

4.11 Vulnerability of Pollination Ecosystem Services

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Glossary

Bridging plants Plants utilized in habitat restorations to provide resources for pollinators during resource-poor time periods.

Ecosystem services A set of resources and processes provided by ecosystems that contribute to human well-being.

Food security The availability and access to sufficient, safe, and nutritious food for a community or individual.

Framework plants Plants utilized in habitat restorations to provide resources necessary for supporting large numbers of pollinator species or individuals.

Phenology Plant and animal life cycle events that are often periodic and usually influenced by seasonal variations in climate.

Pollination The process by which pollen is transferred from anthers to stigma, initiating sexual reproduction and formation of the fertilized fruit or seed.

Pollinator networks A visual display of plant–pollinator interactions, usually based on visitation or pollen-load data.

Pollinator network connectance The proportion of plant–pollinator links observed in a network (links/species).

Pollinator network nestedness Where specialists interact with subsets of species with which generalists also interact, creating a ‘nested’ structure.

Perhaps one of the most critical yet understudied factors affecting the decline of global pollinator populations and pollination services are alterations in local and regional climatic conditions. In the past few decades, humans have significantly altered climatic conditions due to the emissions of aerosols, and of greenhouse gases, including CO₂, and from land management practices (NRC 2005) consequently impacting wild species distributions and population dynamics across the world (reviewed by IPCC 2001; Parmesan 2007; Parmesan and Yohe 2003). Because most pollinators are completely reliant on plants for food resources, pollinator populations may be both indirectly affected by changes in the abundance, spatial distribution, and timing of flowering in plant populations, and

directly affected by the climate of the regions in which they occur. Thus, the discussion of climate impacts on pollination services requires an analysis of both direct and indirect interactions between climate, plants, pollinators, and the many threats to plant and pollinator populations (Figure 1).

In this chapter, we review scientific literature surrounding four key topics: (1) the ecological interactions related to pollination services and vulnerability, (2) the ecosystem services provided by native pollinators and their potential alteration, (3) mitigation possibilities for improved pollination acquisition, and (4) the resulting policy implications (Figure 1). Given the large scope of this topic, we focus on insect pollinators, which are one of many pollinator groups

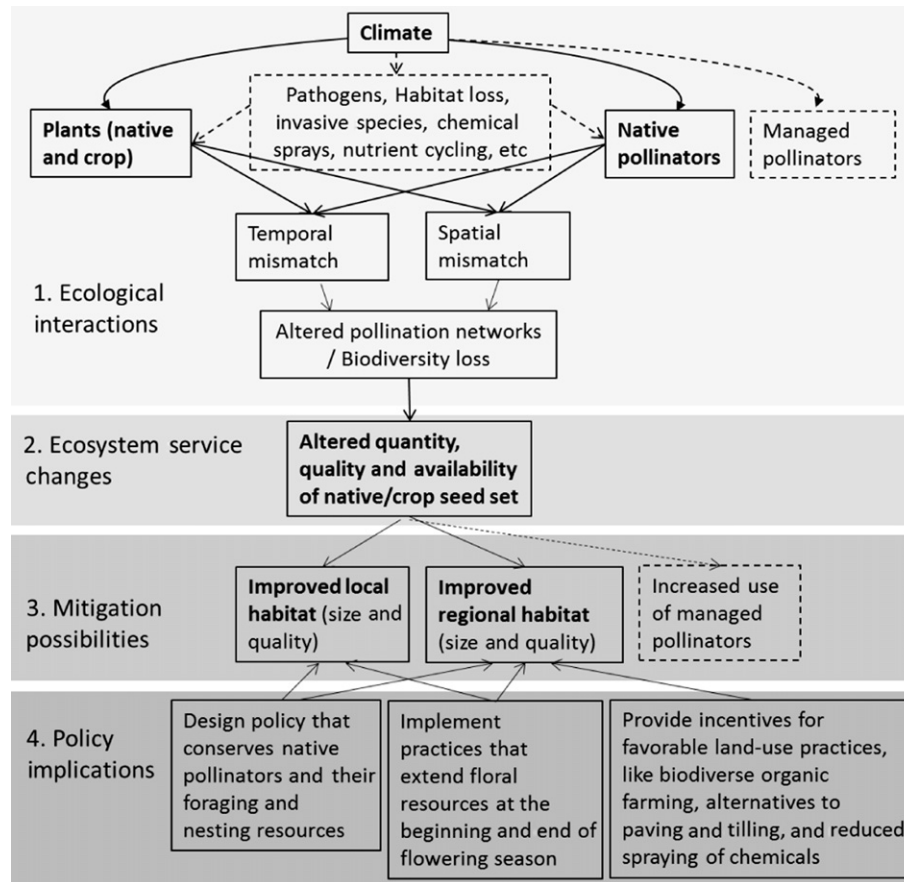


Figure 1 Framework showing how climate influences plants and pollinators, and thus the availability and quality of ecosystem services. Part 1 of the figure is adapted from Hegland, S. J., A. Nielsen, A. Lazaro, A. L. Bjerknes, and O. Totland, 2009: How does climate warming affect plant-pollinator interactions? *Ecol. Lett.*, 12, 184–195, and the remaining parts indicate the change in ecosystem services and role of management practices and policies on pollination services, respectively. Dashed lines and arrows indicate areas not covered by this review.

(e.g., birds, mammals), but are the most economically important pollinator groups globally (Roubik 1995; Winfree et al. 2011a). Because very little literature is available on the direct impacts of climate on pathogens, chemical sprays, and other threats to pollinators, we only speculate on these topics and advise that greater research is required for an understanding of these factors. Because one of the objectives of this review is to provide ecologically informed management suggestions for improved pollination services, we focus on native pollinators, which have the potential to provide sustained pollination services. Compared to the services provided by a single species of managed pollinator (e.g., the honey bee), species-rich communities of wild pollinators can provide redundancy in terms of pollinator services (Kremen et al. 2004) and thus may provide services that are more stable over time (Garibaldi et al. 2011) and in the face of environmental change. However, we suggest that climate impacts on managed pollinator communities are topics of great importance and require further study. Overall, by summarizing the literature relevant to climate impacts on native pollinators, we provide generalizable and ecologically informed management suggestions for scientists and policy makers across communities and ecoregions.

4.11.1 Ecological Interactions

4.11.1.1 Pollination Services

Ecosystem services are the set of ecosystem functions that contribute to human well-being and include provisioning, supporting, regulating, and cultural services (Daily 1997; Millennium Ecosystem Assessment 2005). Pollination of plants by animals is both a regulating and a supporting ecosystem service. As a regulating service, it is essential for the reproduction of pollinator-dependent plants that supply humans with foods, fiber, forage, biofuels, firewood, timber, and medicine. The contributions of pollination services to human well-being may be direct or indirect. Direct contributions include fruit or seed production of pollinator-dependent food, fiber, biofuel, and forage crops (e.g., alfalfa, apple, blueberry, canola, cherry, cucumber, cotton, longan, macadamia, melon, raspberry, squash, soy, and sunflower). Indirect contributions of animal pollination include the reproduction of tree species valued for timber (e.g., mahogany, White et al. 2002), sown crops in which the vegetative parts are eaten, seed production (e.g., lettuce, broccoli, carrot), vegetatively propagated crops in which animal pollinators are required for breeding only (e.g., potatoes, banana), and pollinator-dependent plants with

medicinal properties [e.g., *Catharanthus* spp., which include the famous Madagascar periwinkle (reviewed in Klein et al. 2007; Miyajima 2004)]. As a supporting service, pollination is essential to maintain populations of pollinator-dependent wild plants (Aguilar et al. 2006) that then provide additional ecosystem services, such as erosion control, water filtration, carbon storage, and habitat for biodiversity (discussed in greater detail in the following sections, reviewed in Kremen et al. 2007).

Of these various contributions to human well-being, scientists have to date only rigorously quantified importance of pollination services to food crop production (e.g., effects of animal pollination on fruit and seed yield, and on seed production for crops in which vegetative parts are eaten). These studies have shown that 75% of all crop species depend on animal pollinators to produce fruits or seeds, either partially or completely, supplying 35% of global crop biomass (Klein et al. 2007). Importantly, these crops also supply the majority of certain essential micronutrients in plant-based food, such as dietary lipid (74%), vitamins A (70%), C (98%), E (35–66% of tocopherols) and folate (55%), and minerals calcium (58%) and fluoride (62%) (Eilers et al. 2011). Since some crop production from animal-pollinated crops is due to self or wind pollination, the total amounts of biomass and micronutrients due to yield increases from animal pollination will be less than these numbers, but remain substantial (Eilers et al. 2011; Klein et al. 2007). Worldwide, the pollination services for food crop production, including both those provided by managed bees imported to crop fields and those freely provided by wild bees, were recently valued at €153 billion/year (prices from year 2005), 9.5% of global crop value (Gallai et al. 2009).

Neither the micronutrient nor the economic calculations include the contributions of vegetative crops for which animal pollinators are needed for seed production or breeding. We also lack recent quantitative analyses of the indirect contributions of pollinators to meat and dairy production via forage production (e.g., alfalfa, McGregor 1976), as well as, any calculations of pollinator contributions to fibers, medicinals, botanicals, firewood, timber, and other useful plant species, both cultivated and wild. As 87% of wild plants are pollinator dependent (Ollerton et al. 2011), these contributions are likely to be large.

We can conclude that the contributions of pollinators to human well-being are many and varied. To the extent that wild pollinator species provide these services, then growers do not have to pay beekeepers to supply them, reducing input costs for growers, as well as, food prices for consumers (Chaplin-Kramer et al. 2011; Winfree et al. 2011b). Wild pollinator species still provide sufficient pollination services in certain regions (e.g., Winfree et al. 2007b; Winfree et al. 2008) or in favorable environments within regions (e.g., Garibaldi et al. 2011; Kremen et al. 2002), but in general, with the intensification of agriculture and the loss of natural habitats, both the magnitude and stability of wild pollinator richness, visitation rates, and pollination services have declined in landscapes around the world (Garibaldi et al. 2011). In fact, these declines in pollination services occurred despite no observed declines with intensification in the abundances of the honey bee, *Apis mellifera*, a managed species which growers frequently import to their fields for pollination services.

Declines in the abundance and richness of wild pollinator populations are therefore already having subtle consequences for the human food supply, although these are largely masked by the presence of managed honey bees (Garibaldi et al. 2011). Such effects may intensify as managed honey bees have suffered dramatic declines in some regions (Neumann and Carreck 2010), probably due to synergistic effects of disease, environmental stress, and pesticides (Potts et al. 2010), and wild pollinators are also declining, especially in intensive agricultural landscapes (Garibaldi et al. 2011; Winfree et al. 2009). Declines in wild pollinators will also have large consequences for the reproduction of wild plant populations (Aguilar et al. 2006) that are likely to ramify in their effects on food chains and ecosystem services, potentially affecting both wildlife and humans.

What are the major factors causing wild pollinator declines? Several recent synthetic analyses focusing on bees, the principal pollinators of most crops and many wild plant species, note the loss or degradation of habitat as the principal factor in declining richness and/or abundance (Bommarco et al. 2010; Williams et al. 2010; Winfree et al. 2009). At the landscape scale, meta-analysis showed that pollinator richness and abundance were significantly affected by extreme habitat loss or simplification, but not by moderate habitat loss (54 studies, Winfree et al. 2009); conversely, favorable management practices in farming or grassland landscapes (such as organic farming or set-asides on farmlands or grazing intensity for grasslands) had significant positive effects on abundance and richness of pollinators only in simplified (<20% of non-crop habitats), but not complex landscapes (46 studies, Batary et al. 2011). Guild characteristics affected the response of bees to different habitat disturbance types, as shown in a quantitative synthesis of 19 studies including over 600 bee species; in particular, above-ground nesters and social species were more sensitive to various types of disturbances than below-ground nesters and solitary species (Williams et al. 2010). Social species were negatively affected by pesticide use, but this factor was not significant overall or for other guilds (Williams et al. 2010). Additionally, a few recent studies have shown that pesticide application can have negative impacts on native bee species abundance and richness (Tuell and Isaacs 2010), and declines occur at both local and landscape scales and are more likely to occur after multiple applications (Brittain et al. 2010). However, very little is currently known about the complexities of pesticide impacts on wild pollinators and further research is required to understand the influence of specific pesticide application techniques and chemicals on pollinator life history and behavior in the field.

4.11.1.2 Sensitivity/Vulnerability of Pollination Services

4.11.1.2.1 Temporal Mismatch

Our understanding of the effects of climate on pollination services is weak, in part because determining individual plant and pollinator responses to climate is a vast task, and scaling those responses up to the community level is challenging, given the complexity of such interactions. Pollinator visitation to plants is a community-level phenomenon—merely knowing the species present does not necessarily indicate how they will interact to provide pollination services. In particular,

behavioral changes in pollinator foraging may play an important role (e.g., Greenleaf and Kremen 2006) in determining the effects of climate on pollination services. Climate may cause changes in the quality, quantity, and timing of floral rewards in space, and pollinator behavioral responses to those changes are difficult to predict. Furthermore, pollinator behavior is layered on top of changes in pollinator timing and abundance in space. We may begin to piece together potential effects of climate on pollination by considering evidence for each of these pieces separately. To determine the sensitivity and vulnerability of pollination services to climate, we will first review what is known about how plants and pollinators themselves are being affected. (Much of this work has been reviewed previously by Burkle and Alarcon (2011) and Hegland et al. (2009).)

Although the phenologies of some insect pollinators and many plant species have been shown to be affected by warming, few studies have found temporal mismatches in plant–pollinator interactions. Honey bees, bumble bees, and some butterflies are active earlier with warmer temperatures (e.g., Dennis and Sparks 2007; Gordo and Sanz 2006; Sparks et al. 2010) and many plant species are flowering earlier with warmer temperatures, as well (e.g., Amano et al. 2010; Fitter and Fitter 2002; Miller-Rushing and Primack 2008; Sparks et al. 2000). The majority of reported phenological changes for plants and pollinators show advanced activity, yet some show delayed phenology (e.g., Doi et al. 2008; Von Holle et al. 2010), illustrating the need for detailed, and possibly species specific, investigations of different systems before generalizations can be made. In addition, variability in early-season phenologies of plants, and to a lesser degree, butterflies, is increasing (Menzel et al. 2006). When flowering phenologies were experimentally advanced and plants were placed in an unmanipulated community (e.g., the phenologies of pollinators were allowed to unfold naturally), few mismatches were observed (Rafferty and Ives 2011). By resampling and comparing plant–pollinator phenologies and interactions with historical phenologies and interactions, it is possible to test the degree to which interactions are being disrupted by phenological changes. In a comparison spanning 120 years, few mismatches in plant–pollinator interactions directly attributable to phenological change were found (Burkle et al. *in prep*). These empirical investigations, though limited in number, suggest that temporal mismatches may not play as large a role in decoupling plant–pollinator interactions as previously indicated by models (Hegland et al. 2009; Memmott et al. 2007).

Despite the lack of evidence for widespread temporal mismatches, given the current degree of changes in climatic conditions in some regions, there are likely some cases in which mismatches have led to declines or extirpations of plant and/or pollinator populations. Demographic consequences of such temporal mismatches, however, are not well understood. Thomson (2010) showed strong direct effects of frost events and snowmelt patterns on the reproduction of glacier lilies. Temporal mismatches of glacier lily flowering and the activity of their pollinators may also limit seed set, though this has not been investigated explicitly. Burkle et al. (*in prep*) have observed the extirpation of half of the bee species historically present in mid-western US forests, though the cause of this bee decline, involving many specialist bees, may not be solely due

to temporal mismatches (see below). Effects of climate on pollinator nesting habits and reproduction are largely unknown and have been identified as an important gap in our understanding (Burkle et al. 2011). Miller-Rushing et al. (2010) outlined a way to better understand the demographic effects of phenological mismatches, including key questions and approaches using experiments, models, and long-term data.

4.11.1.2.2 *Spatial Mismatch*

In addition to temporal mismatches influencing pollination services due to phenological changes in plant and pollinator activity, spatial mismatches may also be as, or more, important. Spatial mismatches between plants and pollinators may occur due to range shifts resulting from climate changes, or due to indirect climate change effects such as habitat destruction and fragmentation. For example, under different climate scenarios, it is possible that humans may use land differently, by altering existing urbanization, development, and/or crop planting patterns, and thus potentially destroying and fragmenting existing habitat. Second, climate can determine the distribution of many plant species, and thus, climate changes can result in spatial shifts in plant populations. Much of the empirical support for range shifts has been performed along elevational gradients in the alpine, where the upward movement of species with warming is relatively straightforward to detect. Plant distributions along elevational gradients can change rapidly with climate, and have been documented as shifting upward in elevation an average of 22 m per decade in the southwestern United States (Kelly and Goulden 2008) and 29 m per decade in western Europe (Lenoir et al. 2008; Walther et al. 2005, 2002). Other studies focused specifically on flowering forbs and their range shifts find similar changes in elevation (Crimmins et al. 2009). In a cross-study comparison, Parmesan and Yohe (2003) found many species, including alpine herbs, to be shifting poleward at an average rate of 6.1 km per decade. In some systems, involving narrowly distributed endemic plants, range shifts may not be possible and declines in species richness have been observed (Damschen et al. 2010). At the other end of the spectrum, some plant species, such as invaders, may adapt and evolve to occupy new environmental conditions associated with climate change, expanding into novel ranges (Gallagher et al. 2010). However, there is also evidence for lack of plant response to recent warming in the alpine, with clones of long-lived plants remaining in the same locations over thousands of years (Bahn and Korner 2003; Steinger et al. 1996). Sherrer and Korner (2010) argue that high microclimatic variation in the alpine would allow plants to ‘escape’ larger scale changes in climatic conditions without moving more than a few meters. Determining which plant species would shift their ranges due to warming and the direction and magnitude of their responses remains challenging.

Few studies have documented range shifts in pollinator species, primarily because knowledge of historic and current distributions are lacking. There are initiatives to map historic pollinator distributions based on museum specimens for comparison to current ranges (Koch *in prep*). In a few studies, butterfly range shifts have been documented to be moving poleward due to climate changes (Bryant et al. 1997; Kerr 2001; Parmesan and Yohe 2003). Changes in pollinator species

distributions are more easily attributed to habitat loss or fragmentation directly (Cane 2001), though the ultimate causes of habitat change may be related to climate shifts and associated changes in human land use. At a local scale of kilometers, loss of historically occurring plant–pollinator interactions can be due to spatial uncoupling in which plants become separated from their pollinating partners in isolated forest fragments (Burkle et al. in prep).

4.11.1.2.3 Alteration of Pollinator Networks

A relatively new method for understanding plant and pollinator interactions at the community level is via the construction of interaction networks (Memmtott 1999; Memmtott et al. 2004; reviewed in Vazquez et al. 2009). In these networks, single lines connecting plants and pollinators indicate the existence of interactions between two species, making it easier to visualize and analyze changes in these interactions. Examined as a whole, the pollinator network can also convey critical information regarding the structure and function of community-level interactions (reviewed in Burkle and Alarcon 2011; Vazquez et al. 2009). Pollinator network analysis has generally shown that, within sites, there is substantial interannual variation in what pollinators interact with what plants, but despite this variation, pollination events still take place, potentially indicating resilience to environmental change. Interestingly, despite natural variation in who interacts with whom, structural properties of community plant–pollinator networks remain fairly constant over time (reviewed in Burkle and Alarcon 2011). For this reason, it is possible to use network metrics, like *nestedness* and *connectance* to indicate, over and above this natural variation, the health and stability of interactions and potential directional change over time due to anthropogenic environmental changes. Highly nested networks are fairly robust to environmental change (Bascompte et al. 2003); thus declines in the nestedness of a network over time can serve as a barometer, indicating loss of functional resilience in plant–pollinator interactions.

Pollination networks can be utilized to understand community-level impacts of climate change via two main approaches: (1) evaluation of networks after simulated biodiversity loss or phenological mismatch and (2) comparison of networks after actual habitat restoration. We discuss both in the sections below, respectively.

4.11.1.2.4 Simulated Biodiversity Loss or Phenological Mismatch

Simulation studies use existing plant–pollinator networks to simulate the effects of environmental change, for example, they help us to understand what happens when we delete species or advance the phenologies of species, as might be predicted by climate warming. For the most part, these simulation studies have found that pollination networks are more robust to the removal of random species than to the selective removal of highly linked species (Kaiser-Bunbury et al. 2010; Memmtott et al. 2004). Many studies have found that the removal of the most-linked pollinator species results in a relatively linear decline of plant species, explained by the nested interaction network topology and a redundancy in pollinator links per plant (e.g., Memmtott et al. 2004). In another simulation study, Devoto and colleagues (2007) removed species from the network that they predicted would exhibit spatial range shifts due to climate-change induced

increased precipitation, and found that removal of these species had fairly minimal impacts on the plant–pollinator network. In another simulation study by Kaiser-Bunbury et al. (2010), the authors allowed species in the network to switch to those that they have known potential to interact with, with the interesting finding that networks could be stabilized following species loss if remaining species could indeed ‘rewire’ to form new interactions. While results from these simulation studies suggest that pollinator networks may be more robust to species loss and range shift than other ecological networks (e.g., Dunne et al. 2002), it is important to keep in mind that plants and animals may be differentially impacted by biodiversity loss, given that pollinators represent higher trophic levels, which are inherently more sensitive to habitat disturbance (e.g., Holt et al. 1999; Kruess and Tschamtkke 1994). Because pollinators are dependent on plants for food, it is not surprising that removal of the strongest interacting species in the network can have the strongest negative impact on simulated animal extinction rates (e.g., Kaiser-Bunbury et al. 2010).

Just a few pollinator network studies have examined the impact of climate on pollinator networks by modeling plant and pollinator phenology (Memmtott et al. 2007, 2010). In these studies, Memmtott and colleagues use existing predictions of temperature changes (e.g., IPCC 2001) to calculate potential phenological shifts in plant and pollinator emergence and senescence, if those predictions are accurate. In their 2007 study, Memmtott and colleagues examined simulated networks where the onset of flowering and flight activity of all plants and pollinators would be advanced by 1, 2, and 3 weeks. Across all three scenarios, they found that 17–50% of all pollinator species, especially those with smaller and more specialized diet breadths, faced reduced floral resources and potential extinction. Similar to the findings of other network studies, the predicted impacts on pollinators were much greater than for plants, though plants still experienced a 50% reduction in pollination activity, likely leading to reduced reproduction and eventual population decline (Memmtott et al. 2007). In a following study, Memmtott and colleagues asked specifically how the sowing of wildflowers changes the impact of simulated climate on the pollinator network. Their experimental planting and simulated climate-impacted network showed that by sowing plant species that bloomed at the beginning and end of the flowering season, the overall period of nectar resource availability could be extended for pollinators. However, it should be noted that these simulation studies did not allow for behavioral flexibility, which might allow for new interactions to develop between plants and pollinators within the system.

Another potential interaction between climate and pollination systems may be the introduction of non-native species into the pollination network (Memmtott and Waser 2002; reviewed in Schweiger et al. 2010), which may occur if non-native species become invasive under those environmental change conditions (reviewed in Dukes and Mooney 1999; Walther et al. 2009). Depending on whether non-native plants interact negatively or positively with native plants, their invasion could stabilize or destabilize pollinator networks. Examination of a plant and pollinator network in central United States has shown that non-native plants are far more common than non-native pollinators (Memmtott and Waser 2002). In this study, non-native plants interacted with significantly fewer

pollinator species than native plants, but were still relatively well connected in the network. Likewise, in another simulation study specifically examining the removal of non-native species, the pollination network's structural integrity was diminished by non-native species loss, due to the high levels of connectivity between alien and native species within the pollinator network (Valdovinos et al. 2009). Thus, if non-native plant species increase overall floral resource availability and duration, they may positively impact pollinator populations in the short term. However, the long-term effects of non-native plant species on pollinator populations are not well known. Invasion, which leads to plant species declines and losses in resource heterogeneity, may negatively impact forager biodiversity, as seen in other systems (e.g., MacArthur and MacArthur 1961; Shmida and Wilson 1985; Tylianakis et al. 2008). Overall, these studies suggest that non-native species play varying roles in pollinator networks, depending on their ability to provide foraging resources and their impact on the native plant community.

4.11.1.2.5 Network Comparison Post Habitat-Alteration

Comparing interaction networks before and after an event (habitat destruction or restoration) can tell us more about the maintenance of pollination services than typical biodiversity studies can. Unfortunately, though empirical research on the spatial and temporal variation of plant–pollinator networks is badly needed, the lack of historic data and the intensive sampling effort required to identify multiple empirically gathered networks has limited research in this area (Hegland et al. 2009). Only a few empirical network studies have specifically examined how habitat alteration impacts network architecture. Forup and Memmott (2005) compared pollinator networks for old intact hay meadows and restored hay meadows (planted with native plants post-agriculture), and found no significant difference between the two in terms of plant or insect species richness or abundance, but did find that old meadows had a slightly higher proportion of potential links between plants and pollinators. In a second study, Forup et al. (2008) examined ancient and restored heathlands and found that, while the plant and pollinator communities were similar, the interaction networks were significantly less complex, in terms of connectance values, in the restored heathlands. These results suggest that even in 'restored' human-altered landscapes supporting similar levels of species diversity, the complexity of plant–pollinator interactions may not be easily recreated, and this may ultimately limit the long-term persistence of plant and pollinator communities. In communities with high degrees of network complexity, such as the species-rich plant and pollinator communities of the tropics (Bawa et al. 1985), network recovery post human-alteration may be less likely.

Most remaining studies have examined plant–pollinator interactions over time within the same sites, and these have largely focused on intra- and inter-annual variations in network dynamics (reviewed in Burkle and Alarcon 2011). Studies comparing networks within a single year have often found substantial species turnover in composition, emphasizing the need to consider plant–pollinator networks for shorter and more biologically relevant time periods (Basilio et al. 2006; Jordano et al. 2003; Medan et al. 2006; Petanidou et al. 2008). One study that examined plant and pollinator interactions on a daily basis, also found pronounced species turnover, and

found that the most connected species, and thus perhaps the most resilient species, were those with the longest flowering–foraging periods (Olesen et al. 2008). Studies that have examined variation in pollinator networks across multiple years have also found a large degree of turnover in species composition, but have surprisingly found that the number of plant and pollinator species, connectance, degree of nestedness, and modularity were conserved over the years (Alarcon et al. 2008; Burkle and Irwin 2009; reviewed in Burkle and Alarcon 2011; Dupont et al. 2009; Petanidou et al. 2008). Overall, these studies indicate that plant–pollinator systems are dynamic, but that pollinators are flexible in resource use, potentially making networks more resilient to climate change. Furthermore, they indicate that high levels of connectance and nestedness allow for functional redundancies in the network, and greater potential resilience to climate change-induced biodiversity loss. However, research on pollinator networks over multiple years is sorely needed (reviewed in Burkle and Alarcon 2011), specifically research which examines how habitat alteration and environmental change impacts complex and spatially explicit pollinator network architectures (reviewed in Gonzalez et al. 2011). These future studies will greatly improve our understanding of environmental change impacts on pollinator community dynamics.

4.11.2 Ecosystem Service Changes

As mentioned earlier in the chapter, plants and pollinators provide a number of critical ecosystem services. Throughout this chapter, we have discussed research indicating that alterations in local and regional climate can disrupt plant and pollinator phenology, potentially leading to population and community alteration. In our discussion of pollinator networks, we have further shown that simulated alteration of plant and pollinator phenology can lead to marked changes in community-level interactions. The consequences of these population-level and community-level alterations on ecosystem services could be various, and include potential changes in the quantity, quality, spatial availability, and temporal availability of ecosystem services. Unfortunately, research that directly examines the impact of the various dimensions of local climate change on pollination service acquisition is rare to nonexistent. In the following paragraphs, we discuss how potential outcomes of warming or warming and drying scenarios, specifically reduction in the abundance and diversity of pollinators, may impact ecosystem services provided by wild plants and native pollinators.

4.11.2.1 Wild Plant Pollination

The impact of pollination disruption on wild plant communities and the ecosystem services they provide is potentially wide-ranging, but largely understudied (Tylianakis et al. 2008). Though more than 75% of wild plant species are dependent on insect pollination for reproduction (Ollerton et al. 2011), the impacts of this dependency on community or population level ecosystem services are not clear. Most existing studies have focused on single-species analyses of wild plant reproductive success across varying habitat treatments (e.g., Fenster and

Dudash 2001; Jules and Rathcke 1999). A recent meta-analysis of these studies has found that self-incompatible pollinator-dependent plant species exhibited greater declines in fragmented habitats than self-compatible plant species (Aguilar et al. 2006), and cross studies, the effects of fragmentation on pollinators were highly correlated with the effects on plant reproduction. Both of these findings suggest that pollination limitation could be a key driver for wild plant population decline. Of the wild plant species studied, 62–73% show pollination limitation (Ashman et al. 2004; Burd 1994), and though the long-term consequences of pollen limitation on population growth are uncertain (Hegland and Totland 2008), simultaneous declines in native plant and pollinator populations suggest a link between these two patterns (Biesmeijer et al. 2006). Thus, wild plants may face declines if their pollinators exhibit climate-induced spatial or temporal change, or general population decay.

Biodiversity loss in wild plant communities can have devastating effects on ecosystem services because wild plants are critical for ecosystem processes in both natural and human-altered landscapes. Aside from providing humans with food, medicines, fuel, and construction materials, wild plants also support important processes in agricultural, rural, and urban landscapes, such as pest-predation (reviewed in Chaplin-Kramer et al. 2011), nitrogen fixation (e.g., Hooper and Vitousek 1997), erosion control (e.g., Philpott et al. 2008), water filtration and storage (e.g., Lin and Richards 2007), and carbon sequestration (reviewed in Hooper et al. 2005). Lastly, wild plants provide habitat needed for the migration of important seed dispersers and serve as plant propagule reservoirs for the recolonization of disturbed habitats (e.g., Jha and Dick 2008). Thus, wild plants are critical for the function and regenerative capacity of natural and human-altered landscapes, and their decline would undoubtedly reduce the depth and range of ecosystem services they currently provide.

4.11.2.2 Crop Plant Pollination

As discussed in the introduction of the chapter, animal pollination is important for crop production and contributes to the stability of food prices, food security, food diversity, and human nutrition (Steffan-Dewenter et al. 2005). An estimated 15–30% of the American diet depends on insect pollination (reviewed in Losey and Vaughan 2006) and globally, the cultivation of pollinator-dependent crops is growing (Aizen et al. 2008). Thus the loss of pollinators, without strategic market response, could translate into a production deficit of an estimated –40% for fruits and –16% for vegetables (Gallai et al. 2009). These studies all suggest that climate-induced pollinator declines or disruptions to crop pollination could result in the alteration or reduction of food quantity, quality, diversity, availability, and nutritional content, potentially compromising global food security.

4.11.3 Mitigation Possibilities

A number of options exist for improving conditions for pollinators and buffering disruption of pollination interactions and general biodiversity loss. Unfortunately, very little research on

pollinator restoration has been conducted specifically in the context of climate. In the following paragraphs, we present mitigation strategies that have been developed with respect to other types of environmental change, as they serve as key starting points for climate-specific restoration strategies. Though many of the practices for pollination restoration are similar, restoration projects can vary in their specific objectives and thus may have different concepts of restoration success (Menz et al. 2011). In particular, we focus on local and regional habitat mitigation strategies that are aimed at increasing the abundance and diversity of native pollinators, but also briefly discuss the challenges and opportunities for better developing pollinator restoration practices in the context of climate. Generally, the best insurance for protecting pollination services in the face of any alteration in local and regional climate involves maintaining or restoring high abundances and diversities of wild pollinators, their food plants, and their nesting resources throughout their current and predicted geographical ranges.

4.11.3.1 Local Habitat Restoration

Research on local habitat restoration strategies is the most well-studied area of pollinator conservation and includes a wide range of on-site practices, such as the sowing flowering strips and installation of hedgerows. Pollinators are dependent on both flowering and nesting resources (Kremen et al. 2007; Potts et al. 2005; Williams et al. 2010; Winfree 2010). Thus, it is essential to consider pollinator nesting and floral resource needs while deciding on the location, size, configuration, and longevity of the restoration. When considering the selection of plants to include in the local restoration, it is also critical to consider nectar and pollen needs of the target pollinator community across their foraging periods (e.g., Dixon 2009; Williams et al. 2010). Some studies suggest the strategic planting of ‘framework’ and ‘bridging’ plants, which respectively, provide resources necessary for supporting large pollinator numbers and provide resources during resource poor time periods (Dixon 2009). Bridging plants may become even more important, if there is a mid-summer decline in floral resource availability associated with warmer conditions (Aldridge et al. 2011). Furthermore, it is important to consider the facilitative and competitive interactions between the plants within the restoration in order to select a mix that optimizes resource availability for pollinators, as well as, reproductive capacity for the plants themselves (reviewed in Menz et al. 2011).

For the restoration location, field margins are the most commonly utilized areas within agricultural areas (Carvell et al. 2004; Meek et al. 2002; Pywell et al. 2006), because they are usually not planted with crop plants and are often long and linear, easing the process of sowing, planting, and weeding. Within crop fields, field margins and adjacent lands, flowering strips, especially those that include non-legume forbs (e.g., Pywell et al. 2006), are a low cost method to provide pollinators with floral resources. These flowering strips have been shown to increase the abundance and diversity of native bees and butterflies for at least a single season, often more (e.g., Potts et al. 2009; Pywell et al. 2006). Resowing of these strips can provide extended resources and also help reduce the

occurrence of weeds (Potts et al. 2009). If a longer term restoration is preferred, hedgerows that include woody perennial plants can potentially provide both nesting and floral resources (Menz et al. 2011).

4.11.3.2 Regional Habitat Restoration

Regional habitat restoration strategies for pollinator conservation include the preservation of unmanaged natural habitat and modifications of existing practices on human-managed lands. A number of studies have shown that the preservation of natural habitat within agricultural areas can lead to higher pollinator abundances, richness, and pollination services for adjacent crops (reviewed in Kremen et al. 2007). Furthermore, the presence of remnant habitats can be critical for the colonization of recently restored habitats (Forup and Memmott 2005; Forup et al. 2008). Human-altered regional habitat can also be used to support pollinator populations, if managed appropriately. Minimizing grazing and cutting of grasslands can increase regional floral resource availability (Duffey et al. 1974; Kruess and schardtke 2002) and insect nest site availability (Morris 2000; Woodcock et al. 2007). Pasture that is infrequently grazed can provide bee populations with important floral and nesting resources (e.g., Morandin et al. 2007), and the reduction of fertilizer application, in conjunction with reduced grazing, has been shown to provide improved habitat for a number of butterfly species (e.g., Erhardt 1985).

Whether natural habitat is preserved or human-managed landscapes are modified for pollinator conservation, it is essential to consider the role of habitat restoration in supporting essential regional pollinator dispersal and migration processes, which may vary depending on pollinator community (reviewed in Menz et al. 2011; Powell and Powell 1987; Ricketts 2001). A number of spatial simulation models of pollinator restoration have shown that the best habitat restoration design for pollinator persistence and pollination service was strongly influenced by the foraging behavior of the target pollinator species (Broisi et al. 2008; Keitt 2009). Thus, restoration should keep in mind the dispersal capacities of target pollinator species (reviewed in Menz et al. 2011). For example, for highly mobile species, the restoration processes can consider creating a 'stepping stone' habitat (e.g., Ottewell et al. 2009), whereas dispersal limited species may need more contiguous linear corridors of high-quality habitat (Tewksbury et al. 2002) to facilitate movement through inhospitable matrices. In fact, within agricultural settings, plant populations connected by corridors (Townsend and Levey 2005; Van Geert et al. 2010) or highly biodiverse matrices (Jha and Dick 2010) have been shown to participate in extensive pollen transfer. Thus, habitat restoration that facilitates pollinator movement has the potential to support improved pollination services across natural and human-altered landscapes, particularly in light of current and plausible future changes in local and regional weather patterns and climate.

4.11.3.3 Pollination Restoration and Climate

The habitat-restoration strategies discussed in this chapter provide only indirect options for buffering global climate change; however, the act of increasing pollinator abundance

and species richness in a community, at the least, increases the probability that a community or population can persist in altered conditions. Increased population densities and gene flow levels usually lead to populations with greater adaptive genetic diversity (sensu Conner and Hartl 2004). These genetically diverse populations are more likely to be comprised of individuals genetically more suited to altered habitat conditions. Furthermore, there is substantial research illustrating that many ecosystem processes are a function of biodiversity levels (e.g., Balvanera et al. 2006; Cardinale et al. 2006; Naeem 2009) and that ecosystem process change is often less marked when biodiversity levels are high, due to the potential functional redundancy among species (Montoya and Raffaelli 2010) and response diversity (the differing responses of different species to the same environmental change) (Winfrey and Kremen 2009). Thus by maintaining high population-level genetic diversity and community-level species diversity, restorations can provide potential safeguards against future ecosystem alterations from climate and other environmental stressors.

Furthermore, it is possible to take the mitigation strategies discussed above and adapt them to the specific situations predicted in global climate model change scenarios. One potential result based on these scenarios is a temporal or spatial shift in species flowering or foraging, which would be likely given that species exhibit varying responses to climate (Parmesan 2007). As discussed in the previous section, one pollinator network study suggests that one way to make pollinator restoration habitats more resilient to future climate conditions is to extend the flowering season of existing restoration areas (Memmott et al. 2010). While this study provides insight into how potential phenological changes could be incorporated into existing restoration plans, there are a vast number of restoration strategies that require further research in the context of climate change. Specifically, future work is needed to examine the role of nesting resources and flowering species density in altered climate conditions.

4.11.4 Conclusions and Policy and Management Implications

While conservation biologists are often focused on taking measures to adapt existing management strategies to whatever climate plausibly could occur in the future or to create new strategies that are more resilient, the goal to develop policies that minimize all human climate forcing needs to be a high priority.

The next line of defense is to ensure that conservation management strategies, both existing and in planning, are designed with climate effects in mind. Many of the recommended strategies for making protected areas more resilient to climate (Heller and Zavaleta 2009) are also those long recommended as best practices for conservation, such as ensuring connectivity between reserves, encompassing latitudinal and elevational gradients within reserves or reserve networks, creating buffer zones around reserves, and ensuring that land-use practices in the matrix are favorable to biodiversity. Given the enormous existing challenges of implementing conservation action successfully (Knight et al. 2008), the concordance between recommended conservation measures for adapting to

climate, including plausible changes in local and regional climatic conditions, and other environmental threats is indeed a welcome relief. This concordance also signals how important it is, in the face of climate risks, to enact a full suite of multi-scale conservation measures on the ground to deal with the multiple, synergistic effects of interacting drivers of local and global extinction (Heller and Zavaleta 2009).

Conservation of pollinator biodiversity falls within this general set of recommendations. Thus, rather than repeating this ground, we focus here on the maintenance and conservation of pollination function, rather than pollinators per se, and recommend five key focal points for policy and management, at local and regional scales.

LOCAL:

- Maintaining pollination function in an area requires maintaining a locally diverse set of pollinator species. Diverse groups of pollinators provide enhanced pollination function, through complementarity and other mechanisms (Hoehn et al. 2008; Klein et al. 2009), and are more likely to withstand multiple, potentially synergistic, threats, through response diversity (Winfree and Kremen 2009). Actions that maintain or restore the diversity of pollinators locally are therefore critically important.
- Maintaining the diversity and abundance of floral resources is a key factor in maintaining the local diversity of pollinators (Potts et al. 2003). Therefore, it is important to enact policies and implement actions that provide floral resources in working lands, including agricultural, urban, pastoral, and plantation landscapes. Such landscapes can support high bee diversity under proper management (e.g., Batary et al. 2011; Cane et al. 2006; Holzschuh et al. 2008; Kremen et al. 2002; Winfree et al. 2007a).
- In restoring plant communities to support pollinators, it is important to ensure that a phenological sequence of plants is established that provide bloom throughout the pollinators' flight season (Menz et al. 2011). For added resilience to climate, specific attention should be paid to enhancing resources at the beginning and end of the flight season (Mommott et al. 2010).

REGIONAL

- Maintenance of the regional species pool is equally important. Extensive research has shown that the landscape scale is an extremely important influence on pollinator abundance and diversity (Garibaldi et al. 2011; Ricketts et al. 2008), and that local scale amelioration of habitat tends to augment pollinator diversity and abundance only in the most simplified landscapes (Batary et al. 2011). Therefore, maintaining sufficient natural habitats at the regional scale is critical for supporting healthy pollinator communities and services (Chaplin-Kramer et al. 2011; Kremen et al. 2002).
- Favorable local scale management practices, such as organic farming practices can have landscape level effects that add to the local effects of such management practices (Gabriel et al. 2010; Holzschuh et al. 2008).

Given the critical role of wild pollinators in maintaining a nutritional human food supply (Eilers et al. 2011; Garibaldi et al. 2011; Klein et al. 2007; McGregor 1976), and the recent

and widespread losses of our principal managed pollinator, *Apis mellifera* (Neumann and Carreck 2010), policies and conservation management plans should accord special attention to maintaining the diversity and resilience of pollinator communities, especially in the face of global climate change.

References

- Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen, 2006: Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.*, **9**, 968–980.
- Aizen, M. A., L. A. Garibaldi, S. A. Cunningham, and A. M. Klein, 2008: Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.*, **18**, 1572–1575.
- Alarcon, R., N. M. Waser, and J. Ollerton, 2008: Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos*, **117**, 1796–1807.
- Aldridge, G., D. W. Inouye, J. R. K. Forrest, W. A. Barr, and A. J. Miller-Rushing, 2011: Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *J. Ecol.*, **99**, 905–913.
- Amano, T., R. J. Smithers, T. H. Sparks, and W. J. Sutherland, 2010: A 250-year index of first flowering dates and its response to temperature changes. *Proc. R. Soc. B Biol. Sci.*, **277**, 2451–2457.
- Ashman, T. L., and Coauthors, 2004: Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408–2421.
- Bahn, M., and C. Körner, 2003: Recent increases in summit flora caused by warming in the Alps. *Alpine Biodiversity in Europe*, L. Nagy, G. Grabherr, C. Körner, and D. B. A. Thompson, Eds., Springer, Berlin, Germany, 437–442.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid, 2006: Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, **9**, 1146–1156.
- Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen, 2003: The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA*, **100**, 9383–9387.
- Basilio, A. M., D. Medan, J. P. Torretta, and N. J. Bartoloni, 2006: A year-long plant-pollinator network. *Austral. Ecol.*, **31**, 975–983.
- Batary, P., B. Andras, D. Kleijn, and T. Tschamtké, 2011: Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B Biol. Sci.*, **278**, 1894–1902.
- Bawa, K. S., S. H. Bullock, D. R. Perry, R. E. Coville, and M. H. Grayum, 1985: Reproductive-biology of tropical lowland rain-forest trees. 2. Pollination systems. *Am. J. Bot.*, **72**, 346–356.
- Biesmeijer, J. C., and Coauthors, 2006: Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.
- Bommarco, R., and Coauthors, 2010: Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B Biol. Sci.*, **277**, 2075–2082.
- Brittain, C. A., M. Vighi, R. Bommarco, J. Settele, and S. G. Potts, 2010: Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic. Appl. Ecol.*, **11**, 106–115.
- Brosi, B. J., P. R. Armsworth, and G. C. Daily, 2008: Optimal design of agricultural landscapes for pollination services. *Conserv. Lett.*, **1**, 27–36.
- Bryant, S. R., C. D. Thomas, and J. S. Bale, 1997: Nettle-feeding nymphalid butterflies: temperature, development and distribution. *Ecol. Entomol.*, **22**, 390–398.
- Burd, M., 1994: Bateman principle and plant reproduction – the role of pollen limitation in fruit and seed set. *Bot. Rev.*, **60**, 83–139.
- Burkle, L., A. T. Knight, and J. M. Chase, in prep: Massive extirpation of mid-western bees.
- Burkle, L. A., and R. Alarcon, 2011: The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. *Am. J. Bot.*, **98**, 528–538.
- Burkle, L., and R. Irwin, 2009: The importance of interannual variation and bottom-up nitrogen enrichment for plant-pollinator networks. *Oikos*, **118**, 1816–1829.
- Burkle, L., T. Griswold, J. Hernandez, D. Inouye, and J. Koch, 2011: *Climate Change and Range Shifts*. IUCN/SSC Conservation Breeding Specialist Group, 528–538.
- Cane, J. H., 2001: Habitat fragmentation and native bees: a premature verdict? *Conserv. Ecol.*, **5**, art. no.3.
- Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams, 2006: Complex responses within a desert bee guild (Hymenoptera: *Apiformes*) to urban habitat fragmentation. *Ecol. Appl.*, **16**, 632–644.
- Cardinale, B. J., J. J. Weis, A. E. Forbes, K. J. Tilmon, and A. R. Ives, 2006: Biodiversity as both a cause and consequence of resource availability: a

- study of reciprocal causality in a predator-prey system. *J. Anim. Ecol.*, **75**, 497–505.
- Carvell, C., W. R. Meek, R. F. Pywell, and M. Nowakowski, 2004: The response of foraging bumblebees to successional change in newly created arable field margins. *Biol. Conserv.*, **118**, 327–339.
- Climate Change 2001: The Scientific Basis. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, Eds., Cambridge, University Press, Cambridge, UK, 83 pp.
- Chaplin-Kramer, R., K. Tuxen-Bettman, and C. Kremen, 2011: Value of wildlands habitat for supplying pollination services to Californian agriculture. *Rangelands*, **33**, 33–41.
- Conner, J., and D. Hartl, 2004: *A Primer of Ecological Genetics*. Sinauer Associates, Inc., 304 pp.
- Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen, 2009: Flowering range changes across an elevation gradient in response to warming summer temperatures. *Glob. Change Biol.*, **15**, 1141–1152.
- Daily, G. C., 1997: *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, 392 pp.
- Damschen, E. I., S. Harrison, and J. B. Grace, 2010: Climate change effects on an endemic-rich edaphic flora: resurveying Robert H. Whittaker's Siskiyou sites (Oregon, USA). *Ecology*, **91**, 3609–3619.
- Dennis, R. L. H., and T. H. Sparks, 2007: Climate signals are reflected in an 89 year series of British Lepidoptera records. *Eur. J. Entomol.*, **104**, 763–767.
- Devoto, M., M. Zimmermann, and D. Medan, 2007: Robustness of plant-flower visitor webs to simulated climate change. *Ecol. Austral.*, **17**, 37–50.
- Dixon, K. W., 2009: Pollination and Restoration. *Science*, **325**, 571–573.
- Doi, H., O. Gordo, and I. Katano, 2008: Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Clim. Res.*, **36**, 181–190.
- Duffey, E., M. Morris, J. Sheail, L. Ward, D. Wells, and T. Wells, 1974: *Grassland Ecology and Wildlife Management*. Chapman & Hall, 281 pp.
- Dukes, J. S., and H. A. Mooney, 1999: Does global change increase the success of biological invaders? *Trends Ecol. Evol.*, **14**, 135–139.
- Dunne, J. A., R. J. Williams, and N. D. Martinez, 2002: Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. USA*, **99**, 12917–12922.
- Dupont, Y. L., B. Padron, J. M. Olesen, and T. Petanidou, 2009: Spatio-temporal variation in the structure of pollination networks. *Oikos*, **118**, 1261–1269.
- Eilers, E. J., C. Kremen, S. S. Greenleaf, A. K. Garber, and A. M. Klein, 2011: Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS One*, **6**, e21363.
- Erhardt, A., 1985: Diurnal Lepidoptera – sensitive indicators of cultivated and abandoned grassland. *J. Appl. Ecol.*, **22**, 849–861.
- Fenster, C. B., and M. R. Dudash, 2001: Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*. *Ecology*, **82**, 844–851.
- Fitter, A. H., and R. S. R. Fitter, 2002: Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.
- Forup, M. L., and J. Memmott, 2005: The restoration of plant-pollinator interactions in hay meadows. *Restor. Ecol.*, **13**, 265–274.
- Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott, 2008: The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *J. Appl. Ecol.*, **45**, 742–752.
- Gabriel, D., S. Sait, J. A. Hodgson, U. Schmutz, W. E. Kunin, and T. J. Benton, 2010: Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecol. Lett.*, **13**(7), 858–869, <http://dx.doi.org/10.1111/j.1461-0248.2010.01481.x>.
- Gallagher, R. V., L. J. Beaumont, L. Hughes, and M. R. Leishman, 2010: Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *J. Ecol.*, **98**, 790–799.
- Gallai, N., J. M. Salles, J. Settele, and B. E. Vaissiere, 2009: Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.*, **68**, 810–821.
- Garibaldi, L., and Coauthors, 2011: Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.*, **14**(10), 1062–1072.
- Gonzalez, A., B. Rayfield, and Z. Lindo, 2011: The disentangled bank: how loss of habitat fragments and disassembles ecological networks. *Am. J. Bot.*, **98**, 503–516.
- Gordo, O., and J. J. Sanz, 2006: Temporal trends in phenology of the honey bee *Apis mellifera* (L.) and the small white *Pieris rapae* (L.) in the Iberian Peninsula (1952–2004). *Ecol. Entomol.*, **31**, 261–268.
- Greenleaf, S. S., and C. Kremen, 2006: Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci. USA*, **103**, 13890–13895.
- Hegland, S. J., and O. Totland, 2008: Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Oikos*, **117**, 883–891.
- Hegland, S. J., A. Nielsen, A. Lazarou, A. L. Bjerknes, and O. Totland, 2009: How does climate warming affect plant-pollinator interactions? *Ecol. Lett.*, **12**, 184–195.
- Heller, N. E., and E. S. Zavaleta, 2009: Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biol. Conserv.*, **142**, 14–32.
- Hoehn, P., T. Tschamtkke, J. M. Tylianakis, and I. Steffan-Dewenter, 2008: Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B Biol. Sci.*, **275**, 2283–2291.
- Holt, R. D., J. H. Lawton, G. A. Polis, and N. D. Martinez, 1999: Trophic rank and the species-area relationship. *Ecology*, **80**, 1495–1504.
- Holzschuh, A., I. Steffan-Dewenter, and T. Tschamtkke, 2008: Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, **117**, 354–361.
- Hooper, D. U., and P. M. Vitousek, 1997: The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.
- Hooper, D. U., and Coauthors, 2005: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, **75**, 3–35.
- Jha, S., and C. W. Dick, 2008: Shade coffee farms promote genetic diversity of native trees. *Curr. Biol.*, **18**, 1126–1128.
- Jha, S., and C. W. Dick, 2010: Native bees mediate long-distance pollen dispersal in a shade coffee landscape mosaic. *Proc. Natl. Acad. Sci.*, **107**, 13760–13764.
- Jordano, P., J. Bascompte, and J. M. Olesen, 2003: Invariant properties in co-evolutionary networks of plant-animal interactions. *Ecol. Lett.*, **6**, 69–81.
- Jules, E. S., and B. J. Rathcke, 1999: Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. *Conserv. Biol.*, **13**, 784–793.
- Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Muller, and A. Cafisch, 2010: The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.*, **13**, 442–452.
- Keitt, T. H., 2009: Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol. Appl.*, **19**, 1561–1573.
- Kelly, A. E., and M. L. Goulden, 2008: Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. USA*, **105**, 11823–11826.
- Kerr, J. T., 2001: Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Conserv. Ecol.*, **5**.
- Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschamtkke, 2007a: Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.*, **274**, 303–313.
- Klein, A. M., C. M. Mueller, P. Hoehn, and C. Kremen, 2009: Understanding the role of species richness for pollination services. *Biodiversity, Ecosystem Functioning, and Human Wellbeing: an Ecological and Economic Perspective*. D. Bunker, A. Hector, M. Loreau, C. Perrings, and S. Naem, Eds., Oxford University Press, 195–208.
- Knight, A. T., R. M. Cowling, M. Rouget, A. Balmford, A. T. Lombard, and B. M. Campbell, 2008: Knowing but not doing: selecting priority conservation areas and the research-implementation gap. *Conserv. Biol.*, **22**, 610–617.
- Koch, J., in prep: Bumble bee distributions across North America based on digitation of historic reference collections.
- Kremen, C., and Coauthors, 2007: Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.*, **10**, 299–314.
- Kremen, C., N. M. Williams, and R. W. Thorp, 2002: Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci.*, **99**, 16812–16816.
- Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp, 2004: The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, **7**, 1109–1119.
- Kruess, A., and T. Tschamtkke, 1994: Habitat fragmentation, species loss, and biological-control. *Science*, **264**, 1581–1584.
- Kruess, A., and T. Tschamtkke, 2002: Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biol. Conserv.*, **106**, 293–302.
- Lenoir, J., J. C. Gegout, P. A. Marquet, P. de Ruffray, and H. Brisse, 2008: A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Lin, B. B., and P. L. Richards, 2007: Soil random roughness and depression storage on coffee farms of varying shade levels. *Agric. Water Manag.*, **92**, 194–204.
- Losey, J. E., and M. Vaughan, 2006: The economic value of ecological services provided by insects. *Bioscience*, **56**, 311–323.
- Macarthur, R., and J. W. Macarthur, 1961: On bird species-diversity. *Ecology*, **42**, 594–598.
- McGregor, S. E., 1976: *Insect Pollination of Cultivated Crop Plants*, Vol. 496, USDA-ARS.
- Medan, D., A. M. Basilio, M. Devoto, N. J. Bartoloni, J. P. Torretta, and T. Petanidou, 2006: *Measuring Generalization and Connectance in Temperate*,

- Year-long Active Systems*. Univ Chicago Press, 1427 E 60 St, Chicago, IL 60637 USA, 245–259.
- Meek, B., D. Loxton, T. Sparks, R. Pywell, H. Pickett, and M. Nowakowski, 2002: The effect of arable field margin composition on invertebrate biodiversity. *Biol. Conserv.*, **106**, 259–271.
- Memmott, J., 1999: The structure of a plant-pollinator food web. *Ecol. Lett.*, **2**, 276–280.
- Memmott, J., and N. M. Waser, 2002: Integration of alien plants into a native flower-pollinator visitation web. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, **269**, 2395–2399.
- Memmott, J., N. M. Waser, and M. V. Price, 2004: Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, **271**, 2605–2611.
- Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price, 2007: Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.*, **10**, 710–717.
- Memmott, J., C. Carvell, R. F. Pywell, and P. G. Craze, 2010: The potential impact of global warming on the efficacy of field margins sown for the conservation of bumble-bees. *Philos. Trans. R. Soc. B Biol. Sci.*, **365**, 2071–2079.
- Menz, M. H. M., R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon, 2011: Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends. Plant. Sci.*, **16**, 4–12.
- Menzel, A., T. H. Sparks, N. Estrella, and D. B. Roy, 2006: Altered geographic and temporal variability in phenology in response to climate change. *Glob. Ecol. Biogeogr.*, **15**, 498–504.
- Millennium Ecosystem Assessment, 2005: Full Reports.
- Miller-Rushing, A. J., and R. B. Primack, 2008: Global warming and flowering times in Thoreau's concord: a community perspective. *Ecology*, **89**, 332–341.
- Miller-Rushing, A. J., T. T. Hoye, D. W. Inouye, and E. Post, 2010: The effects of phenological mismatches on demography. *Philos. Trans. R. Soc. B Biol. Sci.*, **365**, 3177–3186.
- Miyajima, D., 2004: Pollination and seed set in vinca (*Catharanthus roseus*). *J. Hort. Sci. Biotechnol.*, **79**, 771–775.
- Montoya, J. M., and D. Raffaelli, 2010: Climate change, biotic interactions and ecosystem services. *Philos. Trans. R. Soc. B Biol. Sci.*, **365**, 2013–2018.
- Morandini, L. A., M. L. Winston, V. A. Abbott, and M. T. Franklin, 2007: Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic. Appl. Ecol.*, **8**, 117–124.
- Morris, M. G., 2000: The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biol. Conserv.*, **95**, 129–142.
- Naeem, S., 2009: ECOLOGY Gini in the bottle. *Nature*, **458**, 579–580.
- NRC, 2005: *National Research Council: Radiative Forcing of Climate Change: Expanding the Concept and Addressing Uncertainties*. The National Academies Press, 208 pp.
- Neumann, P., and N. L. Carreck, 2010: Honey bee colony losses. *J. Apic. Res.*, **49**, 1–6.
- Olesen, J. M., J. Bascompte, H. Elberling, and P. Jordano, 2008: Temporal dynamics in a pollination network. *Ecology*, **89**, 1573–1582.
- Ollerton, J., R. Winfree, and S. Tarrant, 2011: How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Ottewill, K. M., S. C. Donnellan, A. J. Lowe, and D. C. Paton, 2009: Predicting reproductive success of insect- versus bird-pollinated scattered trees in agricultural landscapes. *Biol. Conserv.*, **142**, 888–898.
- Parnesan, C., 2007: Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.*, **13**, 1860–1872.
- Parnesan, C., and G. Yohe, 2003: A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Petanidou, T., A. Kallimanis, J. Tzanopoulos, S. Sgardelis, and J. Pantis, 2008: Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of speciation. *Ecol. Lett.*, **11**, 564–575.
- Philpott, S. M., B. B. Lin, S. Jha, and S. J. Brines, 2008: A multi-scale assessment of hurricane impacts on agricultural landscapes based on land use and topographic features. *Agric. Ecosyst. Environ.*, **128**, 12–20.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. G. Willmer, 2003: Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.
- Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer, 2005: Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.*, **30**, 78–85.
- Potts, S. G., B. A. Woodcock, S. P. M. Roberts, T. Tscheulin, E. S. Pilgrim, V. K. Brown, and J. R. Tallwin, 2009: Enhancing pollinator biodiversity in intensive grasslands. *J. Appl. Ecol.*, **46**, 369–379.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin, 2010: Global pollinator declines: trends, impacts and drivers. *Trends. Ecol. Evol.*, **25**, 345–353.
- Powell, A. H., and G. V. N. Powell, 1987: Population-dynamics of male Euglossine bees in Amazonian forest fragments. *Biotropica*, **19**, 176–179.
- Pywell, R. F., and Coauthors, 2006: Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.*, **129**, 192–206.
- Rafferty, N. E., and A. R. Ives, 2011: Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecol. Lett.*, **14**, 69–74.
- Ricketts, T. H., 2001: The matrix matters: Effective isolation in fragmented landscapes. *Am. Nat.*, **158**, 87–99.
- Ricketts, T. H., and Coauthors, 2008: Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.*, **11**, 499–515.
- Roubik, D. W., 1995: *Pollination of Cultivated Plants in the Tropics*. Food and Agriculture Organization of the United Nations, 196 pp.
- Scherrer, D., and C. Korner, 2010: Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob. Change Biol.*, **16**, 2602–2613.
- Schweiger, O., and Coauthors, 2010: Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biol. Rev.*, **85**, 777–795.
- Shmida, A., and M. V. Wilson, 1985: Biological determinants of species-diversity. *J. Biogeogr.*, **12**, 1–20.
- Sparks, T. H., E. P. Jeffrey, and C. E. Jeffrey, 2000: An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *Int. J. Biometeorol.*, **44**, 82–87.
- Sparks, T. H., A. Langowska, A. Glazaczow, Z. Wilkaniec, M. Bienkowska, and P. Tryjanowski, 2010: Advances in the timing of spring cleaning by the honeybee *Apis mellifera* in Poland. *Ecol. Entomol.*, **35**, 788–791.
- Steffan-Dewenter, I., S. G. Potts, and L. Packer, 2005: Pollinator diversity and crop pollination services are at risk. *Trends. Ecol. Evol.*, **20**, 651–652.
- Steinger, T., C. Korner, and B. Schmid, 1996: Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia*, **105**, 94–99.
- Tewksbury, J. J., and Coauthors, 2002: Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci. USA*, **99**, 12923–12926.
- Thomson, J. D., 2010: Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philos. Trans. R. Soc. B Biol. Sci.*, **365**, 3187–3199.
- Townsend, P. A., and D. J. Levey, 2005: An experimental test of whether habitat corridors affect pollen transfer. *Ecology*, **86**, 466–475.
- Tuell, J. K., and R. Isaacs, 2010: Community and species-specific responses of wild bees to insect pest control programs applied to a pollinator-dependent crop. *J. Econ. Entomol.*, **103**, 668–675.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A. M. Klein, N. Buchmann, J. Perner, and T. Tscharntke, 2008: Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol.*, **6**, 947–956.
- Valdovinos, F. S., R. Ramos-Jiliberto, J. D. Flores, C. Espinoza, and G. Lopez, 2009: Structure and dynamics of pollination networks: the role of alien plants. *Oikos*, **118**, 1190–1200.
- Van Geert, A., F. Van Rossum, and L. Triest, 2010: Do linear landscape elements in farmland act as biological corridors for pollen dispersal? *J. Ecol.*, **98**, 178–187.
- Vazquez, D. P., N. Bluthgen, L. Cagnolo, and N. P. Chacoff, 2009: Uniting pattern and process in plant-animal mutualistic networks: a review. *Ann. Bot.*, **103**, 1445–1457.
- Von Holle, B., Y. Wei, and D. Nickerson, 2010: Climatic variability leads to later seasonal flowering of Floridian plants. *PLoS One*, **5**, e11500.
- Walther, G. R., and Coauthors, 2002: Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Walther, G. R., S. Beissner, and C. A. Burga, 2005: Trends in the upward shift of alpine plants. *J. Veg. Sci.*, **16**, 541–548.
- Walther, G. R., and Coauthors, 2009: Alien species in a warmer world: risks and opportunities. *Trends. Ecol. Evol.*, **24**, 686–693.
- White, G. M., D. H. Boshier, and W. Powell, 2002: Increased pollen flow counteracts fragmentation in a tropical dry forest: an example from *Swietenia humilis* Zuccarini. *Proc. Natl. Acad. Sci. USA*, **99**, 2038–2042.
- Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts, 2010: Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.*, **143**, 2280–2291.
- Winfree, R., 2010: *The Conservation and Restoration of Wild Bees. Year in Ecology and Conservation Biology 2010*. Blackwell Publishing, 169–197.
- Winfree, R., and C. Kremen, 2009: Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. B Biol. Sci.*, **276**, 229–237.
- Winfree, R., T. Griswold, and C. Kremen, 2007a: Effect of human disturbance on bee communities in a forested ecosystem. *Conserv. Biol.*, **21**, 213–223.

- Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen, 2007b: Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.*, **10**, 1105–1113.
- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen, 2008: Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.*, **45**, 793–802.
- Winfree, R., R. Aguilar, D. P. Vazquez, G. LeBuhn, and M. A. Aizen, 2009: A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, **90**, 2068–2076.
- Winfree, R., I. Bartomeus, and D. Cariveau, 2011a: Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst.*, **42**, 1–22.
- Winfree, R., B. J. Gross, and C. Kremen, 2011b: Valuing pollination services to agriculture. *Ecol. Econ.*, **71**, 1–29.
- Woodcock, B. A., and Coauthors, 2007: The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *J. Appl. Ecol.*, **44**, 60–69.