

# Ecology: Pollinator–Plant Synchrony Tested by Climate Change

Flowering plants could lose their pollination service if climate warming potentially uncouples timing of flowering from pollinator availability. Recent evidence might suggest this effect may be less than feared.

Pat Willmer

The potential effect of climate change on the uncoupling of mutualisms has been a perceived threat for 40 years, especially for pollinator interactions [1]. The threat of unbalanced phenological changes could be compounded in increasingly fragmented landscapes, where habitat specialists cannot readily track climate change [2]. However, recent analyses are indicating that the threat to pollination services may be less than feared, with Bartomeus *et al.* [3] providing the largest and most recent analysis.

We know that plants are tending to flower earlier [4], especially those that flower in early spring, and that insects are often emerging earlier. Long-term data sets suggest that insects may be somewhat more responsive to thermal changes than plants [5], not least because plants are also more strongly affected by photoperiod and often tend to have a chilling requirement, so that some species may even delay their flowering because of the reduction of chilling. Available data on many insects, and specifically on bees, indicate that spring emergence is influenced by a specific degree-day requirement rather than just by temperature threshold. Hence there is potential for mismatch between plant and insect responses to climate change.

Earlier field studies of naturally occurring phenologies reported data for just one or a few plants, or looked at single unusual years, but often did reveal potential problems. One very warm spring in Japan led to serious mismatch and reduced seed set for bee-pollinated plants [6], while there were good correlations of flowering onset and snow-melt timing across 16 years in sub-alpine *Erythronium* [7], the plant being increasingly poorly synchronized with its pollinators in recent years. But two other small studies showed bees changing faster than plants while two showed the opposite, suggesting no clear patterns

of divergence. However, use of modelling to simulate warming has yielded predictions that 17–50% of insect pollinators are likely to experience periods with no available floral resources [8].

Three papers in 2011 have used experimental manipulations to dissect these complex interactions. Rafferty and Ives [9] tested 14 plant species, manipulating flowering onset in greenhouses and then observing insect visitation, and found that species which had already advanced their flowering time received more visits when flowering earlier, whereas species without naturally advanced onset received fewer visits when forced to flower earlier. They suggest that species not constrained by pollinators have already started flowering earlier, whereas pollination-constrained species have not, so that temporal mismatches are not occurring. Parsche *et al.* [10] tested mustard plants in varying habitat ‘islands’; earlier flowering reduced numbers of pollinators (wild bees and hoverflies) and of herbivores, with an increase in seed set, suggesting that some loss of pollinating mutualists was more than compensated for (in reproductive outcomes) by simultaneous escape from antagonists. However, Forrest and Thomson [11] highlighted the problem that data on these insect ‘phenologies’ are based on capture at flowers, and therefore not independent of the plants’ phenology. They allowed for this by setting up standardized bee nesting habitats along an elevational gradient in the Rockies, cross-checked with reciprocal transplants of bees, thus acquiring data on actual bee emergence independent of local flowering times. They found that plant and bee phenologies were rather similarly temperature-dependent, but that plants were more likely to advance their phenology when faced with springtime warming. They also recorded specific uncoupling at some sites, e.g. of *Lathyrus* flowering and *Hoplitis* bee availability.

Bartomeus *et al.* [3] take a grander approach than any other study to date, with data sets for emergence time for 10 bee species across 4 genera, and flowering times for over 100 plants they may visit, over a 130 year span. Taken as a whole, the bees’ phenology has advanced by a mean of 10.4 days, not significantly different from the analogous rates of advance of plant flowering; and in both cases the greater part of this advance has occurred since 1970. Within this broad demonstration of retained synchrony, the earliest bees show the best correlations with climate change, whereas the latest emergers are least well-matched by a thermal model and bumblebees are also less dependent on yearly climate. In practice, it seems that the earliest species are advancing their phenology more quickly (as is also the case for plants). But it is noteworthy that the earliest bee species are also those with the greatest spread in emergence times, perhaps indicating some ability on their part to ‘bet-hedge’.

But what might we be missing here? A number of issues arise from the recent publications. Some show that plants in urban areas are advancing flowering faster, and we need to know more about cities as ‘heat islands’. Most concentrate on bees, but mainly on bees that overwinter as adults; what happens for bees that exist as (more susceptible?) larvae in winter? And variable effects in different habitats remain unclear, for example at altitude where plants flower at the snow-line and where snow-melt may become ever more rapid. Such plants may get an earlier start [12,13] without a corresponding advance in insect emergence; to date there may be merely a reduction in overlap, rather than complete decoupling, but further climate change could be particularly deleterious in these habitats [14]. And perhaps we should be looking for more specific seasonal effects anyway: warmer drier summers can produce midsummer floral scarcity [15], and frost damage on early spring buds can lead to poor flowering [16], both these outcomes being exacerbated by climate change. On a still longer time-base, populations may be forced to move latitudinally over time (already documented for butterflies and bees in temperate zones), and insects may

move faster than plants. Such effects may prove to be more damaging than any local phenological mismatches.

Is synchrony critical anyway? If most plants are generalists and plant–pollinator interactions are diffuse [17], and/or are variable in time and space [18], then the pollination mutualism is likely to be buffered against climate change. In the recent flurry of studies, the bees selected, if truly generalist in terms of effective pollination, are inherently unlikely to be tied to the phenology of just one or a few plants. Hence the vexed question of generalization and specialization [17,18] must come to the fore. Bartomeus *et al.* [3] deliberately selected ‘generalist’ bees, and used plants visited by at least one of these ten bees (though in about a third of cases they settled for a plant species where merely the genus is visited by at least one of the bees, despite their own analysis of bees showing that ‘genus’ is poorly explanatory for recorded variation!). Forrest and Thomson also used bees designated as generalist, as have most of the studies to date. Furthermore, all studies rely purely on *visitation* data and are therefore not necessarily recording effective pollinators, a distinction which is almost invariably skated over but which may be crucial [19]. Rafferty and Ives wisely used both generalist and specialist plant species, and did note that they were using visitation and not pollination records, but assumed that visit frequency would serve as a proxy, though data from my own research group do not support this. Hence, all studies to date may be undermined by

over-reliance on suspect ‘pollinator’ records.

Since pollination interactions are also under threat from habitat fragmentation and from introduced alien species [2,20], it may be prudent to look urgently at some more specialist interactions of native bees and their preferred plants, where these multiple threats in combination could be much more serious. And while existing reports of relatively limited climate-related uncoupling effects for flowers and flower visitors may be transiently comforting, since we know that populations and diversity of bees and other pollinators are in serious decline we cannot afford to be complacent.

#### References

1. Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A., and Totland, Ø (2009). How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* **12**, 184–195.
2. Tylianakis, J.M., Didham, R.K., Bascompte, J., and Wardle, D.A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363.
3. Bartomeus, I., Ascher, J.S., Wagner, S., Danforth, B.N., Colla, S., Kornbluth, S., and Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl. Acad. Sci. USA* **108**, 20645–20649.
4. Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., and Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *Am. J. Bot.* **91**, 1260–1264.
5. Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.* **13**, 1860–1872.
6. Kudo, G., Nishikawa, Y., Kasagi, T., and Kosuge, S. (2004). Does seed production of spring ephemerals decrease when spring comes early? *Ecol. Res.* **19**, 255–259.
7. Thomson, J.D. (2010). Flowering phenology, fruiting success, and progressive deterioration of pollination in an early flowering geophyte. *Phil. Trans. Roy. Soc. B* **365**, 3187–3199.
8. Memmott, J., Craze, P.G., Waser, N.M., and Price, M.V. (2007). Global warming and the

disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717.

9. Rafferty, N.E., and Ives, A.R. (2011). Effects of experimental shifts in flowering phenology on plant–pollinator interactions. *Ecol. Lett.* **14**, 69–74.
10. Parsche, S., Fründ, J., and Tschamtkte, T. (2011). Experimental environmental change and mutualistic vs. antagonistic plant flower–visitor interactions. *Persp. Plant. Ecol. Evol. Syst.* **13**, 27–35.
11. 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.
12. Inouye, D.W., Saavedra, F., and Lee-Yang, W. (2003). Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *Am. J. Bot.* **90**, 905–910.
13. Dunne, J.A., Harte, J., and Taylor, K.J. (2003). Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecol. Monogr.* **73**, 69–86.
14. Kudo, G., and Hirao, A.S. (2006). Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Pop. Ecol.* **48**, 49–58.
15. Aldridge, G.D., Inouye, W., Forrest, J., Barr, W.A., and Miller-Rushing, A.J. (2011). Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *J. Ecol.* **99**, 905–913.
16. Inouye, D.W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353–362.
17. Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., and Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology* **77**, 1043–1060.
18. Burkle, L.A., and Alarcón, R. (2011). The future of plant–pollinator diversity: understanding interaction networks across time, space and global change. *Am. J. Bot.* **98**, 528–538.
19. Willmer, P.G. (2011). *Pollination and Floral Ecology* (Princeton: Princeton University Press).
20. Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., Kühn, I., Moora, M., Nielsen, A., Ohlemüller, R., *et al.* (2010). Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biol. Rev.* **85**, 777–795.

School of Biology, Bute Building, University of St Andrews, St Andrews, Fife, KY16 9TS, Scotland, UK.

E-mail: [p.g.willmer@st-andrews.ac.uk](mailto:p.g.willmer@st-andrews.ac.uk)

DOI: 10.1016/j.cub.2012.01.009

## Visuo-Motor Control: When the Brain Loses Track of the Eyes

In single-units studies, neuronal signals are recorded to assess their significance and, hopefully, their role in controlling behavior. A new study of neuronal signals associated with eye position helps to explain not only how the system normally works, but also how it sometimes fails.

John Schlag

In a recent issue of *Current Biology*, Morris *et al.* [1] report evidence that

the sluggishness of perisaccadic mislocalization in the dark can be explained by the dynamics of eye position signals in the dorsal visual

system. Perisaccadic mislocalization is a bizarre phenomenon. In the dark, it occurs if a spot of light is flashed just as you are making an eye movement (saccade). Asked to point to the site where you think you have seen the flash, it turns out that your pointing is wrong — not just inaccurate — but unbelievably wrong, by as much as 70% of the saccade amplitude [2]! Such a ‘mislocalization’, however, may be just a laboratory curiosity. In everyday life, you make several saccades per second, you blink, but