

EDITORIAL

Plant–pollinator interactions and threats to pollination: perspectives from the flower to the landscape

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Animal pollinators have driven the diversification of plants on the earth for more than 100 million years. The mutualism between plants and their pollinators rests on an exchange: food for pollinators and efficient vectoring of sexual reproduction for plants. This relationship has been shaped by many factors during the course of evolution. Competition between pollinators for access to nectar and pollen, and among flowering plants for the attention of pollinators, has influenced the shape, colour and scent of flowers and the extent to which plants invest in the production of pollen and nectar. While many pollinators are ‘generalists’ and visit a variety of flowering plants to obtain food, close relationships between specific pollinators and plant species have developed throughout the course of evolutionary history. An important issue today, given the widespread concern about wild and managed pollinators, is determining how human activities impact the varied relationships between plants and their insect pollinators.

Insect pollinator declines are being attributed to interactions between multiple stressors including pesticides, pathogens and pests, but there is a general consensus that diminishing forage is of overarching importance (Potts *et al.* 2010; Vanbergen & the Insect Pollinators Initiative 2013; Goulson *et al.* 2015). In other words, the single most pressing issue facing plants and their pollinators is the preservation of habitat. Loss of natural habitat reduces plant diversity and abundance which directly translates into fewer and less diverse sources of forage for pollinators (Potts *et al.* 2003; Senapati *et al.* 2015; Baude *et al.* 2016). Generalist bee species require diverse sources of floral pollen because pollen varies in digestibility and nutritional content and may lack essential nutrients (Roulston & Cane 2000). In addition, an environment that is plant species rich is more likely to have floral resources available to pollinators over longer periods, important for social species with long-lived colonies (Wray & Elle 2015). For pollinators that have specialised relationships with flowering plants like certain solitary bee species (Muller & Kuhlmann 2008), reduction in habitat often translates into critical reduction or elimination of

their specialist plant partner populations. However, loss of natural habitat also impacts pollinators through reductions in nesting sites and in fewer host plants for larvae (as in the case of Lepidoptera). Thus, it is easy to predict that solely through the reduction of food and nesting sites, pollinator populations will decline. The collection of eight papers in this special feature highlights the factors that govern the evolution of plant–pollinator relationships and the characteristics of pollinators and plants that make them resilient to anthropogenic change.

In the opening review, Deepa Senapati and colleagues examine the evidence for landscape impacts on pollinator communities in northern temperate systems (Senapati *et al.* 2017). They deal with assessment methods, the main landscape characteristics that affect pollinators and the success or otherwise of conservation schemes in human-altered landscapes. Although the authors find there have been 250 studies on interactions between landscape and pollinators since the review by Viana *et al.* (2012), the need for work on non-bee taxa and for multiple-year observations is still apparent. Nectar and pollen resources may also be affected differently by landscape change. Baude *et al.* (2016) used historical estimates of vegetation cover and direct nectar measurements to look at nectar resources in Britain, and found clover *Trifolium repens* and three other plant species to contribute more than half of national nectar production. Much greater floral diversity may be needed to meet pollen requirements. The study of Requier *et al.* (2015) in intensive farmland showed that honeybees collected nectar mainly from rape-seed and sunflower, confirming that mass-flowering crops benefit generalist pollinators for limited periods, but their pollen diet was botanically much richer and was derived from semi-natural habitats or from weeds in the crops. For both managed and wild pollinators, the preservation of natural habitat and the maintenance of connectivity and landscape heterogeneity are critical, but the extent to which these factors impact pollinators depends on the species in question. Senapati *et al.* (2017) also highlight the fact that providing habitat for pollinators is likely to improve pollination services for flowering crop species and that urban habitats provide resources that can be unexpectedly rich.

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One factor contributing to habitat loss is the spread of invasive plants. In an increasingly connected world, human activities such as trade, agriculture and tourism have translocated much of the world's flora and fauna across geographical space, and the invasion process has complex associations with pollination. Jane Stout and Erin Jo Tiedeken in this issue (Stout & Tiedeken 2017) focus on the direct interactions between invasive plants and native pollinators (most studies have focussed on the indirect impacts such as competition with native plants for pollinators). On the animal side, invasive flowering plants influence the nutrition, behaviour, health and fitness of pollinators. On the plant side, generalised native pollinators, often in the same functional groups as pollinators in the plants' native range, assist the invasion process. Introduced plants may provide substantial food resources for bees. Bumblebees foraging on the abundant nectar of Himalayan balsam (*Impatiens glandulifera*) have facilitated its successful invasion throughout Europe (Chittka & Schürkens 2001; Emer *et al.* 2015). One avenue of future work recommended by Stout & Tiedeken (2017) is to disentangle the effects of invasive plants *per se* on flower visitors from the effects of adding highly rewarding species to the system.

Honeybees, and more recently bumblebees, have been extensively transported around the world for crop pollination purposes and have also become invasive. Christian Pirk and colleagues in this issue (Pirk, Crewe & Moritz 2017) take a fresh look at the interactions between wild and managed bees. Such interactions are usually assumed to be negative, as when pathogens are transmitted to native bees or between wild or feral colonies and managed populations (Fürst *et al.* 2014; Schmid-Hempel *et al.* 2014). The association between the parasitic mite *Varroa* and the pathogenic DWV virus has been disastrous for beekeeping when coupled with the anthropogenic spread of honeybees (Wilfert *et al.* 2016), and in their review Pirk, Crewe & Moritz (2017) present several scenarios for past and future introductions of the *Varroa* mite. However, they also point out positive interactions between wild and managed bee populations: for example, resilience to *Varroa* in Africa and the Americas is due to the high ratio of wild to managed honeybee colonies. Compared to honeybees, the situation for bumblebees is little known and the authors advise extreme caution in importing foreign bumblebee species into novel environments.

An overlooked impact of land-use change on pollinators involves atmospheric chemistry. Anthropogenic volatile pollutants, generated by industry, cities and traffic, have the potential to disrupt olfactory signals between plants and their pollinators, reviewed by Andreas Jürgens and Mascha Bischoff in this issue (Jürgens & Bischoff 2017). In this category of pollutants, they also include reactive oxygen species such as ozone and volatile organic compounds from introduced crops. Air pollution can affect plant–pollinator interactions in multiple ways: metabolic changes in plants may affect signalling, ‘infochemicals’ are degraded or transformed, background noise is increased and

pollinator perception of plant volatiles is altered. The crucial role of odour cues in pollination has been elegantly demonstrated by Larue, Raguso & Junker (2015) who manipulated the volatile profile of two plant species visited by different pollinators and reversibly changed the patterns of visitation, in spite of the flowers being very different in appearance. Interdisciplinary methods are needed to tackle the key research questions of which air pollutants have the highest impact and what is the extent of their long-term interference with plant–pollinator networks (Jürgens & Bischoff 2017).

Central to the controversy surrounding pesticide use and bee declines is the use of neonicotinoids as seed treatments, because these systemic insecticides are commonly present in nectar and pollen (Godfray *et al.* 2014). However, as well as these synthetic toxins, pollinators have to cope with a variety of natural toxins in both nectar and pollen. Secondary metabolites in nectar influence the ecological interactions between plants and their pollinators in various ways, reviewed in this special feature by Phil Stevenson and colleagues (Stevenson, Nicolson & Wright 2017). They may serve as filters that encourage specialist pollinators and deter less effective visitors; may modify the behaviour of pollinators to make them more flower constant (as when caffeine enhances the memory of floral scent associated with food); and their antimicrobial activity has the potential to protect nectar nutrients from degradation and reduce the impact of disease in flower visitors. In many cases, there is a lack of evidence for direct impacts on plant fitness, so that pleiotropic effects (due to defence functions elsewhere in the plant) are not easily ruled out. Whether effects are harmful or beneficial depends on the concentration in nectar of the chemical involved (and secondary metabolite concentrations are typically higher in pollen than nectar). Stevenson, Nicolson & Wright (2017) make a plea for a wider research focus that moves beyond the effects of nectar alkaloids of bee-pollinated plant species.

Compared to how bees assess and obtain nectar rewards, their preferences for pollen, a more complex food and sometimes the only reward offered, have been relatively neglected. Furthermore, the impact of human activity or plant species invasions on pollinators is likely to depend on whether pollinators visit plants for nectar only or whether they must acquire both nectar and pollen (Emer *et al.* 2015). The review by Elizabeth Nicholls and Natalie Hempel de Ibarra (Nicholls & Hempel de Ibarra 2017) on possible mechanisms used by bees to assess pollen rewards fills this gap. The concept of specialisation in bees refers to pollen foraging, which suggests that they possess the ability to distinguish between pollen sources, but mechanisms for assessing the nutritional value of pollen are little understood. Visual, olfactory, gustatory and mechanical cues may all be involved (Ruedenauer, Spaethe & Leonhardt 2015), as well as feedback from larvae. Learning and memory in bees are usually studied using sucrose rewards, but this review shows that bees also learn

to associate floral features with pollen. Nicholls and Hempel de Ibarra point out that, unlike nectar, pollen is a substance that is usually collected by bees rather than being consumed at the flower, so the assessment of pollen quality is likely to be different to the ways bees assess the quality of nectar. However, the difficulty of acquiring pollen from anthers, like the effort required to retrieve nectar, should influence the overall assessment of the value of pollen by foraging bee species.

Much attention has been devoted to the role of specialisation in pollination ecology, not without confusion and controversy. In this issue, Scott Armbruster (Armbruster 2017) clarifies the use of the term specialisation on three levels: ecological (pollination involving one or a few kinds of plants and animals), phenotypic (having specialised flowers or morphologies) and evolutionary (showing transitions towards increased specialisation). Extreme morphology does not always mean ecological specialisation: for example, long tongues in bees and lepidopterans enable them to drink nectar from a broad range of both short- and long-tubed flowers. Asymmetrical specialisation is common (Vázquez & Aizen 2004) and there appears to be a general tendency for specialised flower visitors to forage from generalist flowers and vice versa. A clear example of asymmetry is seen in pollination by hawkmoths (Sphingidae) of unrelated long-tubed flowers showing convergent evolution in tropical and subtropical regions of Africa and the Americas; this is the topic of the final paper by Steve Johnson and colleagues. In a global scale morphometrics study, Johnson *et al.* (2017) have analysed hawkmoth proboscis lengths, flower lengths and the degree of specialisation in nine biogeographical regions spread across the Old and New Worlds. At a regional level, proboscis lengths of hawkmoths show discontinuous frequency distributions which tend to be matched by tube lengths of the night-opening flowers that they visit. The tight association is more apparent in plants with long-tubed flowers (specialists) than in their animal partners, the long-tongued hawkmoths (extreme generalists). Such trends may indicate that the evolution of plant and pollinator traits does not progress reciprocally but rather that pollinators exert strong pressure on floral traits that suit them (Whittall & Hodges 2007). Interestingly, the long-tongued hawkmoth pollination guild in South Africa includes several exotic plant species that are invasive (Johnson & Raguso 2016), indicating that the major pollinator *Agrius convolvuli* rapidly adapts to forage on plant species not encountered previously in its evolutionary history. The study of Johnson *et al.* (2017) is particularly valuable for bringing together a large body of data on moth-flower relationships (including analyses of pollen loads) collected across several species-rich tropical regions.

It is already 20 years since Buchmann & Nabhan (1996) wrote '*The Forgotten Pollinators*' to alert us to the fact that wild pollinators are declining around the world. The collection of papers presented here makes it clear that plant-pollinator mutualisms remain a fascinating topic for study,

but the disruptions to these mutualisms are still of pressing concern. Clear evidence is becoming available that pollinator declines in abundance and diversity can be attributed to human-induced changes in their nutritional resources. For the UK, there is the correlation found by Baude *et al.* (2016) between historical assessment of nectar resources and records of pollinator extinctions, with declines during peak agricultural intensification in the middle of the 20th century being slowed or even partly reversed in subsequent years. Across the USA, Koh *et al.* (2016) find opposing trends in crop expansion and wild bee abundance. One environmental disturbance that has increased in momentum since publication of '*The Forgotten Pollinators*' is global climate change. The consequences of warming temperatures for pollination services include possible mismatches in the phenology of plants and their pollinators (Memmott *et al.* 2007) and range shifts as identified in bumblebees (Kerr *et al.* 2015). These effects of global warming are inextricably linked to habitat loss and fragmentation, and to biological invasions: this is an undoubted challenge for future research in pollination ecology.

The stimulus for this special feature was a workshop held at the University of Pretoria in March 2015, funded by the Royal Society and the National Research Foundation of South Africa under the SA-UK Scientific Seminars Initiative. It was apparent at the workshop that researchers from the UK and South Africa face very different pollination landscapes. Internationally, research in pollination ecology and the assessment of pollinator problems is strongly biased towards northern temperate regions, and Africa is poorly represented (Viana *et al.* 2012; Archer *et al.* 2014). In Europe, biodiversity is limited (but well documented), beekeeping is intensive and the landscape is relatively homogeneous with intensive agriculture and relatively little wild land area. In contrast, Africa has a far lower proportion of arable land and much greater biodiversity, but little is known about pollinators and human interference in pollination (including pesticide use: Muli *et al.* 2014) is much less. Against the background of future population growth, predicted rapid urbanisation and associated anthropogenic pressures, there is much greater potential in Africa for current and future loss of plant and pollinator biodiversity. On a more optimistic note, there is also enormous potential for improved production of animal-pollinated crops to feed the growing human population.

This special feature is accompanied by a virtual issue; also, we draw attention to a previous cross-journal virtual issue on pollinator ecology in *Functional Ecology* in January 2014.

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