REVIEW AND SYNTHESES

How does climate warming affect plant-pollinator interactions?

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Abstract

Climate warming affects the phenology, local abundance and large-scale distribution of plants and pollinators. Despite this, there is still limited knowledge of how elevated temperatures affect plant-pollinator mutualisms and how changed availability of mutualistic partners influences the persistence of interacting species. Here we review the evidence of climate warming effects on plants and pollinators and discuss how their interactions may be affected by increased temperatures. The onset of flowering in plants and first appearance dates of pollinators in several cases appear to advance linearly in response to recent temperature increases. Phenological responses to climate warming may therefore occur at parallel magnitudes in plants and pollinators, although considerable variation in responses across species should be expected. Despite the overall similarities in responses, a few studies have shown that climate warming may generate temporal mismatches among the mutualistic partners. Mismatches in pollination interactions are still rarely explored and their demographic consequences are largely unknown. Studies on multi-species plant-pollinator assemblages indicate that the overall structure of pollination networks probably are robust against perturbations caused by climate warming. We suggest potential ways of studying warming-caused mismatches and their consequences for plant-pollinator interactions, and highlight the strengths and limitations of such approaches.

Keywords

Abundance, climate warming, distribution, global change, interaction, mismatch, mutualism, network, phenology, pollination.

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INTRODUCTION

Observational evidence from all continents shows that many ecosystems are affected by regional and global climate changes, particularly temperature increases (IPCC 2007). A growing number of studies suggest that climate change may be one of the biggest anthropogenic disturbance factors imposed on ecosystems today (Walther *et al.* 2002; Parmesan 2006). Because of the cumulative evidence of a close relationship between greenhouse gas emissions, through human use of fossil carbon, and global change (IPCC 2007), there has been a surge of scientific interest in the ecological and evolutionary effects of climate warming. Studies have shown that both the distribution and phenology of many plants and animals are biased in the directions predicted from global warming in the last few decades (Parmesan 2006), indicated by a global advancement of spring events by 2.3 days per decade and a species range shift of 6.1 km

per decade towards the poles (Parmesan & Yohe 2003). For organism groups involved in pollination interactions, this is evident through recent changes in flowering phenology, e.g., onset of flowering (Sparks *et al.* 2000; Fitter & Fitter 2002; Miller-Rushing *et al.* 2006) and the first-appearance dates of butterflies and migrating birds (Roy & Sparks 2000; Gordo & Sanz 2005, 2006). Whether climate warming will affect ecosystem functioning depends on how interactions among species are influenced. Several studies have shown alterations in trophic relationships and energy-flows in both predator-prey and plant-herbivore interactions as a consequence of rising temperatures (e.g., Stenseth & Mysterud 2002; Visser & Both 2005; Durant *et al.* 2007).

Pollination interactions are important as they benefit both biodiversity and humans. A great diversity of plants and animals – mainly insects, but also some birds, lizards and mammals- depend mutually on each other for pollination and food, and their interactions may influence population

persistence. There has been a growing appreciation of the importance of the ecosystem services provided by pollination interactions (e.g., Allen-Wardell *et al.* 1998; Ricketts *et al.* 2004; Klein *et al.* 2007), and it has been suggested that we may be in the middle of a global pollination crisis (Steffan-Dewenter *et al.* 2005; Biesmeijer *et al.* 2006), but also questioned (Ghazoul 2005). Recent reviews have indicated that knowledge of the effects of climate warming on mutualistic interactions is still limited (Walther *et al.* 2002; Visser & Both 2005), and that the current interest in pollination interactions has not yet resulted in much empirical research on how climate warming may affect this ecosystem service (Kremen *et al.* 2007; but see Memmott *et al.* 2007 for a simulation approach). Speculations on the disruptions of plant-pollinator interactions due to climate change are often brought forward (e.g., Harrington *et al.* 1999; Visser & Both 2005; Parmesan 2006), but few empirical studies exist to verify whether such disruptions do occur and reports still appear largely anecdotal.

As a first step in determining the possible effects of climate change on pollination interactions, we review the evidence of altered phenologies, abundance and distribution in plants and pollinators as a response to climate warming, and outline how these changes may influence the interactions among them. We review the nature of the current phenological response to rising temperatures in plants and pollinators and the magnitude of this response in the species groups. We present the existing evidence for phenological and distributional asynchrony, that is temporal or spatial mismatches, between plants and pollinators, and examine their potential consequences for pollination interactions. This paper also discusses the potential buffers that plant-pollinator systems have against climate warming by synthesizing information from network studies and other fields addressing the impact of, and robustness to, environmental perturbations. Finally, we present and discuss relevant research questions and approaches to reveal potential effects of temperature caused mismatches and their consequences for pollination interactions.

HOW DOES CLIMATE WARMING AFFECT FLOWERING PLANTS AND POLLINATORS?

Phenology

Many organisms respond to changes in temperature by altering their activity and metabolism. Therefore, anthropogenic induced temperature increases have the potential to affect the phenology of both plants and pollinators. Until recently, the strength and direction of the phenological responses to increasing temperatures was mainly unknown. Indeed, it had not been shown whether phenological shifts occurred at all in natural communities in response to climate change. However, in the last decade there has been increasing interest in phenological responses to climate warming (Post & Inouye 2008; Rosenzweig *et al.* 2008) and much of the knowledge on climate warming effects comes from phenological research.

Onset of flowering is regularly used to measure the arrival of spring in temperate habitats. Many plants appear to have reacted to increasing temperatures by earlier flowering during the last 20–50 years (Fitter & Fitter 2002; Fig. 1). In Europe, 78% of the observed time series provided such a trend (Menzel *et al.* 2006), which concurs with findings from

Figure 1 Framework showing how climate warming may affect the phenology and, distribution of plants (left panel) and pollinators (right panel) and thereby creating temporal or spatial mismatches in plant-pollinator interactions. In the lower half of the panels we show how and by which key factors the demography of the mutualistic partners are likely to be affected. The pathway until the mismatches is largely known, whereas the mismatches and the subsequent effects are still mostly unknown and requires additional research.
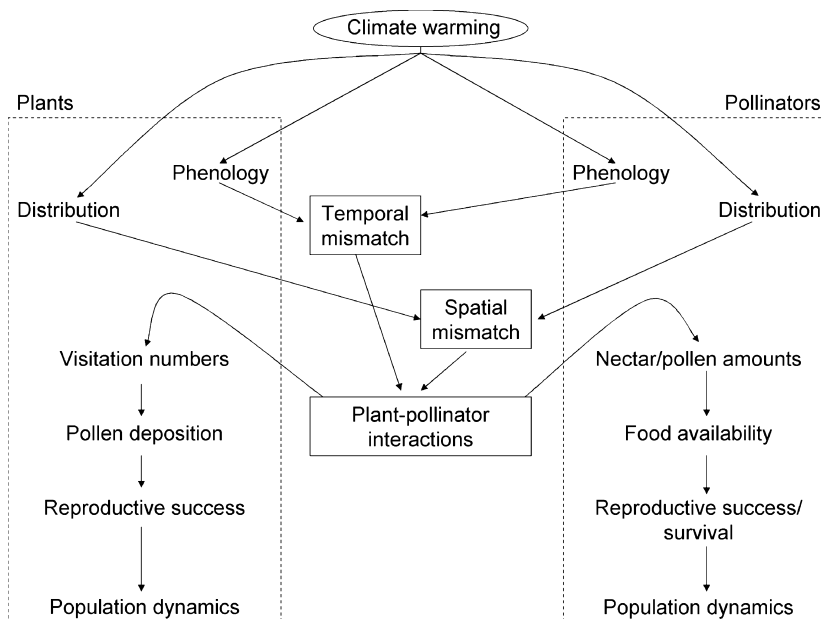
other parts of the northern hemisphere (Sparks *et al.* 2000; Miller-Rushing *et al.* 2006, 2007). Insect-pollinated plants generally react more strongly to increased warming than wind-pollinated plants, and species flowering early in the season appear to be most sensitive (Fitter & Fitter 2002; Miller-Rushing *et al.* 2007), an indication that these species have thermal-sensitive phenologies. In general, the onset of flowering appears to be correlated with the mean temperature in the month of flowering or the months prior to flowering (Sparks *et al.* 2000; Menzel *et al.* 2006). However, other factors may co-vary with temperature and be important for the observed patterns (see Future Research). The responses of flowering onset to increasing temperatures were linear in most cases (Sparks *et al.* 2000; Fitter & Fitter 2002; Gordo & Sanz 2005; Menzel *et al.* 2006), which could be important for plant interactions with pollinators. Although it is obvious that such linear responses cannot continue perpetually, Sparks *et al.* (2000) found significant linearity within the observed range of temperature variations for 24 of 25 British plant species from which 23 flowered earlier with increased temperatures (see Fig. 2 for an overall trend). To better understand the impacts of climate warming, the above mentioned generalizations of species' responses are important. We emphasize, however, that some species may not flower earlier as a response to increased temperatures (e.g., 22% of the species included in Menzel *et al.* (2006)). Also, other potential cues for flowering initiation include photoperiodicity, precipitation, soil humidity and snow melt (Inouye *et al.* 2003; Price & Waser 1998) as well as a particular combinations of cues (e.g., Lambrecht *et al.* 2007; see also Future Research). If climate change disrupts the relationships among the environmental cues which plants use to initiate flowering, past combinations of cues might reappear at novel times in the season (Price & Waser 1998; Stenseth & Mysterud 2002; Visser & Both 2005), resulting in 'bizarre' flowering times. Furthermore, phenological responses of plant species to previous temperature increases do not indicate whether plants' future responses to temperature will continue as linear, level off or follow some other relationship (see below and Fig. 2; see also Fig. 1 in Sparks *et al.* 2000). Such future responses not only depend on a plant species' direct response to temperature or other cues, but may be modified ecologically, or evolutionary, by the interactions with its pollinators (Fig. 2).

Flowering duration is another phenological aspect of great significance, both for plant reproduction and pollinator food supply. There is clear evidence for prolonged growing seasons in many plant communities in Europe during the last decades (Menzel & Fabian 1999), but the length of the flowering season appears less affected, especially for later-emerging species that show a more variable response to climate warming (Miller-Rushing &
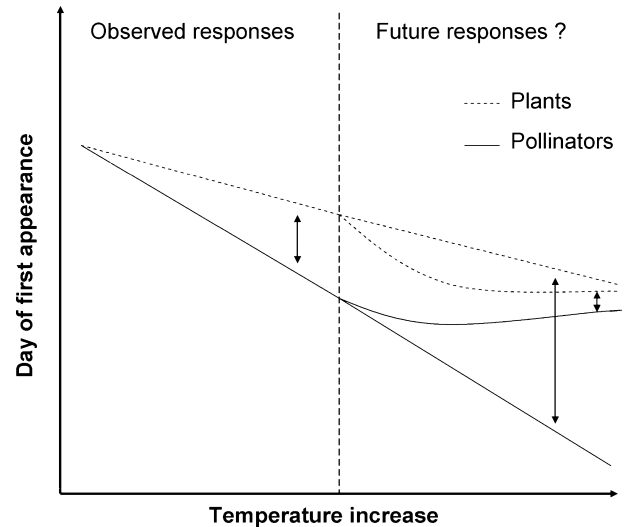

Figure 2 The linear relationships between climate warming and appearance dates in pollinators (flight activity) and plants (flowering) as currently observed, and some potential future development of this relationship. The nature (i.e. linear response) and the magnitude (slope) of responses (i.e. strongest in pollinators) are based on the few available studies (e.g., Gordo & Sanz 2005), and must therefore be viewed as an approximation of how climate warming may shape temporal plant-pollinator mismatches. The length of the arrows visualizes the relative magnitude of temporal mismatch between plant and pollinator. The lines connected by the short arrow (under future responses) illustrate one possible future situation where the adaptation of plant and pollinators to future climates are influenced by the interaction among them and the mismatch is dampened. The lines connected by the long arrow shows an extrapolated projection of the general current trend where phenologies are mainly influenced by temperature resulting in a potential further increase in the mismatch.

Primack 2008). For example, warming experiments in alpine regions have found both indications for prolonged flowering (Dunne *et al.* 2003) and no change in flowering duration (Price & Waser 1998).

Most pollinators are insects and, because insects are small and poikilothermic, it is likely that temperature will be critical for their life cycle development and activity patterns (Fig. 1), which is particularly evident in alpine and arctic regions (Totland 1994; Hodkinson *et al.* 1998). Butterflies are appealing organisms frequently attracting public attention. As a result, long-term butterfly monitoring programmes exist in several countries and studies based on such data have documented a close positive relationship between first appearance date and temperature (Roy & Sparks 2000; Forister & Shapiro 2003). Across climatic zones in Europe, the date of first emergence of butterflies is strongly correlated with temperatures in the month of, or previous to, appearance (Roy & Sparks 2000; Gordo & Sanz

2006). Roy & Sparks (2000) also showed that peak appearance of butterflies came earlier and flight duration was prolonged during a warming period from 1976 to 1998, both variables potentially influencing the interactions with the plants they pollinate.

Bees are the most important pollinators for many wild and cultivated plant species. Long-term data from Spain, spanning more than 50 years, show a clear relationship between the first appearance dates of *Apis mellifera* L. (the honey bee) and early spring temperatures (Gordo & Sanz 2006). Honey bees can be considered good indicators of climate change as they overwinter in the adult phase, and appear to react quickly to increases in spring temperatures (Gordo & Sanz 2006). Likewise, data from Nature's Calendar project (available online at http://www.nature-scalendar.org.uk) indicate that bumble bees have advanced their spring flight times by *c.* 2 weeks from 2001 to 2007 (Sparks & Collinson 2007), probably caused by higher soil temperatures that terminate queens' winter hibernation (Alford 1969). As for plants, available data indicate a linear relationship between temperature and pollinator phenology and that the effect is strongest in early-season events within the span of observed temperature changes (Roy & Sparks 2000; Forister & Shapiro 2003; Gordo & Sanz 2005, 2006; Menzel *et al.* 2006; Fig. 2).

Abundance and distribution

Temperature-driven changes in flower abundance may have a large impact on pollination interactions. Increased reproductive effort (i.e. number of flowers) appears to be one commonly observed response to experimental warming in the arctic and alpine (e.g., Arft *et al.* 1999). On the other hand, observational studies have shown that increasing spring temperatures may decrease flower abundance (Inouye *et al.* 2003) and affect species' abundance in contrasting ways within a community (Tyler 2001). In both of these studies, the temperature effect is weaker than in warming experiments, probably due to interactive effects of precipitation and humidity. Mass flowering, i.e. masting, is also generally positively affected by high temperatures (Schauber *et al.* 2002). Increased flower abundance within a community may affect the reproductive success of plant species, for example through increased visitation rates as a result of altered pollinator behaviour and composition of the pollinator community ultimately increasing out-crossing rates and seed production (e.g., van Treuren *et al.* 1994; Hegland & Totland 2005). Conversely, increased flower numbers on individual plants may cause higher selfing rates due to increased geitonogamy (e.g., Vrieling *et al.* 1999).

Increased flower numbers may also affect pollinators, as food availability appears to be one of the most important factors governing the activity and population density of many pollinator species (Steffan-Dewenter *et al.* 2002; Westphal *et al.* 2003; Hegland & Boeke 2006; Steffan-Dewenter & Schiele 2008). Evidence of direct temperature mediated effects on the abundance of pollinators is relatively rare. However, information from pollination studies along altitudinal or latitudinal gradients (proxies for temperature influence) may infer how pollinator assemblages could be affected by climate warming. For example, flies appear to become more abundant in colder and wetter areas whereas bees are often more abundant in warmer and drier habitats (Arroyo *et al.* 1982; McCall & Primack 1992; Totland 1993; Lázaro *et al.* 2008), suggesting that the composition and dominance of pollinator assemblages may change with climate warming.

Climate is a strong determinant of the geographical range of species (e.g., Moen 1999; Fig. 1) and, although precise information of species' geographic range is relatively difficult to obtain, some generalizations about climate warming effects can be made. Large climatic oscillations have occurred during historical time and have caused changes in species distributions. For example, during major glaciations, species distributions compressed towards the Equator and descended from the mountains, while during warmer inter-glacial periods, species migrated toward higher latitudes and altitudes (e.g., Taberlet *et al.* 1998; Hewitt 2000). Recent range expansions of lepidopterans and tree-line dynamics show similar patterns; they are moving towards higher latitudes and altitudes as forecasted by climate warming scenarios (Parmesan 2006). Kelly & Goulden (2008) showed that nine out of ten dominant plant species on a Southern California mountain had made a mean (+ 65 m) elevational shift upwards the last 30 years. In Norway, alpine vascular plants have shown altitudinal expansions and increases in abundance and diversity during the last century (e.g., Klanderud & Birks 2003).

MISMATCHES BETWEEN PLANTS AND POLLINATORS

The occurrence of mismatches

Plant-pollinator interactions can be disrupted in at least two ways; through temporal (phenological) and spatial (distributional) mismatches that may change the availability of mutualistic partners (Fig. 1). Mismatch occurs when the original mutualistic partners experience reduced sharing of habitat either in time or space, leading to a partial or complete trophic decoupling (Stenseth & Mysterud 2002; Visser & Both 2005). Memmott *et al.* (2007) simulated how global warming might affect a highly resolved plant-pollinator network. They found that, depending on the phenological shifts applied, between 17 and 50% of all pollinator species suffer from disruption of food supply due

to temporal mismatch. They showed that specialized pollinators were most likely to be left with no food plants, but that generalist pollinators could also experience considerable diet reductions following phenological shifts. The variation across species in phenological responses to climate warming may also uncouple many plant-pollinator interactions because the pollinators cannot track all their ancestral hosts, if some flower earlier and some later (e.g., Menzel *et al.* 2006; Memmott *et al.* 2007). As many pollinators visit plants quite opportunistically (e.g., Petanidou *et al.* 2008) such a phenological decoupling may result in the emergence of novel plant-pollinator interactions. Gordo & Sanz (2005) examined the nature of phenological responses of both plants and pollinators to increasing temperatures on the Iberian Peninsula, investigating the slopes of the responses as indications of a mismatch between the mutualistic partners. They found that both Apis mellifera and Pieris rapae advanced their activity period more than their preferred forage species, resulting in a temporal mismatch with some of their main plant resources. This result agrees with how herbivorous insects respond to climate warming in relation to food-plant availability; insect phenologies advance more than plant phenologies (Visser & Both 2005; Sparks & Collinson 2007; Fig. 2). In contrast, Kudo *et al.* (2004) found that early flowering plants in Japan advanced their flowering during a warm spring, whereas bumble bee queen emergence appeared unaffected by spring temperatures resulting in a decreased seed-set in bumble bee-pollinated plants. Thus, direct temperature responses and the occurrence of mismatches in pollination interactions may vary among species and regions.

We know of no reports that have shown climate-driven spatial mismatches in pollination interactions, and there is less evidence of such spatial mismatches in ecological interactions in general compared to temporal decoupling (Devoto *et al.* 2007; Durant *et al.* 2007; Schweiger *et al.*, in press). However, Devoto *et al.* (2007) simulated climate-driven range shifts along a rainfall gradient and found that relatively few species would go extinct and that the pollination systems appeared resilient to climate changes (here, rainfall), even when assuming that pollinators had no flexibility in host plant utilization and a total dependence of plants on pollinator visitation for reproduction and population persistence.

Consequences of mismatches

Synchronized timing of mutualistic partners may be important for efficient pollination of plants and survival of pollinators (e.g., Fig. 1). Therefore, one of the major concerns related to global warming and pollination interactions is the demographic consequence of mismatches between plants and pollinators. Assessments of how

pollination interactions might respond to climate-driven mismatches must be speculative, because little is known about how warming affects the demography and population dynamics of the involved partners (see also Fig. 1). Furthermore, the effect of climate-driven changes in food (for pollinators) and pollinator availability (for plants) is difficult to predict because our knowledge on the relative importance of bottom-up and top-down forces in population regulation is still poor (e.g., Steffan-Dewenter & Schiele 2008). If mismatches are to seriously affect pollinator demography, pollinator population densities and distributions must be controlled by bottom-up forces (sensu Durant *et al.* 2007), such as flower abundance. Likewise, whether mismatches will significantly influence plant demography depends on the extent to which plants are top-down controlled through effects of pollinator abundance on pollen availability and mobility (sensu Elzinga *et al.* 2007).

In plants, a mismatch with important pollinators could reduce pollen deposition through altered visitation (quantity or quality of floral visits), potentially increasing pollen limitation (e.g., Fig. 1). Among plant species, limitation of reproduction due to insufficient pollination is common (Ashman *et al.* 2004). However, the impact of pollen limitation (i.e. a top-down force) on population dynamics, and its relative importance compared to resource limitation (i.e. bottom-up forces), is still poorly understood, although a few studies have shown that increased seed set or seed mass after supplemental pollination can positively influence recruitment, survival and population growth rates of flowering plants (Hegland & Totland 2007; Price *et al.* 2008; see Fig. 1). Another consequence of mismatches is the cascading effects they might have on species interactions occurring later in the season. A crash in early-emerging pollinator populations may affect both early and later flowering species and sequentially flowering species may facilitate each other through maintenance of pollinator populations (Waser & Real 1979). Moreover, in northern regions many plants depend on bumble bees for sufficient pollination. If nest development is restricted by a mismatch between early emerging bumble bee queens and their main food plants, such early season events may influence pollination services later in the season.

In pollinators, we can expect that a mismatch with important forage species primarily will reduce food accessibility through altered availability of carbohydrates (nectar) and proteins (pollen), subsequently affecting pollinator survival and reproduction (e.g., Boggs & Ross 1993; Fig. 1). The effects of mismatches on pollinator population dynamics may be more severe than with plants, because pollinator dependence on nutrition often is more absolute than flowering plant species' dependence on pollination. For example, the reproductive success of hummingbirds may be determined by the degree of matching (both timing and

peak abundance) with its main flower resources (Waser 1976). In such cases, the potential for bottom-up control on pollinators' population dynamics appears evident. The generally shorter life span of pollinators, especially insects, compared to plants makes them more sensitive to climate variability (e.g., Morris *et al.* 2008), and this may be one reason why the population dynamics of many pollinators vary profoundly in time and space (e.g., Williams *et al.* 2001). Knowledge of the effect floral abundance (i.e. resource availability) has on pollinator population dynamics appears limited, but a recent study by Steffan-Dewenter & Schiele (2008) showed that bottom-up forces, including food availability, were more important than top-down forces (such as rate of parasitism) in regulating the population dynamics of a solitary bee species. An extended flowering period or increased food availability per flower in response to higher temperatures (e.g., Petanidou & Smets 1996) may partly compensate for diet reductions due to mismatches in time and space. Importantly, it is not only the presence or absence of an interacting species that determines the output of a mismatch, but also their abundance, because most plants and pollinators are generalists utilizing several mutualistic partners and many mismatches are only partial (e.g., Memmott *et al.* 2007). Altered abundance of the interacting species can potentially compensate for or strengthen the consequences of trophic mismatches (Durant *et al.* 2007).

Buffers against mismatches

Despite potential negative effects of mismatches, there are also innate properties found in plant-pollinator interactions that might buffer against their impacts. One prolific study approach the last decade has been to view ecological communities and systems as networks. Pollination ecology has, by studying entire plant-pollinator systems, been able to illustrate some of the robustness that exists in natural systems of mutualistic interactions. Plant-pollinator networks are very heterogeneous with the bulk of species having relatively few interactions, whereas a few species have many more interactions than expected by chance (Jordano *et al.* 2003; Vazquez & Aizen 2003). Overall, there are more generalist species in pollination networks than previously thought and strict one to one specialist relationships are rare in nature (Waser *et al.* 1996). This generalist tendency in pollination interactions may itself ensure that most species are not severely affected by climate-driven mismatches. Moreover, plant-pollinator networks display a nested structure, where a core of generalist species interact with each other, while most specialists interact only with these generalists (Bascompte *et al.* 2003). Furthermore, most pollination interactions are highly asymmetric, meaning that if a plant is very important to a pollinator (a high percentage

of the pollinator's visits are to this particular plant), the importance of this pollinator to the plant is low (a low percentage of the visits received by the plant comes from this pollinator) (Bascompte *et al.* 2006). The nested structure and pre-dominantly asymmetric nature of the interactions within plant-pollinator networks have been shown to stabilize these systems and make them less sensitive to species extinctions, disturbance and habitat loss (Jordano 1987; Memmott *et al.* 2004; Fortuna & Bascompte 2006). Such perturbations may create mismatches that resemble those expected after climate change. Regardless of these buffering properties, loss of generalist plant species in particular, may put other species of pollinators and plants at higher risk for extinction (e.g., Memmott *et al.* 2004).

Studies on variations in plant-pollinator network properties through time have only recently started to appear (e.g., Olesen *et al.* 2008; Petanidou *et al.* 2008; Alarcón *et al.*, in press). Knowledge of such temporal variation in plant-pollinator interactions is crucial for understanding how these systems are affected by altered climatic conditions. The cited studies all show that plant-pollinator interactions are highly dynamic and both the species comprising the networks and the links change dramatically through time. One consequence of this variation is that plant-pollinator systems may be robust against both temporal and spatial mismatches between pairs of species. The dynamic structure of the mutualistic networks might therefore act as a buffer against cascading effects of loss of species and links within the network, although mutualistic networks could also reach a tipping point and collapse under severe disturbance (Memmott *et al.* 2004; Fortuna & Bascompte 2006).

Evolutionary responses to mismatches

The phenology of species has evolved to match environmental conditions. It is, however, reasonable to believe that plants and pollinators may have different mechanisms underlying their phenology and respond to different environmental cues (Visser & Both 2005). Studies suggest that the activity of both plant and pollinating insects show linear relationships with current increases in temperature (e.g., Sparks *et al.* 2000; Gordo & Sanz 2005; Fig. 2). Despite this apparent similarity in responses, the magnitude (i.e. the slopes) of responses may diverge, resulting in a mismatch (Fig. 2). A central question is whether the responses of plants and pollinators to increasing temperatures will be parallel or whether the partners will halt or accelerate their future response relative to the other (Fig. 2). The answer lies in the potential for adaptation and whether such adaptations will be driven mainly by temperature or whether the interaction itself may shape the organisms' future responses. Fig. 2 gives some possible future developments of species' phenological responses.

Temporal mismatches among plants and pollinators may alter selection pressures that plants and pollinators exert on each other, and result in rapid evolution in pollination and reproductive traits in plants and foraging and phenological traits in pollinators as indirect responses to climate warming. A pre-requisite for such rapid genetic change is a sufficiently large fitness consequence of the experienced mismatch (Davis *et al.* 2005; Skelly *et al.* 2007). Moreover, to what extent climate warming affects selection pressures depends on whether the species use temperature as cues to track changes in the phenology of their mutualistic partners (see also Future Research). Rapid evolution in response to climate change has been documented for both insects and flowering plants (Davis *et al.* 2005; Franks *et al.* 2007; Skelly *et al.* 2007). Species' generation times may be decisive for their potential to respond to rapid direct or indirect changes of climate warming (Davis *et al.* 2005). Thus, plant species with contrasting life-histories may respond with different speed and pollinators, which generally have shorter generation times, may evolve faster as a response to changing climate conditions than their food plants (see also Morris *et al.* 2008).

FUTURE RESEARCH

Temperature plays an important role in the life of plants and pollinators, and in the interactions among them. Although temperature is the factor most often studied, many other environmental factors and cues (see also Phenology and Evolutionary responses to mismatches) may also be of great influence and potentially affect species phenology, abundance and distribution. Firm predictions of future impacts of climate warming on ecological interactions may both require knowledge of the importance of different cues to phenology and the covariance between temperature and other cues. Thus, future research focus must include not only direct temperature effects on pollination interactions, but also indirect and correlated effects of climate change. One goal should be to assess separately the direct and indirect effects of climate warming on plant-pollinator interactions. Moreover, different cues or combinations of cues may have a disproportionate influence on phenological events across species, ecosystems and climatic regions. For example, it appears that bumble bee queen emergence in the Rocky Mountains is tied to snowmelt, as is also the case for the plants they pollinate (Inouye 2008). The activity of insects can also be strongly influenced by photoperiodicity and this effect generally increases with altitude and latitude (Bradshaw & Holzapfel 2007) potentially counteracting warming impacts. Mismatches may occur if photoperiodicity is a more important cue for insect emergence (e.g., Bradshaw & Holzapfel 2007) than for onset of flowering. Studies should simultaneously assess the importance of different cues in both plants and pollinators. In addition, we know much less about potential biological effects of climate warming on ecological interactions in the tropics than in temperate areas. One central question is whether the relative importance of different environmental cues to species' phenologies may differ across altitudinal or latitudinal gradients?

The evolutionary response to climate warming and climate-driven mismatches is of great importance for the persistence of ecological interactions. For example, it is still unclear whether genetic shifts (see Evolutionary responses to mismatches) will be fast and strong enough to prevent species extinctions under predicted climate change scenarios (Davis *et al.* 2005; Parmesan 2006; Skelly *et al.* 2007). Understanding the contexts in which evolution should be considered as a possible and plausible response vs. those in which it is not a likely response, remains a critical challenge for scientists studying ecological effects of climate change (Skelly *et al.* 2007). Future research should aim at determining the capacity of adaptive, evolutionary changes in plant and pollinator species with contrasting life-histories (Davis *et al.* 2005), coupled with studies on the indirect evolutionary consequences of climate warming through changes in species interactions.

Long-term studies and simulation approaches

Long-term monitoring programmes, specifically designed to track changes in pollination services and pollination interactions in time, are rare, expensive and time-consuming (but see Gordo & Sanz 2005, 2006; Williams *et al.* 2001; Ghazoul 2005 for some examples). Ideally, such programmes should involve long-term monitoring, consisting of standardized sampling (e.g., Memmott 1999; Westphal *et al.* 2008) of flowering plants and pollinators, and their interactions. Such sampling schemes should fulfil certain criteria. To achieve reliable data on climate-driven changes in species assemblages, or the effects of mismatches, studies need to use a high taxonomic resolution, include data on abundance and demography and should preferably cover different climatic zones. An alternative to initiating new long-term monitoring studies would be to resample previous plant-pollinator interaction studies (e.g., Petanidou *et al.* 2008), and examine if observed changes may have been driven by recent climate change. It is important that such resampling procedures control for the large inter-annual variability in species abundance and link-structure that typically occur in these systems (e.g., Petanidou *et al.* 2008; Olesen *et al.* 2008).

Perhaps the most proactive research approach, which also could serve the need for rapid actions and changed conservation policies, would be to develop more advanced and realistic simulation models aimed at predicting future

responses to climate change. Earlier simulation studies have shown that pollination networks may be quite resistant to perturbations (Fortuna & Bascompte 2006; Memmott *et al.* 2004), but that they may also experience significant structural changes when perturbed (Vazquez & Simberloff 2003; Aizen *et al.* 2008). Insight on the relative importance of various cues (see above) may also be used to validate assumptions made about climate-driven shifts in phenologies or distributions in simulation models (e.g., Memmott *et al.* 2007; Devoto *et al.* 2007) or projections, such as those illustrated in Fig. 2. In a recent study, Deutsch *et al.* (2008) used empirical fitness curves related to the thermal tolerance of insects across the globe and related this to the expected geographical variation in climate warming during the next century. Interestingly, they found that tropical insects were most likely to experience deleterious effects of warming due to their narrower thermal tolerance, despite the relatively lower temperature increase expected in tropical habitats. Identification of such fitness curves of thermal tolerance for plants and their pollinators, or potential niche spaces (e.g., Schweiger *et al.*, in press), could enable simulations of potential future mismatches among mutualistic partners. Simulations of altered nectar production under changed temperatures could also be a useful approach for a better understanding of the relationship between food availability and pollinator population growth.

Estimating consequences of mismatches

Species may, as mentioned above, not only react directly to climate warming, but also indirectly via changes in the availability of their mutualistic partners. A prime priority for future research should be to examine whether climate-driven temporal and spatial mismatches between plants and pollinators do occur and subsequently examine the potential ecological and evolutionary consequences of such mismatches (Fig. 1). Elucidating the complex effects of climate warming, combined with other human-driven changes of habitats on species and their interactions, requires an awareness of the possibilities and limitations of such research approaches. When developing experimental protocols to assess climate-driven mismatches, a major challenge becomes the differences between plants and pollinators in their space use (plants are sessile, pollinators are mobile). The population dynamics of pollinators are probably controlled by resource availability such as floral resources and nesting sites at a landscape scale, whereas plants mainly are controlled by factors at the local patch scale (e.g., pollinators and/or nutrients). To overcome these scale-related restrictions, a feasible approach would be to assess potential consequences of temporal and/or spatial mismatches on plant-pollinator mutualism, if they occur. For example, a temporal mismatch may be created by warming

up plants to accelerate their flowering development; 'forcing' them to reach anthesis before their main pollinator is available, and thereafter track how their pollinator visitation, reproductive success and population dynamics is affected by such a mismatch. A similar approach would be to transplant flowering plants along altitudinal gradients to simulate both flowering advancement and delay. It should be kept in mind that the effective population size, representing mate availability, will likely be reduced in such experiments causing a confounding factor that is not directly related to climate.

Because many plants and pollinators are generalists (e.g., Waser *et al.* 1996), studying the outcome of a single interaction between two mutualistic partners exposed to a mismatch, where the partners operate on different spatial scales, may be problematic and unrealistic. We can envision one situation where manipulation would be efficient, albeit ethically questionable due to the rarity of such interactions and the involved species. In highly specialized symmetric interactions, where one plant species is pollinated by one pollinator species and where the pollinator has a restricted home range (e.g., some solitary bees), one could speculate that simultaneous experimental manipulation of both plant and pollinator densities would be achievable. Such an experiment could focus on altering the factors that are predicted to change in a warmer climate, and measure the population responses of both partners.

As for many studies of biological responses to climate change, effects of temperature-mediated mismatches on plant-pollinator interactions often have to be studied through observational data (e.g., Parmesan & Yohe 2003). Observations along natural gradients of climate conditions (e.g., Devoto *et al.* 2005) may be one potentially powerful tool to study effects of climate change on ecological interactions, particularly if they are combined with experiments designed to elucidate possible underlying mechanisms for the responses observed. For example, one could study how the magnitude of pollen limitation in plants (as a proxy for pollinator availability) changes along altitudinal gradients (as a proxy for climate change) (e.g., Gügerli 1998; Totland 2001). Alternatively, one could manipulate the availability of pollinators (e.g., by using cages that exclude pollinators, completely or partially, from flowers) along natural gradients of climate conditions. Such an approach could enable an assessment of how altered abundance or composition of pollinators, for example as a simulation of a mismatch, may affect plant reproduction, recruitment and subsequent population and community dynamics under different climate conditions (see Fontaine *et al.* 2006 for an example).

Manipulating the availability of flowers to assess how that may impact populations of pollinators is very time and cost intensive because it requires manipulations of flower

availability over large spatial scales. This might still be possible in species-poor systems with low flower abundance, or where pollinators have highly restricted foraging ranges. Manipulation of resource availability and subsequent assessment of population dynamics of pollinators may be one way of estimating potential consequences of mismatches (see Steffan-Dewenter & Schiele 2008 for a field example). Comparing demographic processes of pollinator populations under different resource conditions, for example different types of natural or cultivated landscapes, may be an observational approach to improve knowledge on population dynamics of pollinators.

It is also important that we improve the way mismatches are quantified. Several studies of phenology use first appearance dates (both flowering and flight) as indications of mismatch. However, this variable only represents a subset of the individuals in a population, whereas the mean advancement of phenology might matter more for how climate warming affects the persistence of mutualistic interactions. Likewise, it is not necessarily the change of distributional extremes of species geographical ranges that matter for their interactions with other species, but rather the change of their optimum or mean distribution (Kelly & Goulden 2008; Lenoir *et al.* 2008).

CONCLUSIONS

The phenology, geographic distribution and local abundance of plants and pollinators appear to be affected by recent climate change (Figs 1 and 2). Nevertheless, the current knowledge of the potential ecological consequences of increasing temperatures is limited and often must be deduced from indirect evidence or basic ecological knowledge of pollination interactions or studies of the mutualistic partners separately. Timing of both plant flowering and pollinator activity appears to be strongly affected by temperature, and their response appears to be linear within the limits of temperature fluctuation observed during recent decades (Fig. 2). Thus, plant and pollinator responses to climate warming may act in concert, although there may be considerable variation in the thermal sensitivity across species. There is also limited information on the relative importance of the factors controlling the phenology, distribution and abundance of plants and pollinators. Whereas temporal mismatches between plants and pollinators in early season have been documented, spatial mismatches have so far not been observed. The demographic consequences of mismatches are still little known (Fig. 1). Although current knowledge suggests that plant-pollinator systems may be resilient to perturbations, such as those caused by climate warming, it is premature to conclude whether increased temperatures in general will be unfavourable or positive for the persistence of many pollination interactions.

Pollination ecologists are faced with a tremendous challenge if we want to understand how future climate change might affect plant-pollinator interactions (see Future Research), and reveal the importance of climate warming relative to other human modifications of natural habitats for the persistence and stability of these interactions. We believe the most important future research directions will be to monitor whether climate-driven temporal or spatial mismatches between plants and pollinators really do occur and subsequently to estimate their potential consequences for pollination interactions. The relative contribution of climate-change driven direct and indirect effects on population dynamics of species, through the effects on pollination and food availability, need to be understood in greater detail. Ultimately, this insight could enable us to better understand how community properties may change by climate-driven plant-pollinator mismatches.

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