



Invasive species in *pollination networks*

Steve Johnson shows us that we need to study birds and bees, and even moths, to understand how plant invasions work.

In this age of efficient transport across land, sea and air, the Earth has become a global village. Travel and trade between countries has led to the introduction of countless plant and animal species into regions where they had never occurred naturally before. Most of these alien species do not survive outside the pampered confines of human settlements, but some eventually become naturalised and even invasive, and some transform natural ecosystems. This process of invasion begins when alien species become incorporated into the various ecological networks that sustain life. This article discusses pollination networks, the web of interactions between plants and their animal pollinators.

Bees and pollination networks

Pollination (the transfer of pollen between flowers) is needed for most plants to produce seeds and reproduce. In turn, flowers provide the food needed by many groups of insects, including bees, most butterflies and moths, and many flies and beetles, as well as vertebrates such as nectar-

feeding birds and bats.

Should we be concerned that invasive species will disrupt pollination networks in South Africa? One way of answering this question is to look at what has happened to pollination networks in other places when alien plants and pollinators have been introduced. A compelling example is that of the honeybee (*Apis mellifera*). This species, native to Africa and Europe, has been domesticated for thousands of years and is the most widely utilised pollinator of crop plants. It was introduced into North and South America where it had never occurred naturally, and being a super-generalist that can obtain food from a very wide range of flowers, it did not take long for the species to become naturalised. It has now seriously disrupted natural ecosystems in countries such as Argentina. The first introductions were of the European subspecies of the honeybee, but later introductions of the far more aggressive African subspecies gave rise to the much-hyped phenomenon of the 'killer bees' (or 'Africanised honeybees') of South and Central America.



Invasion meltdown

An important group of social bees that do not occur naturally in South Africa are bumblebees (genus *Bombus*). They are found naturally in the northern hemisphere and in some parts of South America. Like honeybees, bumblebees are super-generalist insects and, after being introduced to New Zealand and Tasmania, they rapidly became naturalised. They have disrupted many natural pollination mutualisms, but more alarming is their effectiveness in pollinating large-flowered invasive plant species from the northern hemisphere, such as the notorious *Rhododendron ponticum* and Paterson's curse (*Echium plantagineum*). This is what biologists call an 'invasion meltdown', and it happens when invasive species promote the success of other invasive species. Given the ecological concerns raised worldwide, it is unlikely that the South African government would sanction the introduction of bumblebees to this country. There is, however, a danger that bumblebees may be introduced to South Africa by a misguided individual, as was apparently the case in Tasmania. Not only could this lead to an invasion meltdown by promoting the spread of invasive plant species that originate from the native range of bumblebees, but it could also seriously jeopardise our local carpenter bees (genus *Xylocopa*), which are about the same size as bumblebees and occupy a similar ecological niche of feeding from large, deep-

The South American tree tobacco (*Nicotiana glauca*) is invasive in South Africa where it is pollinated by sunbirds that exhibit unusual hovering behaviour to reach the nectar. Image: Anton Pauw

Opposite page: Carpenter bees (genus *Xylocopa*) in South Africa perform a similar pollination role to bumblebees (genus *Bombus*) in Europe. If *Bombus* species were to be introduced to South Africa, they would compete with carpenter bees for access to rewards from large flowers such as this *Brunsvigia radulosa*. Image: Steve Johnson

tubed flowers. Carpenter bees are solitary and more specialised than bumblebees and likely to come off second-best when faced with competition for nectar resources from bumblebees. Bumblebees may also compete with our native honeybees, with negative consequences for honey production, crop pollination and pollination of native plant species.

Invasive plants and local pollinators

To become invasive, introduced (alien) plants must have an assured means of reproduction. Many alien plants are capable of producing seeds through self-pollination and thus do not have to rely on local pollinators for reproduction. Another way of assuring reproduction is for these alien plants to become incorporated into local pollination networks. Pollinators in the introduced region become substitutes for the original pollinators in the native range of the plant species. An example is the small tree tobacco (*Nicotiana glauca*) which is pollinated by hovering hummingbirds in its native South America. Some



The convolvulus hawkmoth pollinates Macowan's crinum lily which is indigenous to South Africa. Image: Steve Johnson

scientists would have predicted that this tree would not invade in South Africa because our local sunbirds usually prefer to perch while feeding on flowers, but in fact local malachite sunbirds do visit and pollinate the tree tobacco, and are so eager to reach the nectar that they show the uncharacteristic behaviour of hovering to do so.

Another example of this is the vine (*Ipomoea alba*) whose long-tubed flowers have been seen to be pollinated by the convolvulus hawkmoth (*Agrius convolvuli*) in South Africa. This local hawkmoth substitutes for the hawkmoths that pollinate the vine in its original range in South America. Another invasive species pollinated by the convolvulus

hawkmoth in South Africa is the Asian Formosa lily (*Lilium formosanum*). This lily may be adapted for pollination by the convolvulus hawkmoth, which occurs naturally in Asia, so allowing the Formosa lily to become easily incorporated into the South African hawkmoth pollination network.

What happens to local pollination networks when alien plant species are introduced? If no local pollinators are suitable, then plants are unlikely to become incorporated into these networks and become invasive (unless, of course, they are capable of self-fertilisation or extensive vegetative reproduction, as in the case of water hyacinth (*Eichhornia crassipes*)). However, as revealed in the above examples, in many cases local pollinators, including honeybees, will visit and pollinate the flowers of invasive species. Alien plant species can compete with local plants in terms of pollinator attraction. They may act as 'magnet species' that increase pollinator abundance in invaded communities, but do so by drawing pollinators away from other native plant communities.

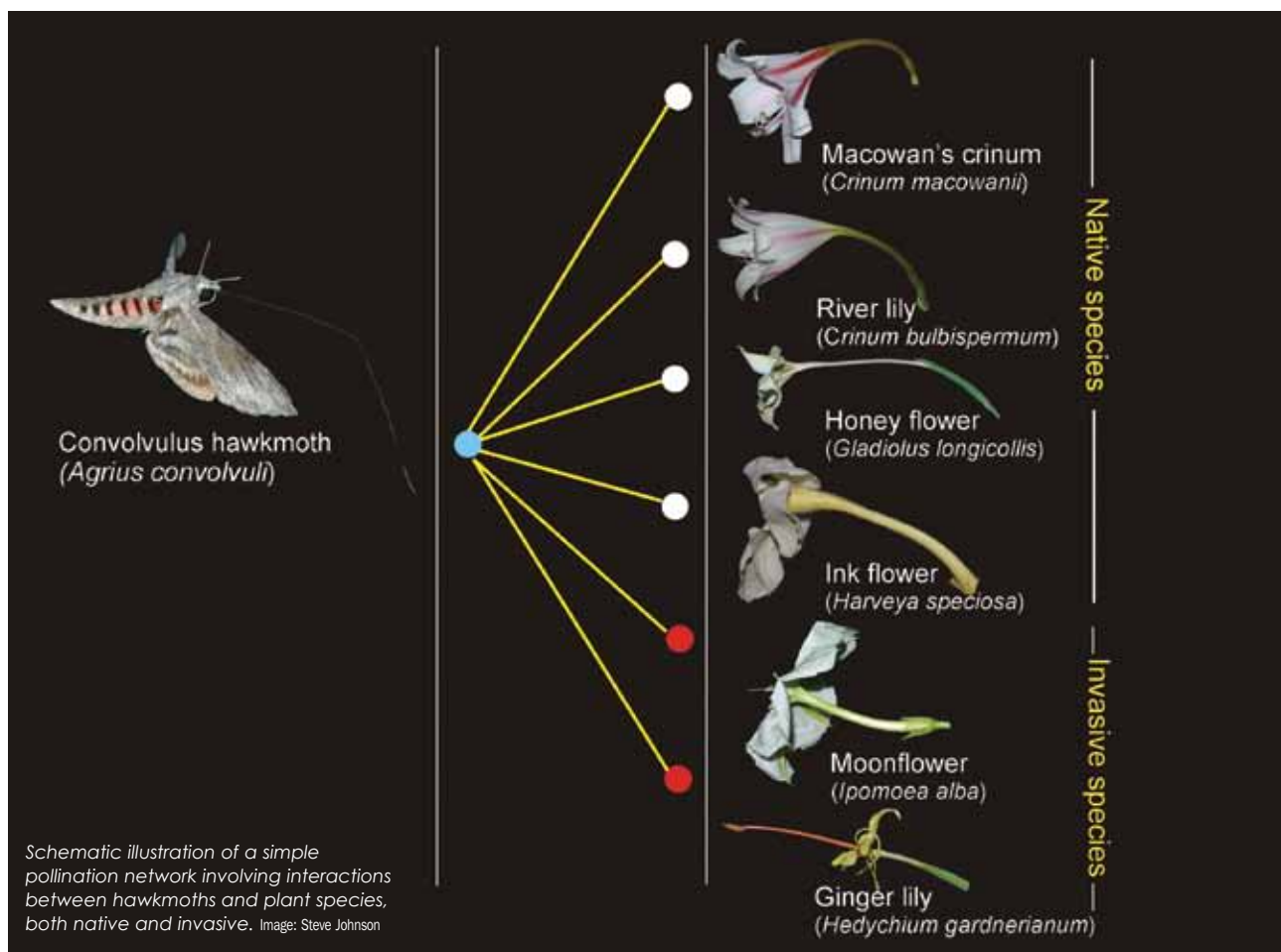
Some bee-keepers are actually in favour of alien plant species such as Australian bluegums that produce copious amounts of nectar, as they boost honey production. This is not necessarily a problem if the interaction is mainly between managed hives and stands of bluegums, as long as there are other ecological filters that prevent invasion by these introduced plant species. If, however, the activities of honeybees on flowers of alien plants causes these plants to become invasive, then the cost to the country will obviously soon exceed the benefits in terms of honey production.

Safe and unsafe plant introductions

How then do we determine which plant species are safe for introduction and which are not? Plant species that can self-fertilise or reproduce by cloning are obviously risky because they do not need to become incorporated into pollination networks. Some plants, such as the common European dandelion (*Taraxacum officinale*) and the much more dangerous trifid weed (*Chromolaena odorata*), have an



The convolvulus hawkmoth pollinates the Asian Formosa lily in South Africa where the lily has become invasive. Image: Steve Johnson



unusual form of reproduction known as apomixis, which allows them to produce seeds by cloning, in other words they don't need pollinators. For plants that do need pollinators, you can try to predict whether a local pollinator is likely to substitute for the pollinators in the introduced plant's native range. This is not always easy to do, as in the case of the tree tobacco that substituted its hummingbird pollinators for sunbirds that unexpectedly hover while feeding on flowers.

It is also important to consider the possibility of an invasion meltdown. *Rhododendron ponticum* (common rhododendron, a major invader in the UK), which is currently cultivated in South Africa, could become seriously invasive if bumblebees were to be introduced here.

Invasive plants that are cross-pollinated by local insects will continue to develop new genetic combinations, which may accelerate the process of invasion. For example, the purple loosestrife (*Lythrum salicaria*) is a European plant species that has become invasive in North America. It is cross-pollinated by the native bumblebees of North America and, through the new genetic combinations that arise from sexual reproduction, has undergone rapid evolution and is now spreading into new territory in Canada.

Controlling invasive aliens

The fight to combat invasive organisms is a tough battle in terms of both the manpower needed to control their spread and the difficulties in making scientific predictions about which species are likely to do so in the future. One of the biggest challenges, however, is to make the public aware that the beautiful plants in their garden may actually be dangerous, and that cute fuzzy pollinators such as bumblebees may actually be harmful if introduced. One of the main roles of science is to encourage us to think objectively about problems, and not to be seduced by the

Pollination networks

Network analysis was originally developed in biology for the study of food webs, but can be applied to the study of mutualistic interactions. Networks are usually drawn as nodes representing species connected by lines representing interactions. Pollination networks describe the pattern of interactions between plants and flower-visiting animals in local biological communities. Plants or animals that interact with many other organisms are generalists, while those that interact with just a few are specialists.

Pollinators that perform a similar role are considered to belong to the same functional group. Many plant species are specialised for pollination by a particular animal functional group. A general property of pollination networks is that the animals that pollinate flowers are mostly generalists, while flowers are more specialised. For example, some plants have flowers that are specialised for pollination by hawkmoths (the functional group in this case), but the hawkmoths themselves may visit dozens of different plant species. There are some examples of reciprocally specialised mutualisms, such as those between figs and their specific wasp pollinators, but these are relatively rare in nature.

It is also important to realise that not all interactions between flowers and flower-visiting animals are mutualisms. Bees will often rob flowers of their nectar by biting through the side of the corolla without pollinating the flower, and plants, in turn, may use mimicry to trick insects into visiting flowers without actually providing a reward of pollen or nectar.

apparent beauty in a plant or animal. It is not too late to stop future biological invasions by identifying plants and animals that have just begun to become incorporated into natural ecosystems or that have the potential to do so. **Q**

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