abundance in higher elevations and colder climates where harsher conditions cause other pollinators such as small solitary bee species to be scarce (Kearns 2001; Totland 1993). Wasps and ants are also considered to be pollinators of native plants, but unlike their close relative the bee, they are not as efficient in their role (National Research Council 2007). These insects have relatively hairless bodies and lack pollen carrying structures, so it is mainly by accident that while they are sipping on nectar they inadvertently cross-pollinate the flower they are visiting (National Research Council 2007).

1.2.3. Pollination is key to a pollinator's reproduction

Pollination is not only key to a plant's reproduction, but it is also critical to pollinator life cycles. Some insect pollinators, like ants, are generalists and tend to use pollen as only part of their diet. However other species, especially bees, rely on the plants they pollinate for almost all their nutritional resources. Pollinators predominately visit flowers for one simple reason: to obtain food. Flowers provide food to pollinators in the form of pollen and nectar. Pollen is one of the main provisions gathered on most bee foraging trips, and is not only used for provisioning natal nests, but also eaten by female bees that are producing eggs (Michener 2000). In a few cases adult butterfly, fly (syrphids), and beetle species may eat pollen, but for the most part pollen is gathered by adult bees to provision their nests and ultimately provide food for young larvae. Within each pollen grain there is a vast array of substances such as carbohydrates, proteins, fats, vitamins, minerals, amino acids and enzymes, each playing an essential role in pollinator diets (Dafni 1992).

Nectar is a finite product produced by a flower until the plant is fertilized or the flower dies (Raven et al. 2005). Nectar is one of the rewards offered to pollinators with the chance that while it sips the sweet liquid nutrition, the plant in turn receives pollination. While some plants produce a greater number of flowers and hence more nectar, other flowers are themselves exceptional nectar producers, these tend to be pollinated by animals such as birds and bats (Raven et al. 2005). Flower nectar is mainly made up of the sugars sucrose, fructose, and glucose and is therefore a quick source of energy for pollinators, some species such as butterflies relying on this as their only food source as adults (Proctor et al. 1996). Other pollinators, such as bees, will mix it together with pollen to provide as food resources for their growing offspring.

1.2.4. Pollination in economical and ecological terms

Pollination is essential to the crops we grow for our food and to the sustainability of our natural ecosystems, and it is therefore important from an economic as well as an ecological standpoint. In economic terms, insect pollination provides valuable services that increase crop productivity and yield for food resources that humans are contingent upon (Kevan and Phillips 2001; Kremen et al. 2002; Klein et al. 2007). Concerning crops for human consumption, pollinators contribute \$153 billion to the production of human food worldwide (Gallai et al. 2009), 35% of these crops requiring animal pollination (Klein et al. 2007). Ultimately plants are used by humans and animals for seeds, fruits, and vegetables that they can obtain. Humans also use plants and their products in the manufacturing of foods, fiber, drugs, and fuel used in their lives every day (National Research Council 2007).

In ecological terms, insect pollination services help to support plants and therefore food webs within natural ecosystems resulting in sustaining and promoting plant biodiversity leading to enhanced habitat for wildlife communities (Gilgert and Vaughan 2011). With enhanced biodiversity of plants and animals in these communities recreational, fishing, and hunting opportunities abound for all to enjoy.

In supporting a diverse plant community, ecosystems further benefit in the practical services provided to them such as water filtration, soil development, flood mitigation, carbon sequestration, and erosion control (National Research Council 2007; USDA 2012). Native bees use these diverse ecosystems for nesting, overwintering, and foraging resources and are able to provide enhanced pollination services to adjacent agricultural croplands. Their pollination services supplement honey bee pollination and can hedge against recent honey bee shortages (Losey and Vaughan 2006; Chaplin-Kramer et al. 2011). Furthermore, healthy diverse

ecosystems can provide the aesthetic, cultural, and spiritual values that many humans desire in offering them the opportunity to connect with nature.

1.3. What is Phenology?

Phenology is the study of the timing of life cycle events that can change according to season or climate conditions (Forrest and Miller-Rushing 2010). For centuries amateur naturalists and outdoor enthusiasts have intentionally or unintentionally followed the timing of spring phenological events such as the arrival of migratory bird species, the date of the lake ice breakup, and also the first flowering dates of plants. Phenology is regulated by a variety of environmental cues which can be different for plant and animal species and differ within plant-animal interactions. Photoperiod, temperature, soil moisture, precipitation, and timing of snowmelt are some of the cues that have the potential to influence the phenology of plants and animals.

Presently environmental change is displaying various forms. These changing environmental conditions have the potential to not only affect functioning at the ecosystem level, but also at the individual organism level in interactions that are shared between species (Sparks and Menzel 2002; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Phenological shifts in relation to changing environmental factors has become a popular and well studied subject (Beebee 1995; Myneni et al. 1997; Crick and Sparks 1999; Peñuelas et al. 2002), with a particular focus on flower phenology (Bradley et al. 1999; Fitter and Fitter 2002; Bai et al. 2011; Grab and Craparo 2011). For the purposes of this review I will be focusing on environmental change as influenced by alterations in temperatures, precipitation patterns, and atmospheric CO₂ levels along with their ultimate effects on the phenology of plants, pollinators, and their interactions.

CHAPTER 2. FLOWERING PHENOLOGY

2.1. Evidence for Change in Flowering Phenology Across Time

The timing of flower bloom is a critical stage in a plant's life cycle and it is sensitive to climate fluctuations, such as variation in temperature or precipitation. Variations in the cues of temperature and precipitation have been linked to climate change as increasing levels of CO₂ and other greenhouse gases in the atmosphere are affecting weather patterns globally (IPCC 2007). With increases in temperature, some areas are seeing a noticeable trend toward an advancement of seasonal phenophases, particularly spring, starting around 1985 (Badeck et al. 2004). As discussed below, there is increasing concern that these changes have resulted in subsequent shifts in the flowering times of some plant species.

It is difficult to quantify long-term ecological changes, especially when a particular question or concern is only fairly recent. Fortunately, there have been some opportunities to continue or re-establish data sets of the first flowering dates for a number of plant species. Many people have enjoyed tracking changes in plant flowering phenology, as plants are very sensitive to changes in seasonal climate patterns and flower bloom times are easily observable in nature. Past observations made by such naturalists as 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-19th century (Willis et al. 2008; Miller-Rushing and Primack 2008), among others, have given us valuable records of first flowering dates. Although these records were originally taken to discern the changing of the seasons, in particular the coming of springtime, we can take advantage of these extended data sets to observe how flowering phenology has changed across species in a given location. In the next section I will address the potential

reasons for these changes by focusing on the environmental cues used by plants to determine flowering time, but in this section I will focus on the evidence that flowering time has changed.

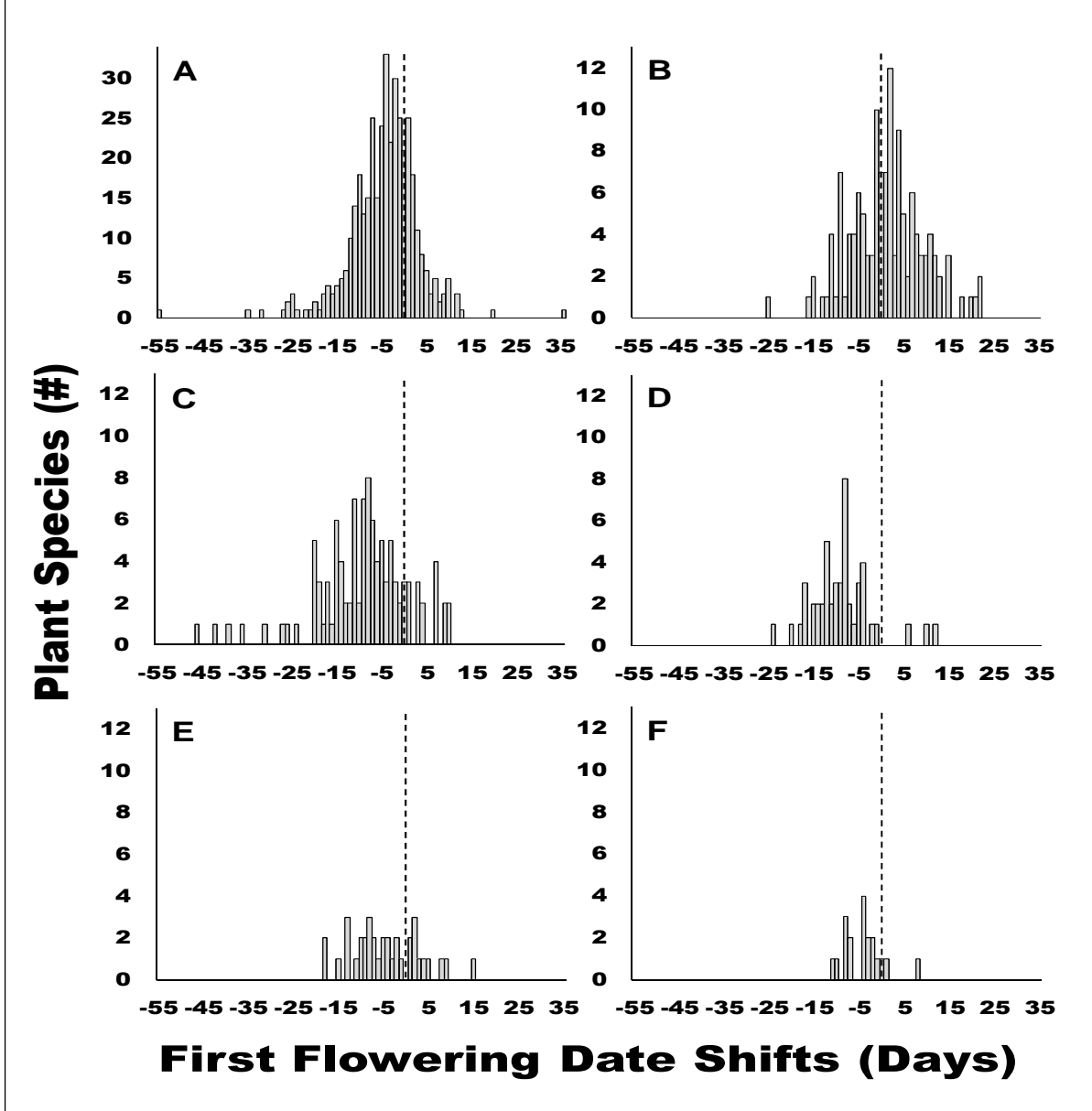
I obtained six studies that quantify the change in first flowering date for multiple plant species in a given location (Table 2). I use these studies to better understand the distribution of changes observed across species at a given location and also across communities of plant species in different locations.

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

Phenology Articles	Species	Years of Study	Analysis	Location & Latitude
Fitter & 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
Bradley et al. 1999	55	1936-1998	Regression	WI, USA; 43.5°N
Bai et al. 2011	48	1963-2007	Regression	Beijing, China; 39.9°N
Cook et al. 2008	19	1928-2002	Regression	NY, USA; 41.8°N

Each panel shows the number of species that were reported to have changed their first flowering date by a given amount. Data was rounded to the nearest day and is binned by day such that bars indicating a change of 2 days are those species that changed by 1.5 days to 2.49 days. Negative values indicate an earlier flowering date now compared to historical information. A dashed line was added to each panel to emphasize the point where there was no change in flowering date. The data in each panel corresponds to the results from a particular study: A) Fitter and Fitter 2002, 385 total species shown; B) Dunnell and Travers 2011, 178 species;

Figure 1. The distribution of phenological changes in first flowering dates for plant species across six different studies.



C) Abu-Asab et al. 2001, 100 species; D) Bai et al. 2011, 48 species; E) Bradley et al. 1999, 55 species; F) Cook et al. 2008, 19 species. Note that because the Fitter and Fitter study provided data from so many more flowering plant species it is shown on a different y-axis than the other studies. There are a number of differences across these studies (Table 2), including how the data was analyzed and presented. To make it easier to compare data across the different studies, I

wanted to find a single number, in days, that indicates the change in flowering phenology for a given species and then use that information to calculate a frequency distribution of changes in flowering phenology (as in Fitter and Fitter 2002). The data was presented in this way for those studies that used the “subtraction” technique (Fitter and Fitter 2002; Dunnell and Travers 2011). With these studies, the authors take the average flowering date for some period of time in the past and then find the difference with an average flowering date for a more current time period. For one of these studies (Dunnell and Travers 2011), I calculated the average flowering date for the most recent period and found the difference. The other studies I used (Bradley et al. 1999; Abu-Asab et al. 2001; Cook et al. 2008; Bai et al. 2011), all looked for changes in flowering phenology by performing a linear regression over time and reporting the slope of that analysis. To make the comparison with the other studies, I multiplied the reported slope from these studies 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 the regression analysis.

The result is six histograms that demonstrate the distribution of changes in flowering phenology across the plant species of these six studies (Figure 1). These figures indicate that for almost all of the studies there is a bias towards more species flowering earlier now than they did during previous records. However, it is extremely important to point out that this trend is not universal. Many of the observed plants are flowering at about the same time as they did in the past or even later than they did previously.

Other studies have reported similar patterns in flower timing in response to recent environmental change (Inouye et al. 2003; Gordo and Sanz 2008; Crimmins et al. 2010; Lesica and Kittelson 2010; Crimmins et al. 2011). These patterns have been predominantly earlier in north and south (Stenseth and Mysterud 2002; Grab and Craparo 2011), with higher latitudes

having a stronger selection to flower earlier (Munguía-Rosas et al. 2011). Some of the observed variation in flowering shifts may be due to the fact that Figure 1 is looking at patterns across time, and not direct correlations with causal environmental factors such as temperature which will also fluctuate from year to year. An additional explanation may come from species-specific responses to any environmental cues that have been changing locally. Both of these explanations to the observed variation suggest that it may be extremely helpful to better understand what environmental cues plants use to determine first flowering date and what evidence there is for changes in those cues leading to changes in flowering phenology.

2.2. Environmental Cues Regulating Flowering Phenology

Plants acquire signals from local environmental cues that prompt them to shift their physiological processes from a focus on growth to that of flowering. Since plants have to balance the time and resources required for different processes, growth and subsequent reproduction cannot both go on forever, but instead must correspond to favorable seasonal conditions such as adequate sunlight, temperature, precipitation, and in some instances pollinators.

Plant phenology is the timing of a plant's life cycle events such as germination, growth, flowering and fruiting, and seed production. The timing and success of each of these stages can be influenced by changing environmental factors (Table 3). However, for the purposes of this paper, I am primarily interested in the timing of the flowering phase.

Flowering and reproduction can be considered the most significant chapter in the plant's life cycle because a plant's primary purpose in life is passing its genes onto successive generations. Since flowering is just one step in the plant's life cycle, a change in the timing of one part of this cycle could influence the timing of flowering, for example a plant that has not

matured enough to flower. Therefore it may ultimately be useful to think of many parts of the plant's life cycle, but for the purposes of this review I will focus on the flowering phase itself.

Flowering is the stage in a plant's reproduction when it is in anthesis or blooming and it is able to be pollinated. The timing of a plant's flowering phase is crucial, as taking advantage of optimal environmental conditions can mean the difference between reproductive success or

Table 3. Examples of the environmental factors that can influence the various stages of a plant's life history.

Plant Life Stage	Influencing Environmental Factor
Seed-	<ul style="list-style-type: none"> ○ Temperature & Moisture (Leopold & Kriedemann 1975)
Germination-	<ul style="list-style-type: none"> ○ Light (Hart 1988) ○ Water initiates germination (Wester 1995) ○ Temperature(Kaufman et al. 1983)
Growth-	<ul style="list-style-type: none"> ○ Forbs-(Lambers et al. 1998) ○ Bulbs- Temperature, not Photoperiod (Tooke & Battey 2010) ○ Grasses- Photoperiod, Temperature & Precipitation (Tooke & Battey 2010) (Epstein et al. 1997) ○ Trees- Precipitation & Temperature (Opler et al. 1976) ○ Optimal growth between 0° C - 40° C (Went 1953)
Flowering-	<ul style="list-style-type: none"> ○ Photoperiod (Leopold & Kriedemann 1975) ○ Photoperiod & Temperature in Temperate Regions (Dunnell & Travers 2011) ○ Photoperiod & Precipitation in Arid Regions (Fischer 1978)
Senescence-	<ul style="list-style-type: none"> ○ Photoperiod & Temperature (Leopold & Kriedemann 1975;Smart 1994)

failure for a species. There are external factors aside from environmental conditions that can influence a plant to flower at a particular time. A plant may time its growth and flowering early in the growing season in order to get a competitive advantage over other plants in the immediate vicinity. A plant can time its flowering to be in synchrony with a neighboring plant to enhance the attractiveness of the combined floral resources increasing the likelihood that both will be pollinated (Rathcke and Lacey 1985). In another example, a dense and diverse flowering plant community can increase the diversity and identity of pollinators that visit a neighboring co-flowering plant (Lazaro et al. 2009). Interactions with animals can also influence flowering. For example, a plant under attack by insect (Bishop 2002; Takahashi and Huntly 2010) or animal herbivores (Augustine and Frelich 1998; Brys et al. 2011) may delay or abandon its flowering altogether due to loss of vegetative mass or stress.

A plant's blooming period is also sensitive to environmental cues. Many of the previously discussed environmental variables undergoing change can influence this timing. For example, resource availability in the form of soil quality and essential nutrients can help determine a plant's overall fitness and the timing of a plant's reproduction (Kaufman et al. 1983). Additionally, within plant communities, the presence of invasive plant species, herbivores, and parasites increases interspecies' competition and may force plants to alter their flower phenology in order to survive (Rathcke and Lacey 1985; Wilke and Irwin 2010).

However, there are three primary environmental cues that are thought to have the broadest influence on flowering times: photoperiod, temperature, and precipitation (Rathcke and Lacey 1985). Below I briefly introduce how each of these environmental cues can influence flowering phenology.

2.2.1. Photoperiod as an environmental cue for flowering

One of the chief external determinants of flowering phenology is photoperiod. Photoperiod influences the flowering response at least partially by the ratio of lightness to darkness in any 24 hour period (Hart 1988). Photoperiod is not only important to flowering, but also in determining many plant life cycle phases such as stem elongation, fruit development, autumn leaf drop in deciduous trees and shrubs, development of winter dormant buds, formation of bulbs and tubers, and development of cold hardiness (Raven et al. 2005). Plants use photoperiod as a means to measure day length and the changing of seasons in order to keep certain physiological processes in synchrony with their environments. The length of uninterrupted darkness of each day is the actual determinant that stimulates plants to flower (Hamner and Bonner 1938).

Plants respond to photoperiod in various ways, but all responses are based on a critical day length, with some plants flowering in response to a short-day length, others a long-day length, and still another group of plants being day-neutral in their response (Garner and Allard 1925; Raven et al. 2005). Short-day length plants such as some tropical species (Opler et al. 1976), strawberries (*Fragaria*), chrysanthemums (*Chrysanthemum*), and ragweed (*Ambrosia*) require light periods of less than a critical upper limit, having a tendency to flower in the early spring or fall (Raven et al. 2005). Even though seasonal changes in day length may be minor in tropical locales, plants growing in these regions do respond to the small changes in photoperiod evident at those latitudes. On the other hand, long-day length plants such as *Arabidopsis* (Ausin et al. 2005) and alfalfa (*Medicago*) (Major et al. 1991) tend to flower in the summer and require light for periods that are longer than a lower limit of critical day length. Late summer and fall blooming species tend to be more closely associated to photoperiod than any other

environmental cue or trigger (Jackson 1966). Day-neutral plants such as some tropical species (Opler et al. 1976), sunflower (*Helianthus*), and maize (*Zea*) (Raven et al. 2005) take their cues to flower from environmental stimuli other than photoperiod. Certain plants require multiple combinations of day length requirements such as long-short-day length and short-long-day length in order to flower.

2.2.2. Temperature as an environmental cue for flowering

Another environmental factor working in conjunction with photoperiod and influencing flowering phenology is temperature. Germination, fertilization, maturation, along with flowering is typically controlled by environmental temperature (Henderson et al. 2003). In a number of plants flowering is initiated following a period of adequate warm temperatures along with days that are free of frost that can harm new vegetative tissue. For example, in temperate and alpine environments flowering is timed to coincide with warmer temperatures in order to ensure that plants will not flower prematurely while snow is still present (Forrest and Thomson 2010).

Increasing daily temperatures acts as a stimulus to those flowering plant species that are characteristically spring and early summer bloomers (Jackson 1966) such as Red-osier dogwood (*Cornus sericea* L.) (Smithberg and Weiser 1968) a temperate woody species, (Reader 1983) and perennials (Van der Pijl et al. 1972) that take their signal to flower from warming temperatures. Annual plant species generally have an advantage as they start their growth early in the spring, yet even in a deciduous forest habitat with increased light and moisture availability annual plant growth cannot be initiated if colder temperatures persist (McKenna and Houle 2000). Arctic-alpine plants distributed across wide latitudinal ranges can have varying ecotypes that grow and flower under differing temperatures and photoperiods (Mooney and Billings 1961). In contrast, some plants need to experience a temperature-photoperiod interaction where exposure to colder

temperatures in the winter incites spring plant growth eventually leading to flowering during the critical day length (Chouard 1960). From time to time site locality and exposure (Jackson 1966) together with lower seasonal temperatures (Totland 1997a and 1997b) may lead to an actual delay in reproduction and flowering phenology.

2.2.3. Precipitation as an environmental cue for flowering

Water provides a vital resource for plants and in many instances precipitation or lack thereof supplies the environmental cue for flowering. Trees established in Brazilian Atlantic rain forests (Morellato et al. 2000) and other neotropical plants typically bloom during the rainy season (Croat 1975). If a second rainy period follows the dry season some tropical species take the opportunity and flower a second time (Croat 1975; Opler et al. 1976; Alvim et al. 1978; Fischer 1978; Hodgkinson and Quinn 1978; Putz 1979). Many trees and shrubs in the tropics go through a dormancy period during dry times, resuming reproduction only when they receive the stimulus from rainfall (Daubenmire 1974; Opler et al. 1976; Valdez-Hernandez et al. 2010). In certain cases the occurrence of rainfall releasing plants from water stress is the stimulus necessary to initiate flowering, such as in coffee (*Coffea* L.) (Went 1957) and other tropical trees (Borchert 1983). In other cases, erratic rainfall events in arid and semi-arid environments can hinder anthesis, leading to decreased plant productivity and seed-set (Fischer and Turner 1978, de Dios Miranda et al. 2009). In alpine environments, plants tend to flower earlier, sometimes even during late winter in cold conditions or under the snow (Rathcke and Lacey 1985, Galen and Stanton 1991). Timing of first flowering is actually determined by timing of snowmelt for *Mertensia fusiformis* (Forrest and Thomson 2010) and *Androsace septentrionalis* (Inouye et al. 2003). Deciduous trees in temperate climates time their flowering with the dry season, prior to leaf development so that their wind dispersed pollen can be distributed easily (Clark 1893;

Robertson 1895; Grainger 1939). For the same reason, wind pollinated trees in tropical climates flower during the dry season after they have lost their leaves (Frankie et al. 1974; Opler et al. 1980; Foster 1982).

2.3. Evidence and Consequences of Environmental Change to Flowering Phenology

In the previous sections I illustrated some of the evidence that flowering phenology for some species has been changing over time, and I have introduced the idea that there are three environmental cues that are known to be the most prominent influence of flowering time in different plant species. In the following sections, I look for the evidence that changing environmental cues may be directly linked to changes in flowering phenology. Since photoperiod is not strongly influenced by climate change, I do not refer to that as an environmental cue, but instead focus on temperature and precipitation, as well as CO₂. While CO₂ is not normally considered one of the primary environmental cues influencing flowering time, there is some evidence that changing CO₂ concentrations can influence flowering time as well.

2.3.1. Flowering phenology response to temperature change

Plants respond to temperature as an environmental cue and changes in temperatures within a locality have the potential to alter the flowering phenology of a plant. Recently increased average global temperatures of 0.2°C per decade have been recorded with future warming over the next two decades projected to be another 0.1°C to 0.2°C (IPCC 2007). These “warming trends” have not been evenly distributed across the globe, but are varying from one continent and region to another (Schwartz et al. 2006), with some areas actually experiencing a tendency toward cooling.

Even though the global warming trends may seem relatively minimal so far, recent reviews have reported a general advancing of plant and animal species phenology associated with temperature increases (Fitter and Fitter 2002; Penuelas et al. 2002; Parmesan and Yohe 2003; Menzel et al. 2006; Bertin 2008; Tooke and Battey 2010). Spring flowering phenophases are becoming earlier mainly due to the effects of climate change and increased early spring temperatures in regions of North America (Bradley et al. 1999; Schwartz and Reiter 2000; Abu-Asab et al. 2001), Europe (Fitter and Fitter 2002; Ahas et al. 2002; Menzel et al. 1999 and 2006), the Mediterranean (Gordo and Sanz 2010), Australia (Hovenden et al. 2008), China (Zheng et al. 2006), and Japan (Kudo et al. 2004), but regional trends also exist. Flowering phenology of trees such as the apple (*Malus* Mill.) (Penuelas et al. 2002), pear (*Pyrus* L.) (Grab and Craparo 2011), and Japanese cherry (*Prunus serrulata* L.) (Abu-Asab et al. 2001; Miller-Rushing et al. 2007) is earlier due to advancement of the spring season. At present cherry trees in Japan are flowering earlier than any other time in the past 1,200 years due to temperature increases associated with urban development (Primack et al. 2009). Cherry trees of the Washington, D.C. area have also been found to bloom 2.4 days earlier than 30 years ago (Abu-Asab et al. 2001). Lilac (*Aubrieta*), grape (*Vitis* L.), and apple (*Malus* Mill.) flower phenology has advanced by 2-8 days in the northwestern region of the United States (Wolfe et al. 2005). In addition, spring flowering succulents growing in the southwestern United States have been found to be influenced by warmer spring temperatures (Crimmins et al. 2010).

Changing temperature is often the main environmental factor associated with changes in the timing of seasons. Spring phenology has been found to be advancing more consistently than summer or autumn timing (Bradley et al. 1999; Menzel and Fabian 1999; Fitter and Fitter 2002; Penuelas et al. 2002; Walther et al. 2002; Gordo and Sanz 2005 and 2010; Wolfe et al. 2005;

Menzel et al. 2006; Miller-Rushing et al. 2007) with spring flowers tending to bloom earlier and end of season flowers tending to bloom later (Dunnell and Traverse 2011; Sherry et al. 2011). In certain cases there are plant species that are not advancing their bloom dates at all (Bradley et al. 1999; Willis et al. 2008; Lesica and Kittelson 2010; Dunnell and Traverse 2011). Species that are not advancing in response to environmental change may be those that receive their flowering signals from other cues such as photoperiod or precipitation. This lack of plasticity in their makeup may lead to diminished fitness over time. In fact, one study conducted on the east coast of the US observed that a number of plant species lacking plasticity in response to local temperature changes have been decreasing in abundance (Willis et al. 2008).

Not only has the timing of spring been changing recently, but the growing season has been lengthening in the Northern Great Plains over the past three and a half decades (Dunnell and Traverse 2011), demonstrating a 12 day increase in North America and an 18 day increase over the past two decades in Eurasia (Penuelas and Filella 2001). Lengthening of the growing season by an average of 10.8 days in Europe has been attributed to temperature increases related to climate change (Menzel and Fabian 1999). A longer growing season may ultimately lead to changes in flowering time as well if the right resources are available longer or at different times.

2.3.2. Flowering phenology response to precipitation change

Changes in the pattern of precipitation events can affect the phenology of flowering of plants in causing modifications to typical bloom periods. Alterations in precipitation patterns can affect amount of snowfall or snowpack witnessed in a given year and can influence snowmelt dates and subsequently flower timing of alpine plants (Inouye et al. 2003) and plants growing in northern latitudes (Post and Stenseth 1999). For example, reduced winter snow amounts along with deficient snowpack led to premature exposure of the subalpine early

blooming perennial two lobe larkspur (*Delphinium nelsonii*) to severe cold temperatures and conditions of early spring, delaying its flowering (Inouye and McGuire 1991). Additionally, spring flowering was advanced and bloom time lengthened in plant species in Norway after warm and wet winters (Post and Stenseth 1999). Earlier snowmelt along with higher precipitation amounts the previous year in the Rocky Mountains of North America advanced the flowering of the glacier lily (*Erythronium grandiflorum*), an early spring blooming alpine plant (Lambert et al. 2010).

Precipitation increases can advance the flowering phenology of plants growing in semi-arid grasslands in the western US. Presently, advances that are being witnessed in these regions are occurring at a faster rate than humid-temperate areas, as precipitation is an important driver in xeric regions (Lesica and Kittelson 2010). The desert and montane flowering plant species found within the southwestern US are particularly influenced by monsoon rains that commonly occur during the month of July (Crimmins et al. 2010). In addition, high levels of autumn precipitation in semi-arid regions are associated with an advance in spring flowering the following year, whereas a decrease in autumn rainfall can result in a delay in spring flowering phenology (Crimmins et al. 2008; de Dios Miranda et al. 2009). In unusual cases, water stress has been found to be an important determinant of flower induction, with an increase in water actually inhibiting flowering (Bernier et al. 1981 and 1985).

2.3.3. Flowering phenology response to CO₂ increase

With rising concentrations of CO₂ in our atmosphere, this greenhouse gas has become an environmental cue triggering growth in terrestrial plants. Plant growth and productivity is affected not only by changes in temperature and precipitation that accompany environmental change, but also increases in CO₂ levels in the atmosphere (Hughes 2000). Unlike temperature

and precipitation, CO₂ is increasing at a similar rate across the globe (Tans et al. 1990), acting as an "atmospheric fertilizer" with the potential to affect both wild and agricultural plants alike (Springer and Ward 2007).

Changing levels of CO₂ may influence flowering timing indirectly by changing other aspects of plants. In general, photosynthetic rate can increase as well as water use efficiency in plants exposed to higher levels of CO₂ (Wand et al. 1999) resulting in an increase in vegetative mass. Species composition can be modified due to the varying responses of plants to increasing levels of CO₂, potentially changing the structure and function of a community (Hovenden and Williams 2010). However, rising levels of atmospheric CO₂ are not influencing all plants in the same manner. CO₂ in some cases has been found to have no significant effect on reproductive growth (Wagner et al. 2001), but the maturity time to flowering is reduced (Reekie et al. 1994; Ellis et al. 1995). Changes in reproductive factors such as the quantity of flowers (Erhardt and Rusterholz 1997; He and Bazzaz 2003), nectar (Lake and Hughes 1999; Rusterholz and Erhardt 1998), or pollen (Levetin and Van de Water 2008) can also be altered due to the climate effects of rising atmospheric CO₂.

Flowering phenology can be directly shown to change due to the effects of increasing CO₂ in the atmosphere. In some cases CO₂ increases alone were found to alter flowering phenology through an acceleration in the growth rate of American pokeweed (*Phytolacca americana*), a perennial herb (He and Bazzaz 2003) and common hedgenettle (*Betonica officinalis*) (Rusterholz and Erhardt 1998) causing them to flower earlier. In a meta-analysis done by Springer and Ward (2007), 80% of all crop species studied showed advancement in flowering with rising CO₂ levels. For example, in annual crop species such as barley (*Hordeum vulgare*) and rice (*Oryza sativa*) flowering accelerated under increasing CO₂ (Springer and Ward

2007). However, in previous research studies sorghum (Ellis et al. 1995; Cleland et al. 2006) and rice (Cleland et al. 2006) species have displayed delays in flowering due to elevated CO₂ showing that results can vary from one study to another.

Some plants only demonstrate a change in phenology when CO₂ is combined with other environmental cues. Bird's-foot trefoil (*Lotus corniculata*) accelerated its flowering times when exposed to elevated CO₂ levels and increased temperatures, but delayed its flowering when CO₂ was combined with drought conditions (Carter et al. 1997). Plants that are normally cued to flower by photoperiod have altered their flowering dates in response to changing CO₂ levels. Earlier flowering plant species tend to be more responsive to changes in the environment than later flowering species (Fitter and Fitter 2002), but this is not always the case. In Asteraceae, early-flowering species' bloom times were accelerated when exposed to elevated levels of CO₂, whereas late-flowering Asteraceae species did not significantly advance their timing under the same conditions (Johnston and Reekie 2008). When CO₂ was combined with increased temperatures, the same effect was found (Johnston and Reekie 2008). Canada cocklebur (*Xanthium canadense* Mill.), another plant in the Asteraceae family and an annual cued by photoperiod was not affected by increased CO₂ levels (Kinugasa et al. 2003). Giant foxtail (*Setaria faberii*) has shown a consistent delay in flowering due to increased CO₂ across many studies (Garbutt et al. 1990; Reekie and Bazzaz 1991; Springer and Ward 2007). Recent studies have provided similar results of no response of many wild plant species to elevated CO₂ (Curtis et al. 1994; Garbutt and Bazzaz 1984; Garbutt et al. 1990; McConnaughay et al. 1993; Farnsworth and Bazzaz 1995; Jablonski 1997; Case et al 1998; Rusterholz and Erhardt 1998; Cleland et al. 2006; Rogers et al. 2006; Råmo et al. 2006).

Future environmental change is expected to occur due to the combined effects of temperature variations, alterations in precipitation patterns, and atmospheric CO₂ increases. Studies on plant phenology have attempted to simulate the effects of these environmental factors on the timing of flowering, but researchers have obtained varying results. In one example, application of warming or simultaneous application of warming, drought, and elevated CO₂ resulted in advancement in flowering in grassland composed of grasses, forbs, and legume species (Bloor et al. 2010). On the other hand, in the same study drought and CO₂ increases alone did not significantly advance flowering (Bloor et al. 2010). In a study by Cleland et al. (2006), advanced flowering in grasses was witnessed due to increased temperatures associated with climate change, but demonstrated delayed flowering under elevated CO₂ (680 ppm) alone; simultaneous increases in CO₂ and temperature resulted in no advance in flowering dates. In Bird's-foot trefoil, temperature increase advanced flowering by 7 days and CO₂ increase alone advanced flowering time by 5 days, but the two environmental factors together compounded the affect by advancing flowering by 16 days (Carter et al. 1997). CO₂ and precipitation together can have varying affects on flowering phenology. Plants grown under drought conditions along with increased CO₂ advanced their flowering times, but elevated CO₂ levels did not advance flowering times under saturated conditions (Carter et al. 1997). In southern latitudes, the interaction between increased temperatures and CO₂ in an Australian native temperate grassland resulted in no acceleration in flowering (Hovenden et al. 2008).

Under rising atmospheric CO₂ levels, C₃ plants continue to increase their photosynthetic rate whereas C₄ species generally have only a minimal response. In a study of four C₃ plant species, common groundsel (*Senecio vulgaris*) and annual bluegrass (*Poa annua* L.) advanced first flowering dates under elevated CO₂ levels compared to ambient CO₂, whereas hairy

bittercress (*Cardamine hirsuta* L.) and corn spurry (*Spergula arvensis* L.) did not respond to artificial CO₂ increases (Leishman et al. 1999). In past research C₃ plant species have been documented to be more responsive to elevations in CO₂ levels than C₄ species (Poorter and Navas 2003), but apparently this does not always translate to an advancement in reproduction (Jablonski et al. 2002). In another study of five annuals, redroot amaranth (*Amaranthus retroflexus*), a C₄ plant flowered significantly earlier with increased CO₂ levels while giant foxtail, also a C₄ species, flowered later (Garbutt et al. 1990). Two other C₃ annuals in this study, velvetleaf (*Abutilon theophrasti*) and annual ragweed (*Ambrosia artemisiifolia*) did not advance their flowering significantly demonstrating that C₃ and C₄ plant species growing in the same community may not have a similar response to changing CO₂ in the atmosphere.

2.4. Conclusions on Flowering Phenology

It is clear that at least some species are flowering earlier now than they have in the recent past (Figure 1), although not all species are responding in the same way. Local changes in temperature, precipitation, and CO₂ levels, all have the potential to influence the timing of flowering and each of them alone or working together, could be important for understanding how different plant species will change in the future.

CHAPTER 3. POLLINATOR PHENOLOGY

3.1. Introduction to Insect Pollinator Phenology

Pollinators can be particularly vulnerable when an ecosystem is undergoing a change in environmental conditions. Insect pollinators are dependent upon their interaction with plants in these ecosystems for the food resources they acquire not only for themselves, but also for their offspring. With changing environmental conditions, certain plant species are demonstrating rapid changes in their life cycle phenologies, such as advancements or delays in flowering. Pollinators may not respond in the same manner to these environmental changes. In view of changing environmental conditions and its influence on flowering phenology, will insect pollinators be able to adapt to keep pace with alterations in flowering phenology?

3.2. Evidence for Change in Insect Pollinator Phenology Across Time

As with plants, my first question was to determine what evidence there is for changing phenology in insect pollinators. Unfortunately, there have not been as many long-term data sets for insect pollinators as there have been for plants. However, I did obtain four studies (Table 4) that had the same type of data as I reported for plants. Since these were not studies that were done in conjunction with the previously reported plant studies, there are numerous differences in the locations, study periods, etc. Therefore, I do not intend to draw a quantitative comparison between changes in insects and plants, but instead want to focus on the qualitative distribution of changes in both groups.

To create histograms of the changes in the timing of an insect pollinator's first flight, I performed similar calculations as for the plant studies with a few minor differences. In this case, all four studies used regression and reported the slopes to indicate change, and I used those

slopes to calculate a change in days or reported the change in days provided in the paper. One of the papers (Roy and Sparks 2000), used a different method to calculate change, and in this paper

Table 4. Characteristics of the four studies used to identify changes in pollinator phenology across insect species in a given location (Figure 2).

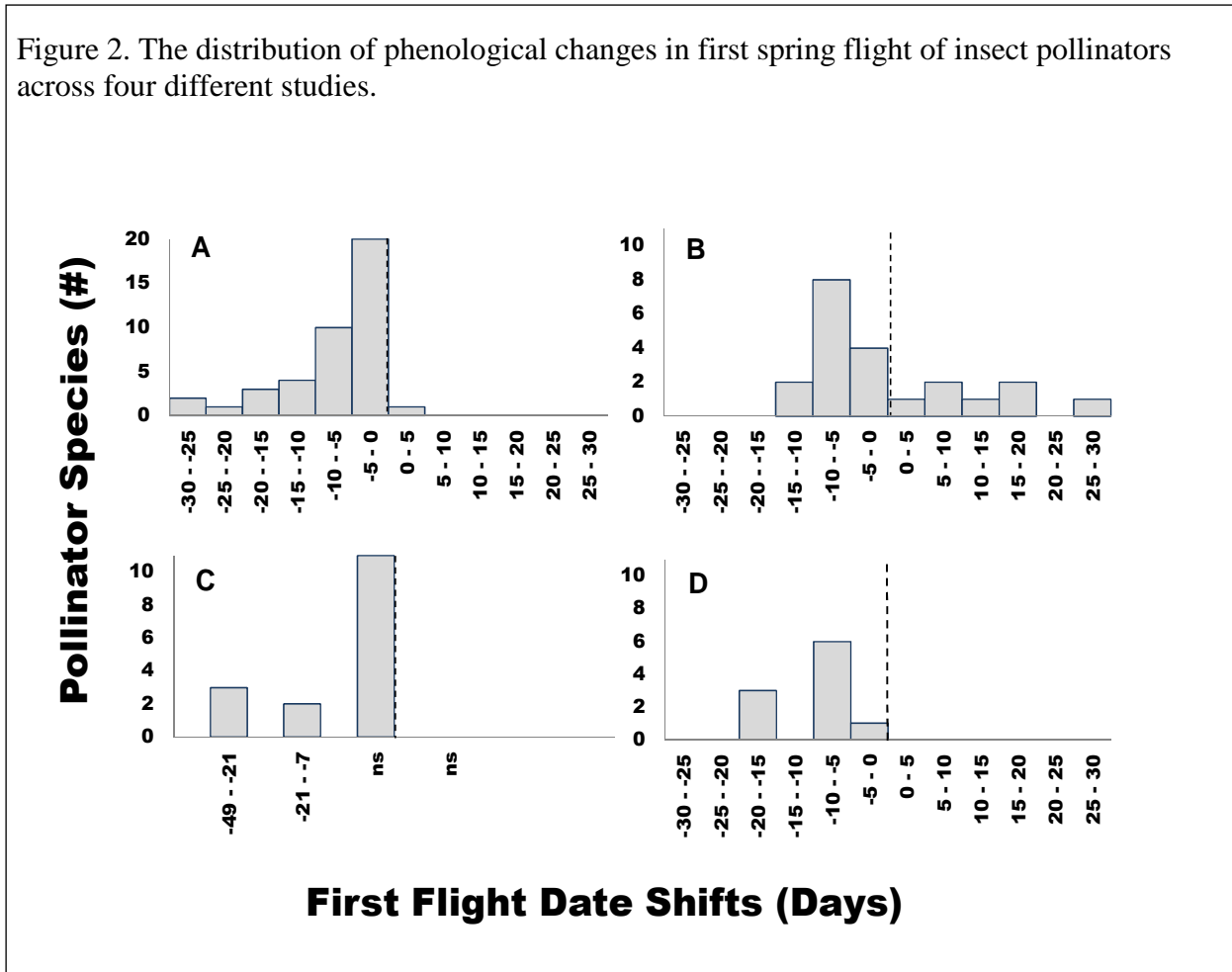
Phenology Articles	Species	Years of Study	Analysis	Location & Latitude
Roy & Sparks 2000	35	1976-1998	Regression	British Isles, UK; 54°N
Forister & Shapiro 2003	23	1972-2002	Regression	CA, USA; 38.6°N
Stefanescu et al. 2003	19	1988-2002	Regression	El Cortalet, Spain; 42.2°N
Bartomeus et al. 2011	10	1880-2010	Regression	Northeast USA; 36-50°N

each species was reported as changes in days per 1°C. Since the paper reports a 1°C change in summer temperature over the study period it was possible to calculate an absolute change in first flight in days. Although this is not as good of a comparison with the other studies, I chose to include it because of the lack of comparable studies.

The result of this is four histograms that can be used to look at the distribution of changes in the first flight of a group of insect pollinators (Figure 2). The first three histograms are for species of butterflies (Figures 2A-C) and the last is for a group of generalist bees (Figure 2D). As in the case of plant flowering, there is evidence that many insect species are having their first flight earlier now than they have in the past. However, also like the plants, there is a wide spread in the distribution of these responses with some species showing no change or even a delayed first flight. Each panel shows the number of species that were reported to have changed their first flight by the given amount. Data was grouped into categories of 5 days except for (C) which was reported at a coarser scale; specifically change in flight was categorized as 3-7 weeks

early, 1-3 weeks early, <1 week early, but not significantly different than no change (ns), or delayed but significantly different. None of the reported species in any of the studies were on the

Figure 2. The distribution of phenological changes in first spring flight of insect pollinators across four different studies.



exact border between two categories. Negative values indicate an earlier date for the first spring flight of the adult insect compared to historical information. A dashed line was added to each panel to emphasize the point where there was no difference in flight date. The data in each panel corresponds to the results from a particular study: A) Roy and Sparks 2000, 35 total species shown; B) Forister and Shapiro 2003, 23 species; C) Stefanescu et al. 2003, 19 species; D) Bartomeus et al. 2011, 10 species. Note that (A) has a different y-axis than the other panels. Once again I looked at the environmental cues that are related to the phenology of pollinators to

help explain why there appears to be a species-specific change over time. In this case, the environmental cues can help us better understand the effects on insect pollinators, while noting similarities and differences between changes to plants and pollinators.

3.3. Environmental Cues in Pollinator Phenology

Pollinators like their plant counterparts, often time their life cycles according to the environmental cues of photoperiod, temperature, and moisture (Leather et al.1993). As with plants, environmental cues could influence the timing of insect flight directly, or it could affect it indirectly by influencing other factors that ultimately influence when insect adults are ready to forage. Here, I focus on the evidence that temperature and precipitation, two of the environmental cues that influence flowering phenology, may also be influencing the timing of pollinators and when they are available to pollinate.

3.3.1. Pollinator phenology response to temperature

Even though photoperiod is considered to be the most reliable cue indicating the changing of the seasons, it is temperature that is the environmental cue directing the phenology of emergence for most insect pollinators. The dormant overwintering stage of a pollinator's life cycle called diapause can be determined by temperature in some species. For instance, in temperate regions that experience climate extremes associated with summer and winter, emergence in bees will only take place after a sufficient period of colder temperatures has occurred. The blue orchard bee (*Osmia lignaria*) is a good example, as this early spring bee emerges only after being exposed to a lengthy cold period followed by warmer spring temperatures (Bosch and Kemp 2003). In the eastern US, *O. lignaria* times its emergence closely to its host the Eastern redbud (*Cercis canadensis* L.) which offers it nectar and pollen early in the season when other resources are in short supply (Kraemer and Favi 2010).

Temperature can also influence the length of the emergence period in pollinators, even within the same species. At higher elevations, bumblebee queens emerge rapidly providing them adequate time to rear the next generation during the short alpine summer (Goulson 2003). On the other hand, bumblebee species in temperate climates are able to emerge slowly over several months due to a longer growing season (Goulson 2003). Subarctic and arctic species of *Bombus* have been found to harmonize their emergence phenology so closely to their host plant that they emerge within one day of willow catkin blooms (Vogt et al. 1994). Butterflies are also very sensitive to environmental cues. Various butterfly species in Spain (Stefanescu et al. 2003) and the UK (Roy and Sparks 2000) exhibit flight dates and flight periods influenced by local temperatures. Phenology records of the Brimstone butterfly (*Gonepteryx rhamni*), confirms that this species first flight dates are not only sensitive to temperature, but also to precipitation (Sparks and Carey 1995).

Just as temperature has been found to be an important environmental cue for emergence in many pollinator species, alterations in seasonal temperatures have the capability to change the timing of pollinator emergence. *O. lignaria* exposed to an abbreviated winter period took a longer time to emerge from overwintering, emerging at a later date than is typical (Bosch et al. 2000). In the same study, overwintering *O. lignaria* were kept at colder temperatures for an “artificially” extended diapause period resulting in synchronization of this pollinator with orchard bloom (Bosch et al. 2000).

3.3.2. Pollinator phenology response to precipitation

In pollinators of arid and tropical regions, emergence phenology or breaking of diapause is synchronized with periods or “seasons” of abundant moisture. *Perdita portalis*, a desert bee, takes its cue to emerge in response to high humidity conditions in the soil rather than temperature

or photoperiod (Danforth 1999). This trait ensures that the bee emerges in the same time frame as its host plant's bloom. Similarly, the solitary bee (*Nomadopsis larreae*), common to arid regions, takes its cue to emerge from its ground nest when rainfall events total 5cm. or more (Rust 1988).

3.4. Conclusions on Pollinator Phenology

As with the timing of flowering in plants, there is evidence that insect pollinators may be changing when they fly, forage, and pollinate. These pollinators also may be responding to some of the same environmental cues that plants are using to determine flowering date. However, all of the work thus far has focused on plants and pollinators as separate species. In the following chapter plants and pollinators will be considered within their relationship, as this interaction may also be influenced by changing environmental conditions.

CHAPTER 4. PLANT-POLLINATOR RESPONSE TO ENVIRONMENTAL CHANGE

4.1. Introduction to Plant-Pollinator Phenology

In the plant-pollinator interaction both species generally rely on and benefit from one another in a relationship that is critical to their individual reproduction. For example, a pollinator receives plant resources in the form of pollen and nectar which facilitate the pollinator's own growth and development and enable it to provide for its offspring. In turn, the pollinator provides the plant a service by collecting and depositing plant pollen while carrying out its foraging visits.

Plant-pollinator interactions operate on the premise that pollinator life cycles will be in harmony or “match-up” with the bloom periods of their preferred flowers. Within this plant-pollinator relationship, changes in the phenology of one species could directly affect the wellbeing of the other. Flowering phenology has been shown to be sensitive to changing environmental conditions in demonstrations of advancement or delay in bloom times of some plant species (see Chapter 2). In some cases pollinators are also advancing their phenologies (see Chapter 3), however we do not know if species are responding in a similar manner since phenological cues can differ across trophic levels. In light of the alterations that have been occurring in plant and pollinator phenologies in response to changing environmental conditions, can plant-pollinator interactions become mismatched?

4.2. Evidence for Change in Plant-Pollinator Phenology Across Time

In the previous section I looked for evidence of changes within and across communities of either plants or pollinators. So far there have been very few studies that have looked for changes in both plants and pollinators in the same area. One recent exception is provided by Bartomeus et al. (2011), who used museum specimens to identify changes in the timing of flight

for a community of generalist bees in the Northeastern United States. They then used published data from the same region of plants that are pollinated by these generalist bees. They conclude that the rate of advancement for their pollinators and their plants were indistinguishable from each other and suggested that these bees are able to keep pace with changing plants. This is the only study I could find that is able to draw these kinds of conclusions, and it is, of course, limited in what species it uses and its area. To investigate changing plant-pollinator phenologies further, it is helpful to review case studies that have focused on particular pairs of species.

Although both plants and pollinators use temperature as an important environmental cue, pollinators may not always respond in the same manner as the plants they frequent. 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 dates (Kudo et al. 2004). Likewise, in the same study, the solitary bee pollinator of yellow star-of-Bethlehem (*Gagea lutea*) was not available when this plant advanced its bloom times resulting in decreased plant reproductive success (Kudo et al. 2004). In a similar case, the glacier lily (*Erythronium grandiflorum* Pursh) experienced pollination limitation early in its bloom period due to unavailability of bumblebee queens to pollinate its flowers (Thomson 2010). This plant is capable of minimal self-pollination, but in the absence of its bee pollinators has nominal fruit set (Thomson 2010). In the case of a mismatch that involved insect herbivory and not a true mutualism mismatch, the larval host plant of Edith's Checkerspot butterfly (*Euphydryas editha* L.) flowered and senesced early due to increased temperatures, leaving the majority of butterfly larvae to die due to lack of food resources (Singer 1972; Parmesan 2003). Migratory butterfly species are displaying earlier spring flight dates over recent years potentially leading to a mismatch with their host plants at

some point in the future. The Red Admiral butterfly (*Vanessa atalanta*) has advanced its migration dates to Britain over the past two decades due to earlier arrival of spring, jeopardizing this butterfly's reproductive success when its larval host plant the stinging nettle (*Urtica dioica*) has been non-responsive to temperature changes (Sparks et al. 2005). Under certain conditions what seems like a mismatch may actually not be a true mismatch at all. *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, a mismatch did not take place because this pollinator is a generalist and was able to use other local flowering resources that were available (Forrest and Thomson 2011). Likewise, *Lathyrus* is frequently pollinated by other visiting insects so it did not suffer from pollination limitation due to this mismatch.

At times pollinators demonstrate plasticity in their phenology and are capable of keeping pace with their host plant, thus avoiding 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, indicating that this pollinator is able to quickly adapt its emergence to coincide with early snowmelt (Kudo et al. 2004). In rare cases pollinators are not demonstrating plasticity in their phenologies leading not only to mismatches in their interactions with plants, but jeopardizing their very survival. The Edith's Checkerspot butterfly typically uses the dwarf plantain (*Plantago erecta*) as a site for laying its' eggs. This butterfly lost synchrony with its host plant when changes in snowpack, dryness, and early arrival of spring resulted in advanced phenology for the plant. Larvae hatched out onto plants that were already past peak maturity forcing them to forage on leaves lacking adequate nutrition. The consequence of this mismatch caused local extinctions of this pollinator along the west coast of

North America, particularly in the Baja California region (Thomas et al. 1996; Singer 1972; Boggs et al. 2003).

4.3. Conclusions on Plant-Pollinator Phenology

The only community-level study of plant-pollinator phenology indicates that both species seem to be changing at the same rate (Bartomeus et al. 2011). However, there are numerous examples here of particular plant species changing their phenology and their pollinator not being able to keep up, with potentially disastrous consequences to the mutualism or interaction.

CHAPTER 5. MANAGEMENT CONSIDERATIONS

The plant-pollinator mutualism plays a pivotal role in maintaining ecosystem function by benefitting primary production in many plant species, therefore supplying essential resources to other wildlife species. If plant-pollinator interactions at this level fail, there can be repercussions through successive trophic levels eventually affecting the entire system. Native pollinators are important not only within natural habitats, but also in agricultural settings for crops requiring pollination services (Kremen et al. 2002; Greenleaf and Kremen 2006; Isaacs and Kirk 2010). For those plants not requiring animal pollination in order to reproduce, pollinators can enhance seed set, improving yield outcomes (Klein et al. 2007; National Research Council 2007). Honey bees perform the majority of pollination for crops requiring this service, but with the recent concern over their decline due to Colony Collapse Disorder (Watanabe 1994) crop pollination by native pollinators is even more crucial (Winfree et al. 2007).

Environmental change has been of increasing concern of late (Parmesan and Yohe 2003; Parmesan 2006), as these changes have the potential to alter the structure and function of ecosystems resulting in degradation of these habitats (Cane 2001; Kremen 2002; Parmesan and Yohe 2003; Root et al. 2003). Furthermore, habitat degradation can lead to impairment of interspecies interactions such as the mutualism shared by plants and pollinators (Cane and Tepidino 2001; Grixti et al. 2009; Winfree et al. 2009; Dicks et al. 2010). New research indicates that changes in environmental factors are leading to shifts in the phenology of plants and pollinators, causing mismatches in their interactions and consequently placing this mutualism in jeopardy (Kudo et al. 2004; Thomson 2010). Considering the importance of this mutualism to ecosystems and to humans, prompt action needs to be taken to ensure that the

plant-pollinator relationship remains vigorous despite any disruption that may occur due to environmental change.

5.1. Management Objectives and Strategies

In order to safeguard plant-pollinator mutualisms and other interactions within ecosystems, conservation measures need to be implemented to ensure that whatever the environmental impact may be on ecosystems, a safeguard is in place to ensure their resilience and adaptability in response to change. This safeguard involves managing these habitats to develop or sustain the vital floral resources that pollinators require. In the following sections I will discuss conservation objectives and strategies in relation to the needs of pollinators and their habitat and also the challenges that are surfacing with regards to this.

Pollinators are crucial to natural ecosystems because of the services that they provide. Just like other animal species, insect pollinators require certain habitat conditions and resources in order to thrive and reproduce. Simply because a habitat appears to be in a natural or wild state does not mean that it contains the essential resources and components necessary for healthy pollinators. Along with uncertain resources, environmental change is threatening to further alter these habitats. Although efforts are being made to predict how environmental change may impact habitats, challenges still remain for managers in balancing conservation efforts with limited funding, time, and perhaps the availability of suitable habitat. With the threat of rapid environmental change looming on the landscape, conservation managers need to anticipate the environmental changes that may occur, as well as the reality of financial limitations involved, and develop objectives and strategies to overcome these challenges.

5.2. Management Goals

Recently the effects of environmental change on pollinators has been brought to the attention of the federal government due to the determined efforts of many national and international non-profit and pollinator conservation organizations. These efforts have culminated in pollinators and their habitats becoming a focal point for conservation. One catalyst that has been put into place to address the requirements of pollinators and their habitat is incorporated into the Food, Conservation, and Energy Act of 2008, commonly known as the 2008 farm bill. In response to the farm bill, the Natural Resources Conservation Service (NRCS) has been asked to take a proactive approach to the habitat needs of pollinators by developing objectives and strategies to work toward three specific habitat goals.

5.2.1. Enhance and protect pollinator habitat

First, in order to provide a healthy habitat for pollinators, adequate nesting and oviposition sites need to be provided within the habitat (USDA 2008). 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 any pollinator conservation plan (Mader et al. 2011). For example, most native bees either nest in the ground or use cavities in dead wood for nests (Vaughan and Black 2007a). Ground nesting bees require the availability of open areas of ground that have the appropriate soil texture that enables bees to tunnel to build their nests. Cavity nesting bees such as the carpenter bee (*Xylocopa*) require old dead trees to excavate for their nests or dead trees with pre-existing tunnels fashioned by beetles to use to lay their eggs. Certain species of cavity nesting bees such as the blue orchard bee will use wood block nests provided by humans in which to reproduce. Wood block nests can provide a ready material for nesting bees 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.

Appropriate timing of habitat management practices such as mowing, haying, grazing, prescribed fire, and pesticide application need to be taken under consideration because these practices can affect pollinator nesting sites and therefore future pollinator generations (Cane 2011; Black et al. 2011). Untimely mowing, haying, or grazing of a habitat may remove plants that are vital as oviposition sites for butterflies and nesting sites for bees (Vaughan and Black 2007a; Black et al. 2011). In the case of grazing, heavy stocking rates can cause ground trampling by hooves resulting in compaction of the soil, making it difficult for ground nesting bees to excavate (Kearns and Inouye 1997). Prescribed fire in the improper season may affect ground nesting bees, especially solitary bees as heat from prescribed fire may potentially reach shallower nesting species (Potts et al. 2003). Nests built by cavity nesting bees, depending on how closely they are located to the ground, can also be at risk (Cane 2011). Butterfly overwintering or oviposition sites can be under jeopardy if fire is timed during the immature development stages of their lifecycle (Swengel 2001; Cane and Neff 2011). On the other hand, well-timed fire treatments can actually benefit ground nesting bees by exposing bare ground for excavating (Campbell et al. 2007). Poorly timed pesticide spraying can also have detrimental effects on pollinators (Kevan 1975; Vaughan and Black 2007b). Developing bees may be affected if pollen containing pesticides has been deposited within their nests (Kearns and Inouye 1997; USDA 2005; Vaughan and Black 2007b). Butterflies in various stages of development from egg to larvae to pupae can be affected by receiving pesticide spray meant for plant insect pests (Russell and Schultz 2010).

5.2.2. Enhance the biodiversity of floral resources in pollinator habitat

Second, in order to provide a healthy habitat for pollinators the biodiversity of floral resources needs to be enhanced and promoted within the habitat (USDA 2008). As mentioned earlier in this review, pollinators require floral resources for their growth, development, and reproduction. Pollinators are dependent upon interactions with plants for the food resources they acquire not only for their own needs, but also for their offspring. With changing environmental conditions, certain plant species are demonstrating rapid shifts in their life cycle phenologies, such as advancements or delays in flowering (Bradley et al. 1999; Abu-Asab et al. 2001; Fitter and Fitter 2002; Dunnell and Travers 2011). Pollinators may not respond to environmental change in the same manner as plants. Due to this, interactions between pollinators and plants may become mismatched, jeopardizing the wellbeing of each species. In order to overcome any mismatch that may occur due to changing environmental conditions, a buffer needs to be created 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 resources for their own energy needs and nectar and pollen to nourish their offspring. Butterflies require the nectar of flowering plants as adults, but also use specific host plants on which to lay their eggs (Kearns and Inouye 1997). In the past, pollinators and their needs were not addressed in conservation planning. Due to the lack of soil conservation standards in our agricultural history and the ensuing dust bowl days of the 1930s and 40s that followed, past habitat conservation plans on farmlands have been designed to maintain soil integrity. For example, the USDA Conservation Reserve Program was created to place previous crop or pastureland under conservation in order to establish long-term vegetation

covers thereby decreasing erosion, water run-off, and sedimentation on these lands. Pollinators were not considered in conservation plans at that time so most lands were planted to grasses as a cost-effective and quick way to establish soil stability (USDA 2012). Presently, with a new focus on the habitat requirements of pollinators, conservation plans need to include the seeding of forbs especially those that will provide quality nectar and pollen resources (USDA 2008).

Management strategies within pollinator habitat need to promote the continued persistence of forbs in the habitat, while discouraging aggressiveness and invasion of unwanted species. Again, appropriate timing of habitat management practices needs to be taken into consideration. Mowing and haying, if timed poorly, will remove plants during bloom depriving pollinators of vital food resources (Noordijk et al. 2009). Additionally, grazing livestock during flower bloom can have devastating results for bee species due to diminished availability of floral resources (Black et al. 2011). In some cases grazing can actually benefit ground nesting bees and butterflies as it can reduce shrub species, opening up area for flowering resources to thrive (Vulliamy et al. 2006). Prescribed fire should be avoided when plants are actively growing or blooming, but proper frequency and timing of fire within plant dormant seasons can supply an eruption of forbs the following spring (Potts et al. 2003). Likewise fire employed to rid a habitat of woody species that are not a historical component of the community can open up the canopy of a habitat, allowing forbs to prosper (Kearns and Inouye 1997). Although pesticides are beneficial to rid habitats of insect pests, pollinators may suffer the same fate if pesticides are applied during periods when pollinators are actively foraging (Kevan 1975; Kearns and Inouye 1997).

5.2.3. Provide a succession of blooming resources in pollinator habitat

Third, in order to provide for a variety of pollinator species and life cycle requirements, a succession of blooming resources spanning the entire growing season should be implemented (Vaughan and Black 2006; USDA 2008). Pollinator species vary in different regions of the country and their life cycles span very short time periods, many times only a few weeks. Many pollinators are generalists in their diet requirements and able to pollinate a variety of floral species.

A number of pollinator diets are much more specialized, pollinating only one or a few floral species. In order 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 in the habitat so all pollinator needs are met. In doing this, floral resources need to be chosen so that there will be overlapping bloom across the spring, summer, and fall seasons, the active period for pollinators. In order to decide which forb species will be most beneficial for pollinators, conservation managers should first determine the pollinator species that are typical to their area so they can provide flowering resources that these species need. Forbs should be chosen based not only on pollinator preference, but also take into consideration those forbs that have historically been a part of these habitats. Wildflower seed can be costly, so determining and planting those species traditionally found within the habitat type will decrease the likelihood of plant failure and decrease the overall maintenance required in the future. Ultimately heterogeneous and well-timed floral bloom available to pollinators throughout the growing season will provide the pollen and nectar resources required for them to not only prosper, but also to face future habitat alterations that environmental change may generate.

5.3. Management Challenges and Opportunities

Pollinator conservation managers have been given the task of protecting and providing quality pollinator habitat in areas that have been degraded or fragmented as a result of human actions. Additionally, they are expected to carry out their task within a culture where pollinators have not been a priority in the past. Opportunities exist for conservation managers and others to increase public awareness of the important role of pollinators and the value of the services they provide to humans.

5.3.1. Develop pollinator conservation habitat

Management practitioners face a challenge in the development of appropriate conservation plans for pollinator habitat. Our wildlands have been increasingly altered by human actions over time, often to such an extreme that the original state of the habitat is unrecognizable or completely absent from the landscape. Every habitat is distinct in the type of climate, soils, hydrology, and topography that is present. In developing plans for pollinator habitat, managers should first take into account the ecological history of the area, how it has evolved through time, and what environmental factors have been natural parts of that history (White and Walker 1997). In order to include the ecological history of an area and therefore habitat requirements, a template of reference ecosystem conditions should be developed for each pollinator habitat. The ecological reference site descriptions and reference plant communities provided through the USDA (USDA 2011) is an excellent resource to utilize when developing pollinator conservation plans. Appropriate plant species that replicate these reference conditions for an area should be chosen, while taking into consideration the cost and availability, well as the overall management objectives for the habitat. In addition, concern for the future effects of changing climate conditions should be contemplated during the planning phase, as historical

plant species that are known to be resistant and resilient species are the ones that will be able to withstand the insults to ecosystems stemming from environmental change. (Harris et al. 2006).

5.3.2. Increase public awareness of the importance of pollinator habitat

Conservation managers have unique opportunities and challenges in promoting and developing pollinator awareness, acceptance, and conservation. For pollinator conservation to be a successful endeavor, managers need to create opportunities to enlighten the public of the importance of pollinators, their habitat, and the services they provide. By and large the public is unaware of the foundational role that pollinators and plants play in natural habitats or how these species could have significance to humans. Oftentimes humans estimate the value of areas set aside for wildlife habitat in monetary terms based only on the services it could offer such as farming, livestock production, development, or hunting. Conserving this same habitat by planting it to native wildflowers for pollinators may be interpreted by some as a wasted and unused space filled with weeds. In order for the plant-pollinator mutualism to be seen as a vital part of the healthy functioning of terrestrial ecosystems, there needs to be a concerted effort placed on educating the public. Education should include not only land managers and practitioners directly associated with the management of pollinators and their habitats, but also governmental policy makers, who have the ability to fund conservation programs, along with the general public who benefit from these conservation actions. The beginnings of public awareness to the needs of pollinators has been raised through efforts such as pollinator monitoring programs like the Backyard Bee Count (The Great Sunflower Project 2012) and the Fourth of July Butterfly Count (NABA 2012) that engage citizen scientist volunteers in active conservation efforts. Likewise, school-aged children are being educated about pollinators and their conservation needs through projects involving monitoring of these organisms and gardening for

pollinators (Pollinator Partnership 2012), among others. We lack knowledge of the ecology of many pollinator species so monitoring programs involving the public can assist conservation managers and scientists in learning more about the life cycles of these species and how they interact with other organisms within their habitats. By increasing our knowledge of pollinator ecology we can move closer to providing the healthy habitats that pollinators require. Healthy habitats full of robust floral resources for pollinators will provide the initial ingredients necessary to build stability into the habitat and safeguard it against the impacts changing environmental conditions may bring.

CHAPTER 6. CONCLUSION

As evidenced in this review, a number of plant and pollinator species have been modifying their life cycle phenologies, in many instances due to sensitivity to warming temperatures, changing precipitation patterns, or increasing atmospheric CO₂ levels. Due to variations in the response of these species' interactions at least some mismatches are already occurring, further complicating the response to environmental change. Phenological advances, delays, or even non-response to environmental changes has been witnessed and documented, but presently we are not able to determine which species will actually respond to local environmental fluctuations. Moreover, we lack knowledge about how plants and pollinators will respond if the pace of changing environmental conditions escalates.

In order to adequately interpret species' response to environmental change, we first need to determine those species most vulnerable to change. Certain pollinating species may be robust and able to adapt to changing conditions within their communities. For instance, social pollinators such as honey bees are not as likely to be as vulnerable to many environmental changes as the colony shares in responsibilities ensuring that all individuals are sheltered, warm, and fed regardless of the environmental conditions surrounding them. Moreover generalist pollinators may be less sensitive to climatic change as their dietary niches are broad, increasing the chance that they will have adequate food resources should a change in local conditions occur. In alpine regions characteristically early spring emergers such as bumblebee queens and males of the *Andrena* spp. may be more resistant to environmental change as they are accustomed to the unpredictable conditions that early spring weather can offer (Forrest and Thomson 2011). Reproductive traits of three species of *Osmia* bees, specialists of the plant family Compositae,

can demonstrate a one year or two year diapause cycle potentially aiding them in “riding out” shorter periods of harsh environmental conditions (Torchio and Tepedino 1982).

Other pollinators may possess species specific traits that make them more vulnerable to changing environmental conditions. For instance, solitary bees have abbreviated life cycles, producing one generation per year, affording them less opportunity to adjust their phenologies to alterations in their environment (Schweiger et al. 2010). Habitat restricted or non-migrating pollinator species will be more vulnerable as they may not be able to disperse in response to modifications in local environmental conditions (Biesmeijer et al. 2006). Moreover, specialist pollinators in the adult or larval stage that are relying on a single or few plant species may be susceptible to change if the host plants they rely on for food resources are no longer available in the habitat (Diamond et al. 2011). As previously mentioned, the Edith’s Checkerspot butterfly (*Euphydryas editha bayensis*) and its’ host plant experienced an interaction mismatch due to the early arrival of spring. Lack of adequate larval food resources led to local pockets of extinctions for this butterfly within its’ northern Baja to southern California range (Thomas et al. 1996; Boggs et al. 2003).

While questions remain regarding the fate of plants and pollinators in the midst of environmental change, the evidence reviewed here implies that environmental change does have the potential to disrupt ecosystems, plant and pollinator species, and their interactions. The phenologies of flowering plants and pollinators are already being altered due to a variety of changing conditions within their communities. Plants and pollinator phenologies are also not necessarily responding to environmental change in the same manner or at the same rates. Changes to the plant-pollinator interaction has the potential to cause repercussions through higher trophic levels, ultimately affecting numerous interspecies interactions. Thus, in light of

the evidence that is mounting regarding the changing phenologies of plants and their pollinators in response to environmental change, it is imperative that we develop an understanding of the influence these changes can have on the species involved in plant-pollinator interactions, as there can be consequences to the functioning and diversity of ecosystems in the future.

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