



Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations?

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Climate change can affect plant–pollinator interactions in a variety of ways, but much of the research attention has focused on whether independent shifts in phenology will alter temporal overlap between plants and pollinators. Here I review the research on plant–pollinator mismatch, assessing the potential for observational and experimental approaches to address particular aspects of the problem. Recent, primarily observational studies suggest that phenologies of co-occurring plants and pollinators tend to respond similarly to environmental cues, but that nevertheless, certain pairs of interacting species are showing independent shifts in phenology. Only in a few cases, however, have these independent shifts been shown to affect population vital rates (specifically, seed production by plants) – but this largely reflects a lack of research. Compared to the few long-term studies of pollination in natural plant populations, experimental manipulations of phenology have yielded relatively optimistic conclusions about effects of phenological shifts on plant reproduction, and I discuss how issues of scale and frequency-dependence in pollinator behaviour affect the interpretation of these ‘temporal transplant’ experiments. Comparable research on the impacts of mismatch on pollinator populations is so far lacking, but both observational studies and focused experiments have the potential to improve our forecasts of pollinator responses to changing phenologies. Finally, while there is now evidence that plant–pollinator mismatch can affect seed production by plants, it is still unclear whether this phenological impact will be the primary way in which climate change affects plant–pollinator interactions. It would be useful to test the direct effects of changing climate on pollinator population persistence, and to compare the importance of phenological mismatch with other threats to pollination.

How great is the threat posed by climate change to plant–pollinator interactions? Most attention has focused on possible impacts of climate change on temporal overlap between flowering and pollinator activity: if phenologies of plants and pollinators are not equally affected by warming temperatures, ‘temporal mismatches’ or ‘phenological mismatches’ might develop – that is, periods during a plant’s flowering season or a pollinator’s active season when interaction partners are scarce or absent, either because their seasonal activity period is already finished or because it has not yet started. Such asynchronies could decrease interaction rates between plants and pollinators (at least over a part of the season), relative to the historical norm to which we assume these organisms have adapted. Decreased rates of interaction might adversely affect populations of plants, pollinators, or both. However, other, non-phenological, impacts of climate change on plant–pollinator interactions are also plausible (Hegland et al. 2009, Willmer 2012). For instance, increasing drought severity might reduce survival, flowering, or nectar production of certain plants (Carroll et al. 2001, Peñuelas et al. 2004), resulting in lower resource availability for flower-dependent animals, lower reproductive potential for those plants, and potentially lower pollination success and plant

population declines as well. Increased atmospheric carbon dioxide concentrations can also have direct effects on nectar production (Rusterholz and Erhardt 1998, Lake and Hughes 1999, Erhardt et al. 2005) as well as on plant growth and reproduction (Jablonski et al. 2002, Poorter and Navas 2003). The relative importance of these varied impacts of climate change on plants and pollinators is difficult to assess.

To appropriately direct research and conservation efforts, we need to know how the threat of phenological mismatch compares to other threats to plant and pollinator populations. To make this comparison, we must 1) determine if mismatch is happening and is likely to worsen with further climate warming, 2) evaluate whether such mismatches will reduce population viability of plants or pollinators, and 3) weigh these reductions against other impacts of environmental change (although here I will focus specifically on climate change). A variety of approaches have been used to assess the first two of these problems, including simulation modelling, analysis of long-term data, and experimentation (Rafferty et al. 2013). Although experimental approaches can provide unique insights, experimentally testing the impacts of climate change on plant–animal interactions poses several logistical and conceptual challenges, as

I discuss below. On the other hand, observational studies are frequently unable to determine conclusively the mechanistic basis for observed patterns. Here, I will review what we have learned so far about mismatches between pollinators and pollinator-dependent plants from both experimental and observational approaches, and then critically evaluate the potential for further experiments and observations to deepen our understanding of climate-change impacts on pollination – including the likelihood of worsening mismatch, the consequences of mismatch, and its relative importance.

Is mismatch happening, and is it likely to get worse?

Temporal mismatches are expected if phenologies of different organisms are regulated by different types of environmental cues, or if phenologies are regulated in different ways by the same type of environmental cue (e.g. responding at varying rates to rising temperatures). Studies evaluating which variables predict seasonal timing of flowering and insect pollinator emergence often find that temperatures are good predictors of both plant and pollinator phenology, at least in temperate and Mediterranean regions (Hegland et al. 2009, Gordo and Sanz 2005, Doi et al. 2008, Forrest and Thomson 2011). Both warm temperatures in spring and cold temperatures in winter seem to be important for temperate-region plants and insects (Bosch and Kemp 2003, Kraemer and Favi 2010, Tooke and Battey 2010, Forrest and Thomson 2011, Laube et al. 2014), although the details of how temperature affects plants and insects may differ. Timing of snowmelt is highly correlated with flowering time and activity periods of many plants and some flower-visiting animals (Inouye et al. 2003, Green 2010, Lambert et al. 2010, Iler et al. 2013b, Kudo and Ida 2013); however, the apparent effect of snowmelt on phenology may be indirect, driven by its effect on soil temperatures – for which long-term data are unavailable. Other factors, such as rainfall and day-length, are known to influence phenology in some habitats and some taxa (Crimmins et al. 2010, Friedman and Willis 2013), but so far there is no information on the role they play in synchronizing plants and pollinators – perhaps because published data on pollinator phenology are lacking for deserts and the tropics. Migratory species (including hummingbirds) may be quite vulnerable to mismatch with their food supply because they must respond to seasonal cues in a different environment than the one to which they are headed (McKinney et al. 2012). However, at least some migratory species are able to adjust the rate of their journey according to climate cues experienced en route (Bauer et al. 2008), suggesting that migrants may be able to time their springtime arrival appropriately even if cues in the winter and summer territories are mismatched.

Observations

We have no information so far to indicate that plants and insect pollinators in a given locality use fundamentally different phenological cues. Indeed, several recent analyses of long-term data suggest similar phenological shifts in plants and insect pollinators in response to climate warming. A large-scale study using museum records of bee activity in the northeastern USA and published data on flowering phenology suggests there have been essentially parallel

changes in plant and bee phenology over the last 130 years (Bartomeus et al. 2011). Similarly, long-term data from Russia show good maintenance of synchrony between first appearances of bumble bees *Bombus* spp. and early-flowering plants (Ovaskainen et al. 2013). Rafferty and Ives (2011) also concluded that the plant species they studied in the midwestern USA were not mismatched with their flower visitors, despite several of these plants having significantly advanced their flowering times over the past century. In a study in Illinois, USA, bees and forbs also demonstrated comparable average phenological shifts over a 120 year period (Burkle et al. 2013). The authors did attribute the loss of certain specific interactions to lack of temporal co-occurrence, but some of these losses may have been due to reduced population sizes rather than independently shifting phenologies (Burkle et al. 2013).

Nevertheless, there are examples of non-parallel shifts in plant and flower-visitor phenology. Gordo and Sanz (2005) documented a growing gap between first appearances of honey bees *Apis mellifera* and cabbage white butterflies *Pieris rapae* and the first flowering of several likely food plants in the Iberian peninsula, suggesting greater temperature-sensitivity on the part of the insects. Long-term data from Japan, in contrast, suggest that flowering of local fruit trees is generally more responsive to temperature than is *P. rapae* phenology (Ibáñez et al. 2010, Ellwood et al. 2012). In fact, by appearing later, the butterfly has become better synchronized with cherry flowering over the years (Doi et al. 2008) – although shrinking butterfly populations seem to play a role in this trend (Ellwood et al. 2012). In any case, while *P. rapae* and *Prunus* spp. may be representative of broader assemblages of flower visitors and plants, it seems unlikely that there is any meaningful interdependence between *P. rapae* and *Prunus* flowers in particular. In contrast, the Japanese woodland ephemeral *Corydalis ambigua* is largely reliant on queen bumble bee visits, and flowering onset of *C. ambigua* appears more responsive than bumble bee emergence to fluctuations in snowmelt date (Kudo and Ida 2013). Consequently, years and sites with early flowering have seen greater mismatch between flowering and subsequent bee appearance (Kudo and Ida 2013). This has not yet led to an increase in mismatch over time, since there has been no detectable temporal trend in snowmelt (despite increasing air temperatures); however, growing mismatch seems a strong possibility for the future.

Even if plants and pollinators respond similarly to environmental cues, they may experience somewhat different environments. For example, Visscher et al. (1994) observed delayed emergence of the andrenid bee *Calliopsis pugionis* relative to its primary pollen source, *Encelia farinosa*, in an unusually rainy year. In this case, the mismatch can be explained by the fact that the bee nests in seasonally flooded pools, while the plant grows in the drier upland areas (the latter being less affected by heavy rainfall). However, it is not expected that flooding episodes (and, therefore, asynchrony) will occur more frequently in the future. In a similar fashion, bees that nest in above-ground cavities in wood or hollow stems are exposed to somewhat different overwintering conditions than the plants they depend on, which may be covered by soil, snow, or water. This difference in microhabitat raises the possibility that above-ground-nesting bees might

(all else being equal) be more prone to mismatch with the flowering of their food plants, compared to bees that overwinter in the ground.

Overall, the long-term data indicate a general maintenance of synchrony – so far – between plants and pollinators, albeit with some exceptions and with the caveat that the available data are strongly biased toward north-temperate locations. Assessing the prospects for future maintenance of synchrony requires experimentation or extrapolation of current trends to future climate conditions, and extrapolation is problematic if we have not correctly identified the actual drivers of phenology. Analysis of long-term phenology data often involves calculating correlations between phenology and a limited number of abiotic variables (e.g. mean temperatures in the months before flowering or emergence, often from a nearby weather station) to identify potential drivers (Sparks et al. 2005, Ellwood et al. 2012, Calinger et al. 2013). This approach can suggest hypotheses about the actual factors controlling phenology. However, correlations based on historical data may fail to identify the actual mechanisms responsible for changing phenology, particularly if the available weather data do not capture the conditions actually experienced by the organisms. For instance, past associations between warming temperatures and advancing phenology may saturate or even reverse themselves if warm temperatures lead to a failure to meet winter chilling requirements (Cook et al. 2012). Forecasts of advancing phenology with earlier snowmelt will also fail if temperature is the true driver and if early snowmelt is not reliably associated with warm temperatures (see Steltzer et al. 2009, Iler et al. 2013a for evidence of such an effect). Although a late snowmelt will inevitably delay soil warming, setting a lower bound on the onset of growth for organisms overwintering below-ground, early snowmelt (while air temperatures are still below freezing) may not hasten development of below-ground organisms. Threshold responses (for instance, in the case of pollinators that are unable to forage above or below certain critical temperatures; Willmer and Stone 2004) and interactions among environmental cues (e.g. photoperiod and temperature) can also invalidate extrapolations based on single-variable linear relationships that may have adequately described phenologies in the past.

Experiments

Experimental approaches in combination with observations hold promise for developing more robust forecasts of future phenological mismatch, but they also have limitations. Outdoor warming experiments (e.g. using open-top chambers or overhead heaters) generally do not manipulate phenology of pollinators, which are most likely to enter the experimental plots from unmanipulated surrounding habitat (although emergence phenology of ground-nesting pollinators could in principle be monitored within the experimental plots). In addition, warming experiments of this type are known to introduce experimental artefacts and underpredict climate-driven change in plant phenology (Wolkovich et al. 2012); despite their natural setting, they cannot therefore be viewed as accurate simulations of future global warming. Growth-chamber experiments provide an alternative approach to testing the simpler mechanistic

hypotheses suggested by historical data – for example, potentially isolating the effects of winter versus spring warming on phenology (Laube et al. 2014) – although they cannot simulate all potentially relevant aspects of future climates (e.g. alterations in precipitation). Many organisms cannot be reared in a growth chamber for their entire life cycle; but dormant, overwintering bees could be reared until emergence. Results of such experiments could be used to parameterize mechanistic, ‘process-based’ phenology models for the species of interest (Chuine et al. 2003, Régnière et al. 2012), which could then be used in conjunction with regional climate models to assess the likelihood of future phenological mismatch in a given region. In some cases, it may be possible to rear plants and pollinators in the same experimental environment to determine whether future temperature regimes are likely to produce mismatch. Such an approach has apparently not yet been attempted with plants and pollinators, but there are precedents with plants and herbivores (Liu et al. 2011, Gillespie et al. 2012). Clearly, once pollinators emerge from dormancy the potential for growth chambers to simulate the larger outdoor environment is greatly reduced – few controlled-environment arenas are likely to provide an adequate spatial scale for a flying insect – but the approach may be useful for studying phenology of pollinator emergence and plant flowering under novel conditions. Regardless, any such experiment must be interpreted carefully, since it does not allow for evolutionary adjustments by the organisms: Confronting a small experimental population with a radically altered climate regime may produce more dramatic effects than would a more gradual change in a larger population.

To summarize so far, the available observational evidence suggests that temporal mismatch between plants and pollinators is not impossible, but it is rare. Furthermore, the environmental conditions that have produced mismatches in the past do not – so far – appear to be increasing in frequency with climate change. Experimental studies will be needed to test whether novel climatic conditions are likely to generate mismatches in the future, but researchers will need to recognize the inferential limitations of any such experiment.

Does plant–pollinator mismatch threaten plant or pollinator populations?

If temporal mismatches between plants and pollinators are a plausible outcome of climatic change, we would like to know how such mismatches will affect population dynamics of the taxa involved. However, linking observed or projected mismatches to demographic outcomes has been a challenge for researchers (Miller-Rushing et al. 2010). Part of the problem is that we lack crucial baseline information: for most populations, we do not know which variables limit population size (Roulston and Goodell 2011) and therefore are poorly placed to make projections about how changes in rates of species interactions will affect population growth rates. We should only expect reductions in temporal overlap between plants and pollinators to cause population declines if it is the availability of suitable pollen (and nectar, in the pollinator case)

that, at least occasionally, regulates those populations. The demographic impacts of predators, parasites, and availability of abiotic resources may frequently be more important, making it challenging – if not completely pointless – to search for demographic consequences of phenological mismatch with mutualists (cf. Miller-Rushing et al. 2010).

Observations

Despite the potentially overriding impacts of resources, herbivores and seed predators, some observational data do suggest impacts of plant–pollinator mismatch on plant reproduction. One long-term study on an early-flowering plant (which included repeated pollen supplementation experiments) has shown that seed set is increasingly limited by inadequate pollination, possibly because of growing phenological mismatch with bumble bee queens, the main pollinators (Thomson 2010). Phenological mismatch with *Bombus* queens is associated with low seed set in the early-flowering *C. ambigua* (Kudo et al. 2004, Kudo and Ida 2013); and, as noted above, mismatch is more pronounced in years with especially early flowering, suggesting that future advances in springtime phenology could increase the frequency of reproductive failure for this plant. Early-flowering plants that are strongly reliant on a single type of pollinator, like those studied by Thomson (2010) and Kudo and Ida (2013), may be most at risk of total mismatch with pollinators and consequent reductions in seed set. On the other hand, such relatively specialized plants should also have experienced stronger selection to synchronize emergence with that of their pollinators; we might expect mismatches to occur comparatively rarely in these taxa in which the consequences of mismatch would be most severe. Later-flowering plants that can be pollinated by a diverse assemblage of visitors should be less vulnerable to declines in reproductive output as a result of phenological changes, even if certain plant–pollinator pairings are disrupted (Bartomeus et al. 2013).

Although pollinator extinctions have been predicted as a consequence of mismatch with food plants (Memmott et al. 2007), I am unaware of any data showing pollinator population declines to be a clear consequence of temporal mismatch with floral resources. Burkle et al. (2013) attributed a substantial fraction of lost plant–bee interactions in their pollination network to phenological mismatch, but it cannot be determined whether the apparent mismatches were a cause or a consequence of pollinator declines. Boggs and Inouye (2012) showed that abundance of the butterfly *Speyeria mormonia* could be partially predicted by availability of *Erigeron speciosus* flowers (an important nectar resource) in the preceding year; however, the association is unrelated to phenological overlap between the plant and the butterfly. A study by Høye et al. (2013) is more relevant to the issue of phenological mismatch: They found a correlation between fly abundance at their Arctic field site and the extent of phenological overlap between community-wide flowering and fly activity in the preceding year. Again, however, it is unclear if the relationship is a causal one, as some Diptera species are not flower visitors (and some are completely non-feeding as adults).

While some butterfly and fly species can certainly be important pollinators for some plants, the insects that seem

most likely to suffer from mismatch with flowering are bees, because of their dependence on floral resources for larval development as well as for adult activity and fecundity. Studies linking vital rates of bee populations to their temporal coincidence with floral resources are scarce. There is evidence that the timing of floral resource pulses affects growth of bumble bee *Bombus vosnesenskii* colonies (Williams et al. 2012), although no effect on colony reproduction has been observed. It seems possible that solitary bees, with their shorter seasonal activity periods, would be more strongly affected by the timing of resource availability. Cavity-nesting bees provide a good candidate system for studying how temporal overlap with particular floral resources affects population vital rates (see Williams and Kremen 2007 for one approach), and studies are under way in Colorado and Arizona, USA, to investigate this question in natural settings (P. CaraDonna). However, for many bee taxa, even basic ecological information – for example, on level of pollen specialization (lecty) or typical foraging range – is currently unavailable and would be very useful in determining the risk of population declines caused by phenological shifts. In fact, many pollinators likely have far greater dietary flexibility than was assumed by Memmott et al. (2007) and would adopt new food sources in situations where preferred plants were lacking. We have substantial evidence that plant–pollinator linkages are flexible and that apparent specialization in a given site or year need not reflect true dependence (Petanidou et al. 2008, Benadi et al. 2014) – although it must be noted that observational studies of visitation networks may underestimate pollen specialization, as many pollen-specialist bees (oligoleges) are generalists when it comes to nectar-foraging (Wcislo and Cane 1996). In addition, we still have little information on how long bees can survive without nectar following emergence, how long they can wait for pollen before they begin nesting, or how far they can fly to reach a good food patch before initiating their nest. At 20°C in the lab, male *Osmia* bees can survive for up to a week without food, depending in part on the size of the individual's fat reserves (Bosch et al. 2010), but metabolic rates would be lower, and longevity would likely be greater, at lower (but still above-freezing) temperatures (Meurisse et al. 2012). Female longevity may be somewhat lower than that of males (Bosch and Kemp 2000), but even so, emergence slightly before appearance of floral resources may be tolerable. It is worth noting that within a solitary bee population, emergence can occur over a period of several weeks (Forrest and Thomson 2011), indicating that imprecision is a normal phenomenon.

If mismatched phenology with floral resources reduces offspring production in bees, there should be strong selection for altered phenology or floral host use (Sedivy et al. 2008). So far, there has been little study of the potential for evolutionary change in phenology in bee populations (or those of other pollinators), but the existence of locally adapted developmental schedules within bee species clearly indicates that adaptive adjustments are possible (Sgolastra et al. 2012). The lack of study in bees contrasts with the situation in plants, in which evolution of phenology is well studied (Anderson et al. 2012, Franks et al. 2007). Given adequate genetic variation, response to selection

should be relatively rapid in bee populations, which often have short (one year) generation times. However, this optimistic conclusion neglects the possibility of conflicting selection pressures and developmental constraints that may limit the range of evolutionary options. This area of study deserves more attention.

Experiments

Manipulative field experiments are one way to test the impacts of plant–pollinator mismatch in the absence of long-term data on plant or pollinator reproductive success. Researchers can directly alter plant or pollinator phenology and monitor changes in interaction strength and population vital rates relative to unmanipulated controls. I will refer to such experiments as ‘temporal transplants’. This approach was used by Rafferty and Ives (2011, 2012) and by Parsche et al. (2011), who manipulated flowering time by growing experimental plants under different light and temperature regimes. Artificially advanced and control plants were then placed in the field to be visited by the local insect community. Rafferty and Ives (2011) found generally high visitation for experimentally advanced plants, although they also detected reduced mean pollinator effectiveness in response to advanced flowering for two species that they studied in detail (Rafferty and Ives 2012). In

contrast, Parsche et al. (2011) observed fewer flower visitors on experimentally advanced plants – but also fewer antagonistic flower beetles, and, perhaps as a result, higher seed set. Just as these authors experimentally altered flowering phenology, one could rear insect pollinators such as *Osmia* bees such that they emerge as adults at different times (as is commonly done for agricultural applications; Bosch et al. 2000) and subsequently monitor their nesting success – although observing post-manipulation fitness of small wild animals is a non-negligible challenge.

However, linking the results of temporal transplant experiments back to climate-change effects on real ecosystems is complicated. For one thing, such experiments manipulate only one component of the community and therefore may not simulate the actual phenological changes expected with climate change. Nevertheless, if sufficient information is available on expected mismatches (see ‘Is mismatch happening...?’ above), it may be possible to manipulate communities such that they do mimic expected future assemblages. Still, there remains a second, conceptual, problem with such an experiment, which is one of scale: Temporal transplants necessarily alter the phenology of only a few small subpopulations, which become islands of advanced or delayed individuals in a sea of unmanipulated individuals (Fig. 1, upper panels). Small, isolated popula-

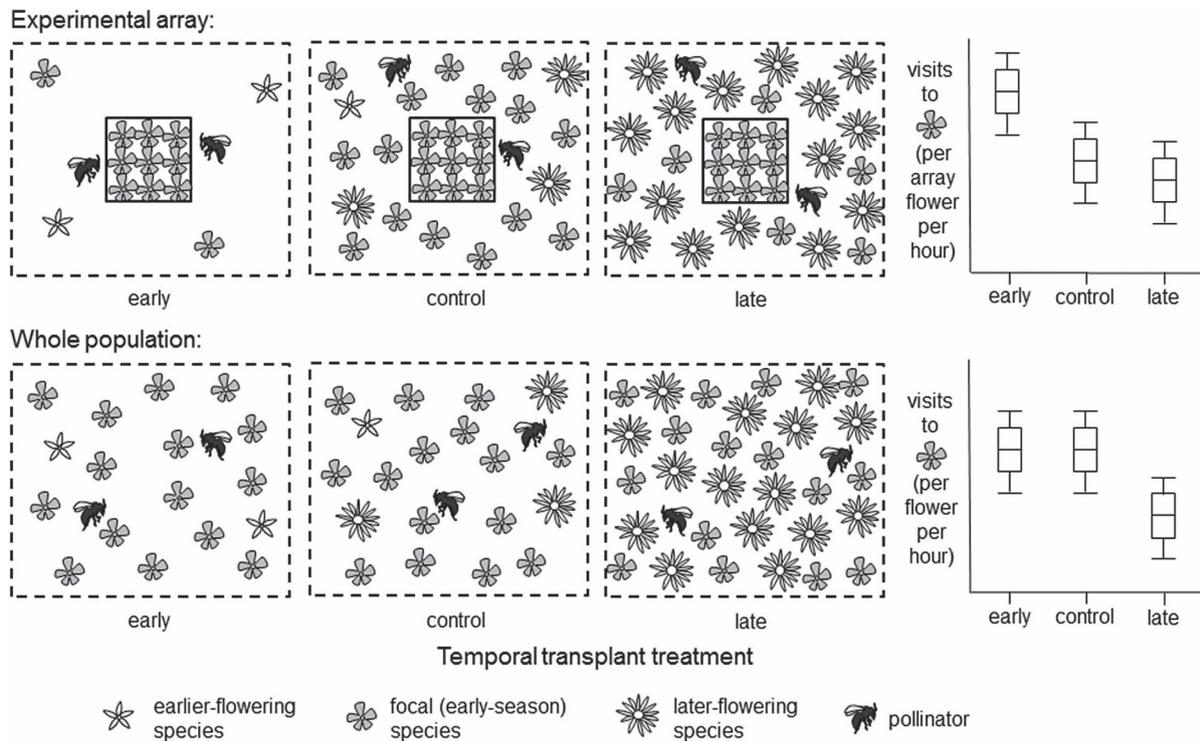


Figure 1. Hypothetical outcomes of temporal transplant experiments with an animal-pollinated plant. Panels to the left show possible experimental set-ups for early, control, and late transplants, respectively. Panels to the right show summary plots of hypothetical results, in terms of visitation to the focal species (the grey flower), assuming that pollinators preferentially visit the species that is most abundant in each panel. Upper panels show small-scale manipulations of single-species experimental arrays, illustrated by the central boxes containing a high density of the focal species (these represent a single replicate; an actual experiment would include multiple replicate arrays). Lower panels show altered timing of peak flowering of an entire plant population relative to other co-occurring plants, at the scale of an entire meadow (a thought experiment). Note that phenologies of other plant species are unchanged, and pollinator abundance is similar in all time periods. Pollinator scarcity early or late in the season would lower the expected visitation rates for those treatments. Variation in size and density of the experimental arrays is not shown here but could also influence pollinator attraction and per-flower visitation rates in arrays relative to surrounding flowers.

tions may suffer from mate-limitation (as noted by Hegland et al. 2009), although it may be possible in some cases to avoid this problem (e.g. by using self-compatible but non-autogamous plants). In addition, isolated populations may be inordinately attractive – or unattractive – to consumers, including herbivores, predators and pollinators (Singer and Wee 2005). A small patch of early-flowering plants, for example, might be mobbed by unusually flower-constant visitors if it is the only concentrated nectar resource in an otherwise largely flowerless landscape (cf. Moise and Henry 2010); conversely, it might be avoided if other types of flowers are more abundant (Smithson and Macnair 1997, Crone 2013). Do the pollination rates observed in an experimental array reflect the rates that would be experienced following population-wide advancements in flowering time (Fig. 1, lower panels)? Perhaps; but not if pollinator attraction and effectiveness are influenced by patch size and context – as they certainly can be (Sih and Baltus 1987, Jennersten and Nilsson 1993, Kunin 1993). Similarly, small, temporally transplanted populations of bees might have access to more floral resources per capita than would real (presumably larger) populations with altered phenologies.

These arguments do not mean that temporal transplant experiments are without value, only that their findings must be interpreted cautiously. For plants, experiments of this type do provide a means of testing for pollinator presence at times outside the usual flowering period (although failure to observe pollinator visits to experimental plants cannot be viewed as conclusive evidence that pollinators are not present). In addition, temporal transplants can be viewed as tests of how selection would operate on rare, phenologically novel mutants – rather than as tests of climate-change effects on species interactions. For example, if bees induced to emerge early exhibit high reproductive success in the field, it suggests that earlier emergence could evolve in the population, provided the necessary genetic variation were present. This viewpoint shifts the focus from ecological effects of climate change to the potential for adaptive change in phenology. Rafferty and Ives (2011) took a similar approach, arguing that the plant species in their experiment which experienced high visitation with advanced flowering would have the greatest potential for evolutionary adjustments in phenology (or would be more likely to have evolved plasticity in flowering phenology). Indeed, several of the seemingly unconstrained species in their study were ones that had shown advances in phenology over the preceding 70 years.

So, does the available evidence suggest that populations are threatened by plant–pollinator mismatch? The scarce observational data show that temporal mismatches with pollinators are reducing seed production in some plant populations, whereas the experimental studies – despite manipulating flowering phenology beyond the natural range of variation – have actually reached somewhat more hopeful conclusions. It is possible that the observational studies have misattributed low seed production to phenological mismatch; however, it also seems possible that the contrasting findings are due to experimental artifacts (e.g. small size of experimental arrays) or to differences among study systems (e.g. use of relatively unspecialized or later-flowering study species for experiments). So far, there is no evidence that phenological disruption has adversely

affected pollinator populations, but this may reflect lack of study rather than invulnerability of pollinator populations. There is clearly room for further research on how mismatches are affecting (or will affect) populations of plants and pollinators, but experimental approaches to this question require careful design and interpretation. It may be most productive to use experiments to study particular components of the problem in isolation (cf. Yang and Rudolf 2010) – for instance, testing the ability of bees to collect or develop on the novel pollens to which they are expected to have the greatest access in future, novel climates (see Williams 2003 and Praz et al. 2008 for methods). While this kind of experiment does not attempt to investigate the impacts of climate change on whole communities of interacting species, nor does it allow pollinators to choose among different available pollens, it can provide useful information on how pollinators might fare when faced with changing overlap with particular floral resources.

How does the threat of phenological mismatch compare to other impacts of climate change?

In addition to potentially driving phenological mismatch, climate change may influence pollination by affecting plant and pollinator populations in other ways. In particular, warming temperatures can have direct (positive or negative) impacts on growth, survival, and reproduction of plants and animals, as can changes in precipitation and increasing climatic variability (Table 1). For example, dry winters are associated with low flower numbers in the following summer for some subalpine plants (Miller-Rushing and Inouye 2009), suggesting low reproductive potential for the plants and low overall resource availability for flower visitors in warmer, drier years. Early snowmelt increases the risk that late-spring frosts will damage the flower buds of certain plants (Inouye 2008); this, too, reduces seed production and availability of floral resources (Boggs and Inouye 2012; as mentioned above). Climatic variability, in the form of extreme winter values of the Pacific Decadal Oscillation index, is associated with population declines in *Parnassius smintheus*, an alpine butterfly (Roland and Matter 2013). The precise mechanisms driving this association are

Table 1. Different types of observed or hypothesized climate-change effects on plant and pollinator populations. Only studies showing likely impacts on survival or reproduction are included. For both plants and pollinators, key papers either documenting or reviewing the phenomenon are listed. For some types of effects, research on pollinators is unavailable. *Not an exhaustive list. Note that studies of drought effects on wind-pollinated trees and grasses are not included here.

Type of climate-change effect	Plants	Pollinators
Heat stress	reviewed by Scaven and Rafferty 2013	reviewed by Scaven and Rafferty 2013
Increased frequency of damaging frost	Augspurger 2013, Inouye 2008	Boggs and Inouye 2012
Loss of insulating snow cover	reviewed by Pauli et al. 2013	reviewed by Pauli et al. 2013
Altered precipitation	Liancourt et al. 2012, Peñuelas et al. 2004*	
Phenological mismatch	Kudo and Ida 2013, Thomson 2010	

unknown, but desiccation in warm winters and cold exposure in cold winters may both be involved. In normally snowy parts of the world, loss of insulating snow cover in warmer winters exposes overwintering organisms not only to desiccation but also to potentially harmful temperature extremes (Pauli et al. 2013). Declining snowpack may have profound impacts on overwinter survival of hibernating bees and dormant plants, but overwintering biology remains relatively unstudied – despite the fact that future warming is projected to occur disproportionately in winter (IPCC 2007). Changes in plant or pollinator population size as a result of any of these variables are just as likely as shifting phenology to alter plant–pollinator interactions.

Although some of the direct effects of climate change on plant populations are relatively well studied (Table 1), there has been little effort so far to compare their ecological importance to that of changing synchrony between plants and pollinators. This may be because the species that have been used to study physiological impacts of warming (frequently wind-pollinated grasses and trees) have generally not been used to study timing of species interactions. The same is true from a pollinator perspective – the relative importance of phenological mismatch and physiological effects of climate change is unknown – but this is unsurprising given the lack of information about consequences of mismatch for pollinators. In the absence of any comparison, it is difficult to know if the attention paid to phenological mismatch over the last decade (Memmott et al. 2007, Hegland et al. 2009, Fabina et al. 2010) is commensurate with the ecological threat it poses.

Observations

One way to determine the relative importance of non-phenological climate-change effects would be to compare projected geographic range shifts (Wiens et al. 2009) with projected temporal shifts (Hodgson et al. 2011), using existing observational data on species' ranges and phenologies. Range shifts are the outcome of population decline and extinction in parts of a species' range combined with population establishment elsewhere; hence, they represent the outcome of demographic processes acting locally. Although joint changes in phenology and distribution in response to climate change have been modelled for individual plants and insects (Chuine 2010, Söndgerath et al. 2012), forecasted spatial and phenological shifts have seemingly not been compared for pairs of interacting species. In principle, either process-based or correlative modelling should allow projections and comparisons of spatial and temporal mismatch, albeit with the caveat that models are unlikely to account for all relevant environmental variables and that projections into novel conditions will therefore be imperfect (Wiens et al. 2009, Buckley and Kingsolver 2012). High-quality range and phenology projections will require large and high-quality datasets – in this case, from sets of interacting species. However, the increasing digitization of georeferenced and dated museum and herbarium specimens makes this type of analysis an achievable goal.

Experiments

Because of the effort required to detect effects of plant–pollinator mismatch on populations, it makes most sense to

build on the few existing long-term studies that have done so to determine how other climate-change impacts measure up. One possibility would be to subject these focal plant species to experimental warming or snow removal, combined with supplemental pollination, to isolate the direct effects of altered precipitation or temperature (within the range expected for that locality) on survival and reproduction, independent of pollinator shortages. (It must be noted, however, that the issues of scale noted above could influence the interpretation of such experiments, particularly with respect to interactions between plants and mobile herbivores or seed predators.) Ideally, results from these experiments would be integrated in a life-table analysis with existing data on mismatch effects on reproduction to allow the effects of different aspects of climate change to be compared in the same currency (population rate of increase).

For pollinators, experimental tests of how climatic conditions affect survival – independent of food supply – would be useful for comparative purposes. Over-wintering conditions could be manipulated (e.g. by conducting snow addition/removal or rainfall manipulations, or by placing overwintering bees in different microhabitats) and the proportion of surviving bees noted in spring. This approach is more easily applied to cavity-nesting bees in experimental trap-nests, since numbers of dead and surviving offspring can be easily tallied by removing and dissecting nest liners in spring; but nest excavations could allow the same methods to be applied to ground-nesting bees. Of course, over-winter survival does not tell the whole story of direct climate-change impacts on pollinators, and other types of experiments would be necessary to evaluate the importance of summertime climate change. One could, for example, observe foraging rates and longevities of pollinators in controlled-climate flight arenas well-stocked with pollen-producing plants. However, it should be noted that actual global warming may not expose pollinators to higher temperatures during their flight periods if it also drives shifts to earlier phenology, altered diel activity patterns (cf. Rader et al. 2013), or changes in behavioural thermoregulation – opportunities for which would be lacking in an indoor environment without the thermal heterogeneity provided by solar radiation and shade.

Conclusions

Because plants and their pollinators are unlikely to respond to environmental variables in an identical fashion – and because, in addition, the microhabitats they occupy may not experience precisely the same environmental conditions – climate change has the potential to shift phenologies of plants and pollinators relative to one another. It is clear from various types of observational data (including long-term and multi-site observations as well as more anecdotal reports) that such phenological shuffling occurs regularly at a low level, with overlap between particular pairs of species increasing or decreasing depending on climatic conditions. More dramatic disruptions, with plant or pollinator suffering complete loss of interaction partners, seem to occur occasionally; and in a few systems these wholesale mismatches may be increasing in frequency with climate change – although this has not yet been demonstrated for

even the best-studied systems. Laboratory and field experiments are useful for isolating the effects of particular environmental variables on phenologies of plants and pollinators, and for measuring phenological responses to environmental variation beyond the range so far observed; but historical observations and climate-model projections will be needed to decide which of the infinite number of possible environmental manipulations to focus on.

To date, primarily observational studies have provided the most convincing evidence that plant–pollinator mismatch can have measurable impacts on plant reproduction, and observational studies are likely to be critical in evaluating impacts on pollinator populations, as well. In principle, experiments allow us to study the fitness effects of phenotypes that do not currently occur in nature (e.g. extremely early-flowering plants). However, because they do not mimic actual effects of large-scale climate change, their results must be interpreted with caution. In particular, researchers need to be attentive to how pollinator behaviour can be affected by the scale of experimental manipulation.

Although we would like to be able to compare the demographic impacts of phenological mismatch with other types of climate-change effects on populations, that goal is not likely to be achievable for many species because of the amount of effort required to characterize the different climate-change impacts. However, the effort need only be focused on those species for which we already suspect that mismatch is important. It is for these species that it would be most useful to know whether mismatch should be our primary concern. Both experiments and observations (and, ideally, demographic modelling as well) would be useful to address this problem.

Because of the multivariate nature of climate change, strictly observational data may lead to false attribution of a phenological pattern to a particular climatic variable; experiments are therefore necessary to tease these variables apart – that is, if we suspect that these variables will become uncoupled in the future. On the other hand, because of the scale at which climate change operates, many of its effects are not experimentally tractable. Applying an experimental approach to a small subset of the system one wishes to study may allow one to disentangle normally correlated variables, but it may also make it impossible to extend the results to large-scale changes. A better ability to forecast climate-change effects on plant–pollinator interactions is most likely to come from thoughtful integration of observational studies and focused experiments.

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References

- Anderson, J. T. et al. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. – *Proc. R. Soc. B* 279: 3843–3852.
- Augsburger, C. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. – *Ecology* 94: 41–50.
- Bartomeus, I. et al. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. – *Proc. Natl Acad. Sci. USA* 108: 20654–20659.
- Bartomeus, I. et al. 2013. Biodiversity ensures plant–pollinator phenological synchrony against climate change. – *Ecol. Lett.* 16: 1331–1338.
- Bauer, S. et al. 2008. The relevance of environmental conditions for departure decision changes en route in migrating geese. – *Ecology* 89: 1953–1960.
- Benadi, G. et al. 2014. Specialization and phenological synchrony of plant–pollinator interactions along an altitudinal gradient. – *J. Anim. Ecol.* 83: 639–650.
- Boggs, C. L. and Inouye, D. W. 2012. A single climate driver has direct and indirect effects on insect population dynamics. – *Ecol. Lett.* 15: 502–508.
- Bosch, J. and Kemp, W. P. 2000. Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). – *Environ. Entomol.* 29: 8–13.
- Bosch, J. and Kemp, W. P. 2003. Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). – *Environ. Entomol.* 32: 711–716.
- Bosch, J. et al. 2000. Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. – *Environ. Entomol.* 29: 874–883.
- Bosch, J. et al. 2010. Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. – *J. Insect Physiol.* 56: 1949–1957.
- Buckley, L. B. and Kingsolver, J. G. 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. – *Annu. Rev. Ecol. Evol. Syst.* 43: 205–226.
- Burkle, L. A. et al. 2013. Plant–pollinator interactions over 120 years: loss of species, co-occurrence and function. – *Science* 339: 1611–1615.
- Calinger, K. M. et al. 2013. Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. – *Ecol. Lett.* 16: 1037–1044.
- Carroll, A. B. et al. 2001. Drought stress, plant water status and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). – *Am. J. Bot.* 88: 436–446.
- Chuine, I. 2010. Why does phenology drive species distribution? – *Phil. Trans. R. Soc. B* 365: 3149–3160.
- Chuine, I. et al. 2003. Plant development models. – In: Schwartz, M. D. (ed.), *Phenology: an integrative environmental science*. Kluwer Academic, pp. 217–235.
- Cook, B. I. et al. 2012. Divergent responses to spring and winter warming drive community level flowering trends. – *Proc. Natl Acad. Sci. USA* 109: 9000–9005.
- Crimmins, T. M. et al. 2010. Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. – *J. Ecol.* 98: 1042–1051.
- Crone, E. E. 2013. Responses of social and solitary bees to pulsed floral resources. – *Am. Nat.* 182: 465–473.
- Doi, H. et al. 2008. Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. – *Climate Res.* 36: 181–190.
- Ellwood, E. R. et al. 2012. Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? – *Oecologia* 168: 1161–1171.
- Erhardt, A. et al. 2005. Elevated carbon dioxide increases nectar production in *Epilobium angustifolium* L. – *Oecologia* 146: 311–317.
- Fabina, N. S. et al. 2010. Sensitivity of plant–pollinator–herbivore communities to changes in phenology. – *Ecol. Modell.* 221: 453–458.
- Forrest, J. R. K. and Thomson, J. D. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. – *Ecol. Monogr.* 81: 469–491.

- Franks, S. J. et al. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. – *Proc. Natl Acad. Sci. USA* 104: 1278–1282.
- Friedman, J. and Willis, J. H. 2013. Major QTLs for critical photoperiod and vernalization underlie extensive variation in flowering in the *Mimulus guttatus* species complex. – *New Phytol.* 199: 571–583.
- Gillespie, D. R. et al. 2012. Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. – *Oikos* 121: 149–159.
- Gordo, O. and Sanz, J. J. 2005. Phenology and climate change: a long-term study in a Mediterranean locality. – *Oecologia* 146: 484–495.
- Green, K. 2010. Alpine taxa exhibit differing responses to climate warming in the Snowy Mountains of Australia. – *J. Mt. Sci.* 7: 167–175.
- Hegland, S. J. et al. 2009. How does climate warming affect plant–pollinator interactions? – *Ecol. Lett.* 12: 184–195.
- Hodgson, J. A. et al. 2011. Predicting insect phenology across space and time. – *Global Change Biol.* 17: 1289–1300.
- Høye, T. T. et al. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. – *Nat. Climate Change* 3: 759–763.
- Ibáñez, I. et al. 2010. Forecasting phenology under global warming. – *Phil. Trans. R. Soc. B* 365: 3247–3260.
- Iler, A. M. et al. 2013a. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? – *Phil. Trans. R. Soc. B* 368: 20120489.
- Iler, A. M. et al. 2013b. Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. – *Global Change Biol.* 19: 2348–2359.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage and floral abundance of montane wildflowers. – *Ecology* 89: 353–362.
- Inouye, D. W. et al. 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). – *Am. J. Bot.* 90: 905–910.
- IPCC 2007. Climate change 2007: the physical science basis. Contrib. of Working Grp I to the 4th Assess. Rep. of the IPCC. – Cambridge Univ. Press.
- Jablonski, L. M. et al. 2002. Plant reproduction under elevated CO₂ conditions: a meta-analysis of reports on 79 crop and wild species. – *New Phytol.* 156: 9–26.
- Jennersten, O. and Nilsson, S. G. 1993. Insect flower visitation frequency and seed production in relation to patch size in *Viscaria vulgaris* (Caryophyllaceae). – *Oikos* 68: 283–292.
- Kraemer, M. E. and Favi, F. D. 2010. Emergence phenology of *Osmia lignaria* subsp. *lignaria* (Hymenoptera: Megachilidae), its parasitoid *Chrysura kyrae* (Hymenoptera: Chrysididae), and bloom of *Cercis canadensis*. – *Environ. Entomol.* 39: 351–358.
- Kudo, G. and Ida, T. Y. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. – *Ecology* 94: 2311–2320.
- Kudo, G. et al. 2004. Does seed production of spring ephemerals decrease when spring comes early? – *Ecol. Res.* 19: 255–259.
- Kunin, W. E. 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. – *Ecology* 74: 2145–2160.
- Lake, J. C. and Hughes, L. 1999. Nectar production and floral characteristics of *Tropaeolum majus* L. grown in ambient and elevated carbon dioxide. – *Ann. Bot.* 84: 535–541.
- Lambert, A. M. et al. 2010. Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae). – *Am. J. Bot.* 97: 1431–1437.
- Laube, J. et al. 2014. Chilling outweighs photoperiod in preventing precocious spring development. – *Global Change Biol.* 20: 170–182.
- Liancourt, P. et al. 2012. Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. – *Ecology* 93: 815–824.
- Liu, Y. et al. 2011. Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity. – *Ecology* 92: 1201–1207.
- McKinney, A. M. et al. 2012. Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. – *Ecology* 93: 1987–1993.
- Memmott, J. et al. 2007. Global warming and the disruption of plant–pollinator interactions. – *Ecol. Lett.* 10: 710–717.
- Meurisse, N. et al. 2012. Low temperature tolerance and starvation ability of the oak processionary moth: implications in a context of increasing epidemics. – *Agric. For. Entomol.* 14: 239–250.
- Miller-Rushing, A. J. and Inouye, D. W. 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species. – *Am. J. Bot.* 96: 1–10.
- Miller-Rushing, A. J. et al. 2010. The effects of phenological mismatch on demography. – *Phil. Trans. R. Soc. B* 365: 3177–3186.
- Moise, E. R. D. and Henry, H. A. L. 2010. Like moths to a street lamp: exaggerated animal densities in plot-level global change field experiments. – *Oikos* 119: 791–795.
- Ovaskainen, O. et al. 2013. Community-level phenological response to climate change. – *Proc. Natl Acad. Sci. USA* 110: 13434–13439.
- Parsche, S. et al. 2011. Experimental environmental change and mutualistic vs. antagonistic plant flower–visitor interactions. – *Persp. Plant Ecol. Evol. Syst.* 13: 27–35.
- Pauli, J. N. et al. 2013. The subnivium: a deteriorating seasonal refugium. – *Front. Ecol. Environ.* 11: 260–267.
- Peñuelas, J. et al. 2004. Noninvasive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north–south European gradient. – *Ecosystems* 7: 598–612.
- Petanidou, T. et al. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. – *Ecol. Lett.* 11: 564–575.
- Poorter, H. and Navas, M.-L. 2003. Plant growth and competition at elevated CO₂: on winners, losers and functional groups. – *New Phytol.* 157: 175–198.
- Praz, C. J. et al. 2008. Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? – *Ecology* 89: 795–804.
- Rader, R. et al. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. – *Global Change Biol.* 19: 3103–3110.
- Rafferty, N. E. and Ives, A. R. 2011. Effects of experimental shifts in flowering phenology on plant–pollinator interactions. – *Ecol. Lett.* 14: 69–74.
- Rafferty, N. E. and Ives, A. R. 2012. Pollinator effectiveness varies with experimental shifts in flowering time. – *Ecology* 93: 803–814.
- Rafferty, N. E. et al. 2013. Phenological overlap of interacting species in a changing climate: an assessment of available approaches. – *Ecol. Evol.* 3: 3183–3193.
- Régnière, J. et al. 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. – *J. Insect Physiol.* 58: 634–647.
- Roland, J. and Matter, S. F. 2013. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. – *Ecology* 94: 190–199.

- Roulston, T. H. and Goodell, K. 2011. The role of resources and risks in regulating wild bee populations. – *Annu. Rev. Entomol.* 56: 293–312.
- Rusterholz, H. P. and Erhardt, A. 1998. Effects of elevated CO₂ on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. – *Oecologia* 113: 341–349.
- Scaven, V. L. and Rafferty, N. E. 2013. Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. – *Curr. Zool.* 59: 418–426.
- Sedivy, C. et al. 2008. Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees. – *Evolution* 62: 2487–2507.
- Sgolastra, F. et al. 2012. Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees of the genus *Osmia*. – *J. Insect Physiol.* 58: 924–933.
- Sih, A. and Baltus, M. S. 1987. Patch size, pollinator behavior and pollinator limitation in catnip. – *Ecology* 68: 1679–1690.
- Singer, M. C. and Wee, B. 2005. Spatial pattern in checkerspot butterfly–host plant association at local, metapopulation and regional scales. – *Ann. Zool. Fenn.* 42: 347–361.
- Smithson, A. and Macnair, M. R. 1997. Density-dependent and frequency-dependent selection by bumblebees *Bombus terrestris* (L.) (Hymenoptera: Apidae). – *Biol. J. Linn. Soc.* 60: 401–417.
- Söndgerath, D. et al. 2012. Large spatial scale effects of rising temperatures: modelling a dragonfly's life cycle and range throughout Europe. – *Insect Conserv. Diver.* 5: 461–469.
- Sparks, T. H. et al. 2005. Examining the total arrival distribution of migratory birds. – *Global Change Biol.* 11: 22–30.
- Steltzer, H. et al. 2009. Biological consequences of earlier snowmelt from desert dust deposition in alpine landscapes. – *Proc. Natl Acad. Sci. USA* 106: 11629–11634.
- Thomson, J. D. 2010. Flowering phenology, fruiting success, and progressive deterioration of pollination in an early-flowering geophyte. – *Phil. Trans. R. Soc. B* 365: 3187–3199.
- Tooke, F. and Battey, N. H. 2010. Temperate flowering phenology. – *J. Exp. Bot.* 61: 2853–2862.
- Visscher, P. K. et al. 1994. Benthic bees? Emergence phenology of *Calliopsis pugionis* (Hymenoptera: Andrenidae) at a seasonally flooded site. – *Ann. Entomol. Soc. Am.* 87: 941–945.
- Wcislo, W. T. and Cane, J. H. 1996. Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. – *Annu. Rev. Entomol.* 41: 257–286.
- Wiens, J. A. et al. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. – *Proc. Natl Acad. Sci. USA* 106: 19729–19736.
- Williams, N. M. 2003. Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). – *Oecologia* 134: 228–237.
- Williams, N. M. and Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. – *Ecol. Appl.* 17: 910–921.
- Williams, N. M. et al. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. – *Ecology* 93: 1049–1058.
- Willmer, P. 2012. Ecology: pollinator–plant synchrony tested by climate change. – *Curr. Biol.* 22: R131–R132.
- Willmer, P. G. and Stone, G. N. 2004. Behavioral, ecological, and physiological determinants of the activity patterns of bees. – *Adv. Study Behav.* 34: 347–466.
- Wolkovich, E. M. et al. 2012. Warming experiments underpredict plant phenological responses to climate change. – *Nature* 485: 494–497.
- Yang, L. H. and Rudolf, V. H. W. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. – *Ecol. Lett.* 13: 1–10.