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LETTER

Global warming and the disruption of plant–pollinator interactions

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Abstract

Anthropogenic climate change is widely expected to drive species extinct by hampering individual survival and reproduction, by reducing the amount and accessibility of suitable habitat, or by eliminating other organisms that are essential to the species in question. Less well appreciated is the likelihood that climate change will directly disrupt or eliminate mutually beneficial (mutualistic) ecological interactions between species even before extinctions occur. We explored the potential disruption of a ubiquitous mutualistic interaction of terrestrial habitats, that between plants and their animal pollinators, via climate change. We used a highly resolved empirical network of interactions between 1420 pollinator and 429 plant species to simulate consequences of the phenological shifts that can be expected with a doubling of atmospheric CO_2. Depending on model assumptions, phenological shifts reduced the floral resources available to 17–50% of all pollinator species, causing as much as half of the ancestral activity period of the animals to fall at times when no food plants were available. Reduced overlap between plants and pollinators also decreased diet breadth of the pollinators. The predicted result of these disruptions is the extinction of pollinators, plants and their crucial interactions.

Keywords

Climate, insects, network, phenology, plants, pollination.

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INTRODUCTION

Pollination of flowers is an essential step in the sexual reproduction of angiosperms. Most angiosperm species rely on insects or other animals, rather than wind, for transfer of pollen among individual plants. The pollinators in turn benefit by obtaining floral resources such as nectar or pollen. Pollination is not only mutually beneficial to the interacting plants and animals, but also serves humanity directly through the yield of many crops, and indirectly by contributing to the healthy functioning of unmanaged terrestrial ecosystems (Costanza *et al.* 1997; Nabhan & Buchmann 1997; Klein *et al.* 2007). Unfortunately, plant and pollinator species are increasingly at risk of local and global extinction from human activities, including habitat loss, altered land use, introduction of alien species and climate change (Kearns *et al.* 1998; Biesmeijer *et al.* 2006). Furthermore, some anthropogenic changes directly threaten pollination interactions themselves. The most obvious example is climate change, which may disrupt the overlap in seasonal timing (i.e. phenology) of flower production and of pollinator flight activity, thus altering the opportunity for interaction between the plants and animals (e.g. Harrison 2000; Wall *et al.* 2003).

The major aspect of climate change, increase in mean global temperature, is associated with an average advancement in the phenology of life history events, including migration and reproduction, in many species. Plants and their pollinators appear to follow this pattern. Over the past century, global warming has advanced the first flowering date of plants, and the seasonal flight activity of some pollinating insects, by *c.* 4 days per degree C on average in temperate zones (see Methods). However, the responses of individual species vary around these averages, so that while most phenologies have been advanced, the degree of advancement has varied, and some phenologies have remained essentially unchanged or have even been retarded.

Our aim in this paper was to explore how future climate change, from the doubling of atmospheric CO_2

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concentration forecast for the period of 2070–2100 (IPCC 2001), is likely to affect interactions of plants and pollinators. We did so by simulating phenological shifts within a real community of plants and pollinators. From 1884 through 1916 Charles Robertson recorded flowers and their pollinators in the prairie-forest transition of western Illinois, USA, identifying all taxa to the species level (Robertson 1929). Robertson's records can be re-cast as a network of 429 plant species engaged in 14 983 distinct interactions with 1419 species of pollinating insects and one species of hummingbird (Memmott & Waser 2002; Memmott *et al.* 2004). This finely resolved qualitative network is an order of magnitude larger than any other available pollination network. Furthermore, Robertson recorded first and last dates of flowering for plant species, and first and last dates on which he made observations of pollinators visiting each plant species. These records allowed us to estimate seasonal timing of flowering and flight activity for each plant and animal species, as well as duration of flowering and flight activity. Extrapolating from phenological shifts observed over the past century, we predict that phenologies of plants and pollinators will be advanced on average by between 1 and 3 weeks by the end of the 21st century, with substantial variation of individual species around the average. Applying this prediction to Robertson's network allows us to determine the extent to which pollinator species may be threatened with local extinction because their temporal overlap with food plants is reduced or eliminated altogether.

METHODS

Pollinator activity periods

Robertson (1929) described a network of plant–pollinator interactions in far more detail than any similar effort to date, which reduces error due to pooling of taxa. However, his phenological records for insects are relatively crude, requiring us to bracket their actual activity periods with minimum and maximum estimates, derived as illustrated in Fig. 1. For each plant species, Robertson gives the first and last dates on which he censused the plant for pollinators, along with a list of all the pollinators. We used these data from 429 plant species; the remaining 27 species studied by Robertson were wind pollinated or had missing census data. As a check on the method we took records for Lepidoptera (butterflies and moths) from Robertson, and correlated them with records from a recent report (Opler *et al.* 2003), such reports being much more common for Lepidoptera than for other types of pollinators. Of the 97 species found in Robertson, 55 were shared with the more recent report. Dates of onset of activity for these species are positively correlated in the two reports (Spearman's $r = 0.49$, d.f. $= 53$, $P = 0.0001$), as are durations of the activity periods (Spearman's $r = 0.51$, d.f. $= 53$, $P < 0.001$, using our maximum estimates of activity periods), indicating that our method is reasonable.

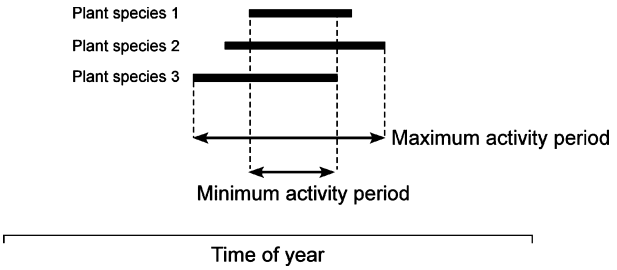

Figure 1 Method for calculating the minimum and maximum estimates of activity period for a hypothetical pollinator species that visits three flower species. The three thick horizontal lines depict the flowering periods during which Robertson (1929) recorded pollinators of plant species 1, 2 and 3 (these periods are either equal to the flowering periods of the plants, or slightly shorter). Robertson did not provide dates of observation for each of the individual pollinator species, but only an overall set of dates for all pollinators to those plants. However, the maximum possible activity period of the pollinator that interests us must be encompassed by the earliest and latest dates for all pollinators, whereas the minimum activity period must be encompassed by the minimum period during which all three plant species flowered simultaneously, given that the pollinator was observed on all three species.

Phenological shifts

We can estimate how flowering phenology in temperate zones will respond to future climate warming, from accounts of responses to recent warming. In the absence of data specifically for western Illinois, we relied on reports of phenological shifts over the past century from multiple northern temperate sites in the USA and the UK. Some of these accounts give the mean shift across species per 1 °C increase in local annual temperature (Fitter *et al.* 1995), or give information readily converted to this scale (Bradley *et al.* 1999; Abu-Asab *et al.* 2001; Primack *et al.* 2004). In other cases we could estimate mean and variance from the authors' figures (Fitter & Fitter 2002), or from values for individual species (Sparks *et al.* 2000). Across five studies from temperate regions of the USA and the UK, first flowering was advanced by 2–6 days per 1 °C, with an overall mean of 4 days. Variation about the mean is approximately normally distributed with a standard deviation equal to the mean (Sparks *et al.* 2000; Fitter & Fitter 2002). In the case of pollinators, butterflies once again appear to provide the only estimates of shifts in onset of the flight season (Rusterholz & Erhardt 1998; Roy & Sparks 2000; Stefanescu *et al.* 2003), and these are very similar to

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those just described for plants. For lack of more complete information, therefore, we used the same values for pollinators as we did for plants.

Current climate models for western Illinois predict an increase in mean annual temperature between 3.5 and 5 °C under doubling of atmospheric CO_2 (derived from Fig. 20 in IPCC 2001). Multiplying these values by the estimated per-degree mean responses of 4 days per 1 °C yields estimates of 14–20 days (i.e. *c.* 2–3 weeks) for the mean advance in phenology. An alternative is to use recent predictions of global average temperature increase, which have a 95% confidence interval of 1.5–6.2 °C and a mean value of *c.* 3 °C (Hegerl *et al.* 2006). This yields a range of predicted phenological shifts of 4 days per °C × 1.5–6.2 °C or *c.* 1–3 weeks, with a most likely shift of 4 days per °C × 3 °C, or *c.* 2 weeks. The simple multiplicative approach used here tacitly assumes that future phenological shifts will scale linearly with the amount of climate warming, which seems reasonable in the absence of better information.

Based on these calculations, we simulated the effect of future climate warming by advancing the onset of flowering of all plant species and of flight activity of all pollinator species in Robertson's web by averages of either 1, 2 or 3 weeks (see Electronic Appendix 1 for details of the simulation model). This range brackets the values calculated above, providing for best- and worst-case scenarios. We left the durations of flowering and activity periods unchanged for all species. Experimental warming did not alter length of flowering seasons in one recent study (Price & Waser 1998), and there is some evidence that adult life cycles of pollinating insects are unaltered or compressed with increasing temperatures (Bosch *et al.* 2000; Karlsson & Wiklund 2005).

Shifts for individual plant and pollinator species were drawn independently and at random from normal probability distributions with mean values of 1, 2 or 3 weeks, and standard deviations equal to the mean (see above). Finally, we assigned 10% of plant species a new phenology chosen not from the normal distribution, but instead taken at random across the entire growing season of western Illinois, which was *c.* 11 months long in Robertson's day (Robertson 1929). If climate change disrupts the correlations among environmental cues plants use to initiate flowering, ancestral correlations are likely to reappear at such novel times in the season (Price & Waser 1998; Inouye *et al.* 2000; Stenseth & Mysterud 2002; Visser & Both 2005; Both *et al.* 2006; Pounds *et al.* 2006; note, however, that qualitative conclusions of our simulations remain unchanged if we omit such assignment; results not shown). By assigning shifts to plants and pollinators independently, and by assigning 10% of plants a 'bizarre' new flowering time, we are assuming that the phenological responses of plants and pollinators are not automatically coupled. This is reasonable on two counts. First, different species are likely to respond to different qualitative or quantitative combinations of environmental cues (e.g. Lambrecht *et al.* 2007), and climate change is unlikely to alter individual cues to the same extents, or to maintain unchanged the ancestral correlations among them. This dissociation of cues has been implicated in the climate-altered temporal overlap between species in a variety of other ecological interactions (e.g. Inouye *et al.* 2000; Peñuelas *et al.* 2002; Stenseth & Mysterud 2002; Edwards & Richardson 2004; Visser & Both 2005; Both *et al.* 2006). Second, plants and pollinators are connected in a web or network of interactions (e.g. Petanidou & Ellis 1996; Memmott 1999; Memmott & Waser 2002), so that individualistic phenological responses for plants will necessarily mean that a pollinator cannot shift timing of activity to maintain unchanged its ancestral associations with all of its food plants. Obligately specialized plant–pollinator pairs might shift synchronously, because they might evolve tightly correlated phenological cues (although little appears to be known about this), but obligate specialization is rare in plant–pollinator interactions (Waser & Ollerton 2006).

We ran 1000 iterations for each of the three magnitudes of phenological shift (1, 2 or 3 weeks) and the two estimates of pollinator activity period (maximum, minimum). For each iteration we then calculated the number of pollinator species that no longer overlapped with any of their original food plants (hereafter 'no food'), the number that experienced temporal gaps in their supply of food plants (hereafter 'gaps'), and the number that suffered periods without food at the beginning or end of their activity period (hereafter 'curtailment'). Figure 2 illustrates the second two of these three types of disruption in food supply.

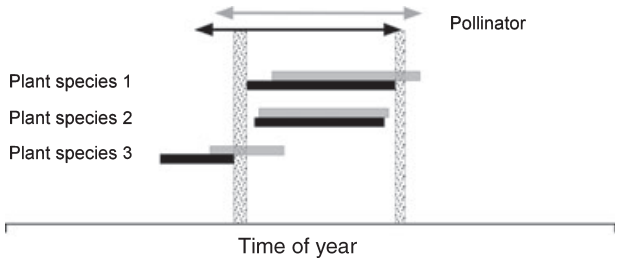

Figure 2 Hypothetical example of shifted phenologies of plants and a shared pollinator that lead to the pollinator experiencing a gap in its food supply and a curtailment in supply at the end of its period of flight activity. The three plant species have been shifted forward (i.e. to the left on the graph) in timing of their flowering (thick black horizontal lines) relative to their ancestral timing (shaded lines), and the pollinator also has shifted (black two-headed arrow vs. shaded arrow). These shifts have produced a gap in food supply (stippled column to left of figure) and a curtailment at the end of the pollinator's flight season (stippled column to right).

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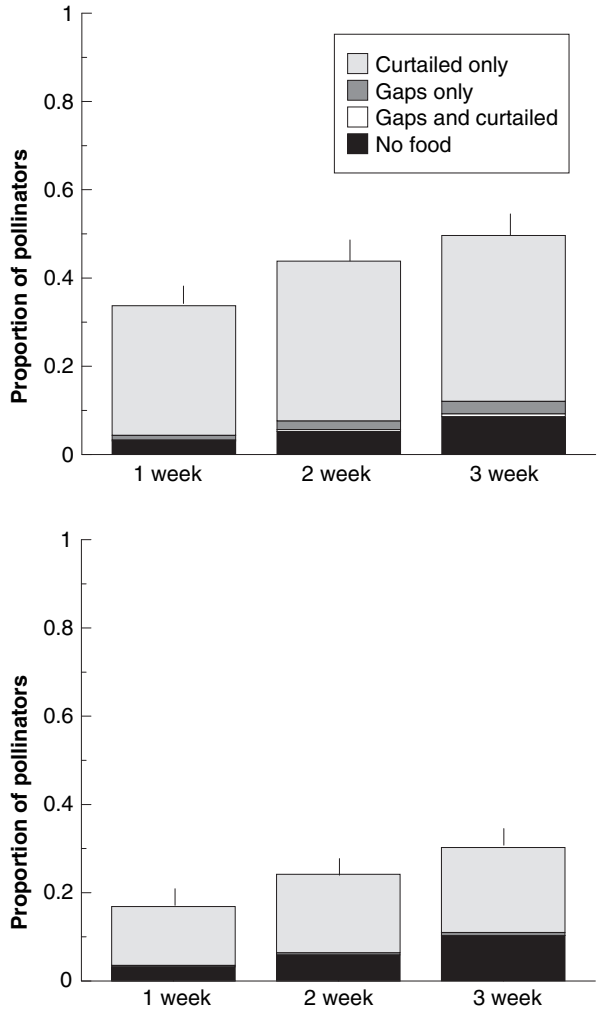

Figure 3 Frequencies of alternative types of food disruption resulting from 1-, 2- and 3-week advancement in mean phenologies. Top: Simulations that used maximum estimates of pollinator activity periods. Bottom: Simulations that used minimum estimates. Values are averages across 1000 model runs. 95% confidence intervals are too small to be presented for all but the curtailments, and gaps + curtailment are too infrequent to show on the stacked graph. The predicted extreme percentages of all pollinator species suffering disruption in food supply (17–50%) derive, respectively, from a mean phenological advance of 1 week coupled with minimum estimates of pollinator activity periods, and from a mean advance of 3 weeks coupled with maximum estimates.

RESULTS

The simulations predict that between 17% and 50% of all pollinator species will suffer disruption in food supply (Fig. 3). The percentage of species suffering disruption increased as mean phenologies advanced from 1 to 3 weeks ($F_{2,14} = 8.08$, $P < 0.05$, ANOVA; see Electronic Appendix 2 for details), and as estimates of pollinator activity period increased from minimum to maximum ($F_{1,14} = 39.76$, $P < 0.0001$, ANOVA; see Electronic Appendix 2). In all the simulations, curtailment was the most common form of disruption, followed by no food, gaps in the food supply and by a very small number (too small to be visible in Fig. 3) of pollinators that suffered both gaps and curtailment. Mean gap lengths ranged from 7.1 days for a mean phenological shift of 1 week with minimum estimates of pollinator activity periods, to 11.9 days for a shift of 3 weeks with maximum estimates; these corresponded, respectively, to losses of 8.3% and 13.9% of the insects' total activity periods (Table 1). There was no difference in the length of curtailment at the start of pollinator activity periods vs. at the end (Fig. 4). Total curtailment increased from 14.5 days for a shift of 1 week with minimum estimates, to 32.0 days for a shift of 3 weeks with maximum estimates, corresponding, respectively, to losses of between 16.9% and 37.2% in total activity periods (Table 1). Overall, therefore, the percentage of shifted pollinator activity period that occurs without overlap with any ancestral food plant might be as high as 51.1% (13.9 + 37.2%).

The pollinators most likely to be left with no food at all were those that use flowers of a small number of plant species. Pollinators that had no food left after a mean phenological advancement of 2 weeks had originally visited a median of one plant species only, whereas those that suffered no loss of food resources had visited a median of nine plants (this and further comparisons are based on maximum estimates of pollinator activity periods; minimum estimates yield qualitatively similar results). Generalist pollinators that feed from flowers of many plant species were also subject to reductions in diet breadth following phenological shifts. In the original Robertson pollination network each pollinator species visited a median of four plant species, whereas after a simulated advancement in plant and pollinator phenology of 2 weeks this dropped to 3.3 plant species (Wilcoxon $W = 1\,856\,843$, $P < 0.0001$). Different insults to pollinators – gaps, curtailment and reduced diet breadth – can also act in combination. For example, the 2-week advancement in phenologies exposed 36% of pollinator species to curtailment, in addition to the reduction in their median diet breadth.

DISCUSSION

Our simulations indicate that shifts in phenology induced by climate change have the potential to disrupt the temporal overlap between pollinators and their floral food resources, assuming no compensating mechanisms. They predict that a substantial fraction of pollinators, particularly the more specialized ones with small diet breadths, are vulnerable to such disruption. Local extinction is the predicted fate of a pollinator that no longer overlaps with any food plants. But

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Model assumptions	Mean gap length (days)	Mean % activity period lost	Mean total curtailment (days)	Mean % activity period lost
1 week, min	7.1	8.3	14.5	16.9
1 week, max	8.3	9.7	16.2	18.9
2 weeks, min	7.5	8.7	22.8	26.6
2 weeks, max	10.0	11.7	24.8	28.9
3 weeks, min	8.7	10.1	28.0	32.6
3 weeks, max	11.9	13.9	32.0	37.2

Table 1 The average extent of pollinator activity period, expressed as days and as percentage of the total activity period, during which no ancestral food plant is in flower, under different model assumptions

The model assumptions range from a mean phenological shift of 1 week with minimum estimates of the length of activity periods, to a shift of 3 weeks with maximum estimates.

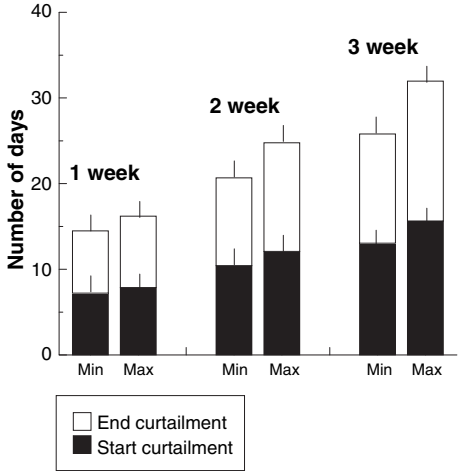

Figure 4 The mean number of days of curtailment in food supply of pollinators for 1, 2 and 3 weeks mean shifts in plant and pollinator phenology. Min = prediction based on minimum estimates of pollinator activity periods; Max = prediction based on maximum estimates. Error bars are 95% confidence intervals from 1000 model runs.

the risk of pollinator extinction is also likely to increase with the probability of gaps and curtailment, and with their length. The few available studies of life histories of pollinating insects subjected to adult food limitation indicate that fecundity and/or longevity are reduced (Murphy *et al.* 1983; Boggs & Ross 1993), which in turn reduces population densities or growth rates (Bijlsma *et al.* 1994), and increases risk of extinction. Even pollinators experiencing no gaps or curtailment, but losing some of their food plants, are likely to suffer population declines from this reduced diet breadth, as relying on fewer plant species will expose them to lower overall densities of flowers and greater temporal and spatial variation in food supply.

Although we have not presented results on the percentages of plants that lose all or some pollinators, the effects on plants in our simulations were symmetrical in basic outline to the effects on pollinators. While plants do not face starvation if they lose pollinators, recruitment of new individuals through sexual reproduction will decline or cease. This will lead to immediate or eventual population declines, depending on longevity of individuals, their capability to spread clonally, their ability to self-fertilize, and the viability and fertility of selfed offspring (Bijlsma *et al.* 1994; Holsinger 2000).

Loss of more specialized pollinators is unlikely to lead to immediate co-extinction of plants they pollinate, because of the topology of networks of interactions among plant and pollinator species. Pollination networks are strikingly nested and asymmetrical, with specialist pollinators tending to visit generalist plants, and specialist plants tending to be visited by generalist pollinators (Petanidou & Ellis 1996; Bascompte *et al.* 2003). Thus, plants are protected, at least in part, from the loss of more specialized pollinators by the presence of other, more generalist, visitors (Melián & Bascompte 2002; Memmott *et al.* 2004). Indeed, temporal and spatial variation in association between plants and pollinators is the norm (e.g. Price *et al.* 2005), to which the common condition of generalization of both mutualistic partners represents one likely adaptation (Waser *et al.* 1996). Nonetheless, apparent resilience of pollination networks to loss of specialists, and adaptation to some level of environmental variability, are no guarantee against eventual loss of more generalized species and decay of functionality of pollination services (Memmott *et al.* 2004; Fontaine *et al.* 2006) in the face of climate change, insofar as climate change will move these systems in a directional fashion beyond their ancestral range of variation.

Forecasts of the loss of pollination interactions must remain imprecise, as there are many gaps in our understanding of how global warming influences the interactions between species. Some of these gaps could bias predictions from the simulations in the direction of *overestimating* detrimental effects of phenological shifts on pollinator food supply. For example, some pollinators deprived of ancestral hosts will be able to use new host plants whose phenologies now overlap with theirs. But in very few cases do we know the potential host range of pollinators, so we must simply

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acknowledge here the possibility that their diet is not always fixed. Similarly, rapid evolutionary change could allow pollinators to track shifting host phenologies. We have not included this effect either, because we see two major hurdles to such tracking. First, because most pollinators visit more than one plant species, and because different plants apparently respond differently to climate change, it is not a foregone conclusion that strong directional selection on phenology will be the net result. Second, even if selection is strong, it is unclear that additive genetic variation will arise by spontaneous mutation of a form that allows a pollinator to use ancestral cues in new combinations to track plants, or that allows a shift to new cues. Rapid evolutionary change that broadens the diets of more specialized pollinators seems more likely, for example, via evolution of the trophic apparatus (compare Grant & Grant 1993), although competition from existing generalists might constrain such change. Finally, it is possible that some lost interactions involving loss of pollinators will be replaced by interactions involving new insect species extending their ranges to higher latitudes, although this might be counterbalanced by ancestral pollinators leaving the area towards higher latitudes themselves.

Other gaps in knowledge could bias predictions from simulations in the direction of *underestimating* disruption of pollination. Although Robertson could not observe all plant species in all years, most were observed in more than 1 year (J. C. Marlin, personal communication). Year-to-year variation, and spatial variation over the local area that he sampled, will mean that Robertson's pooled records overestimate the flowering period for such species in any single year and site, and thus that our simulations underestimate the actual chance of phenological mismatch in a given year. The simulations also underestimate the magnitude of phenological shifts by ignoring those that have already occurred in western Illinois since Robertson's day. Moreover, we assumed a linear relationship between climate warming and phenological shifts in our simulations, meaning that our figures are conservative should a nonlinear relationship prove to be the case. Finally, our approach does not consider the consequences of warming-induced phenological shifts that may be relevant to other pollinator life stages (e.g. larval stages, migratory phases), nor does it consider damage to plant–pollinator interactions arising from extreme weather events driven by climate change (e.g. Harrison 2000; Meehl & Tebaldi 2004).

We conclude that a prediction of serious adverse consequences for pollination interactions is merited in light of these countervailing biases, along with our approach of bracketing the best- to worst-case scenarios. To improve the precision of community-level predictions (the community being the unit that is affected by global warming), ecologists particularly need data on phenological cues and on the behavioural flexibility of pollinators, and on pollinator life cycles. These are areas calling for vigorous research if we are to improve predictions of future change.

Over 30 years ago Janzen (1974) raised the spectre of the 'most insidious sort of extinction, the extinction of ecological interactions'. Here, a community-level approach using the largest available ecological network of interactions suggests that global warming, in addition to its other predicted impacts on species extinctions (Walther *et al.* 2002; Thomas *et al.* 2004), may lead to the large-scale extinction of interactions which are responsible for a key ecosystem service, that of the pollination of plants.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Model details.

Appendix S2 ANOVA for proportion of pollinators suffering disruption.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01061.x

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