

BEES

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Bees (superfamily Apoidea) belong to the large and exceedingly successful insect order Hymenoptera, which also includes wasps, sawflies, and ants. There are currently approximately 25,000 known species of bee, and undoubtedly many more remain to be discovered. All bees feed primarily on nectar and pollen throughout their lives, with the adults gathering food for their sedentary larvae. The life history of bees varies across a spectrum, from solitary species (which make up the vast majority of species) to those that are highly social, living in large colonies with sometimes hundreds of thousands of individuals. The most familiar bee is of course the domesticated honeybee (*Apis mellifera*; Fig. 1), highly valued for its role as a crop pollinator and source of honey.

BEES AS INVASIVE SPECIES

Because of the obvious benefits they provide to humankind, various bee species have been deliberately introduced in parts of the world to which they are not native.



FIGURE 1 The honeybee, *A. mellifera*, now perhaps the most widespread insect on Earth.

The honeybee is thought to be native to Africa, western Asia, and southeastern Europe, although its association with humans is so ancient that it is hard to be certain of its origins. It has been domesticated for at least 4,000 years. Because of its economic value, the honeybee has been introduced to basically every country in the world (being absent only from the Antarctic). It is now among the most widespread and abundant of insects on Earth.

Various bumblebee (*Bombus*) species have also been deliberately introduced to new countries. The earliest successful bumblebee introduction was to New Zealand in 1885 and again in 1906 (no bumblebees naturally occur in Australia or New Zealand). Four species became established and survive to this day. During the late 1980s, the commercial rearing of bumblebees was developed, primarily for pollination of glasshouse tomatoes, and this has since developed into a worldwide trade with in excess of 1 million nests having been exported from Europe to at least 19 countries around the globe. The main trade is in the European species *Bombus terrestris*. As a result of this trade, *B. terrestris* became established in the wild in Japan in the 1990s. In 1992 *B. terrestris* arrived in Tasmania from New Zealand, perhaps having been accidentally transported in cargo. Recently, *B. terrestris* was deliberately introduced to Chile. This is the second U.K. species to arrive in Chile, for *B. ruderatus* was introduced in 1982; it had spread across the Andes to Argentina by 1993, and *B. terrestris* arrived there in 2006.

Other bee species were deliberately introduced far from their native range in the twentieth century. The alfalfa leafcutter bee (*Megachile rotundata*), a native of Eurasia, has been introduced to North America, Australia, and New Zealand for alfalfa pollination. At least six other leafcutter bee species (Megachilidae) have been introduced to the United States for pollination of various crops, mainly from Europe and Japan. The alkali bee (*Nomia melanderi*), a native of North America, was introduced to New Zealand for pollination of alfalfa and has become established.

Because bees are generally regarded as beneficial organisms, should these introductions be a cause for concern? There are a number of possible undesirable effects of exotic bees, including (1) competition with native species, (2) introgression with native species, (3) transmission of parasites or pathogens to native species, (4) pollination of exotic weeds.

Competition with Native Species

The two bee species that are most widespread outside their native range, the honeybee and the bumblebee *B. terrestris*, are both generalists. Honeybees usually visit

a hundred or more different species of plant within any one region and in total have been recorded visiting nearly 40,000 different plant species—and *B. terrestris* is similarly polylectic, having been recorded visiting 419 plant species in New Zealand alone. Honeybees and bumblebees differ from many other flower visitors in having a prolonged flight season; honeybees remain active for all of the year in warmer climates, while bumblebees commonly forage throughout the spring and summer in the temperate climates where they naturally occur. Thus, the wide distribution, broad diet, and long field season of these two bee species mean that their niches overlap with many thousands of different native species.

Of course, demonstration of niche overlap is not proof of competition. If flowers are abundant, there may be plenty of nectar and pollen to go around. In fact it is notoriously difficult to provide unambiguous evidence of competition, particularly in mobile organisms such as bees. Both bumblebees and honeybees begin foraging earlier in the morning than many native insects; they are able to do so because their nests are kept warm through the night. Studies in Tasmania suggest that the combined action of nonnative bumblebees and honeybees removes 90 percent of the available nectar before native bees have begun to forage. This could give these nonnative organisms a competitive advantage over most native insects. This and other studies demonstrate that the presence of high densities of either honeybees or bumblebees can depress availability of floral resources, and there is good evidence that this can displace native organisms from the most profitable flowers. For example, the presence of honeybees on particular nectar sources has been found to deter foraging by hummingbirds.

Asymmetries in competition may also occur because of the ability of honeybees and bumblebees to communicate the availability and/or location of valuable food sources with nestmates, thus improving foraging efficiency. In contrast, the majority of other flower visitors are solitary, and each individual must discover the best places to forage by trial and error. Thus, social species are collectively able to locate new resources more quickly, which again may enable them to gather the bulk of the resources before solitary species arrive.

Asymmetries in competition may not be stable, because the relative competitive abilities of bee species are likely to vary during the day, according to temperature and resource availability, and are likely to vary spatially according to the types of flowers available. Bumblebees and honeybees are large compared to most of the native species with which they might compete. Large bees are

at a competitive advantage in cool conditions because of their ability to maintain a body temperature considerably higher than the ambient air temperature. However, large bees are not always at an advantage. The energetic cost of foraging is approximately proportional to weight; thus, large bees burn energy faster. As nectar resources decline, the marginal rate of return will be reached more quickly by large bees. Thus, large bees are likely to be at a competitive advantage early in the day and during cool weather, but small bees can forage profitably even when rewards per flower are below the minimum threshold for large bees; at these times, honeybees and bumblebees may survive by using honey stores. Small insects are also able to maintain activity in high ambient temperatures, when bumblebees would swiftly overheat. Thus, the relative competitive abilities of different bee species are not consistent, and the strength of competition is likely to vary with time of day, season, and according to what types of flower are available.

Is there evidence that competitive effects of nonnative bees reduce the populations of indigenous species? Studies in Argentina, Israel, and on islands near Japan have all found that native flower-visitor abundance was lower in places where either nonnative bumblebees or honeybees were more abundant. In Japan, the arrival of *B. terrestris* has led to declines in the native bumblebee *B. hypocrita*, and this is thought to be at least in part due to competition for nest sites. However, such studies can be criticized on the grounds that the relationship between invasive bee abundance and declining native bee populations (if found) need not be causative. Increasing invasive bee populations are often associated with increased environmental disturbance by humans, which may itself explain declines in native bees.

The only way to test unequivocally whether floral resources are limiting and competition is in operation is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored. Removal of feral honeybee nests and domesticated hives from part of Santa Cruz Island in California resulted in marked increases in numbers of native bees and other flower-visiting insects. Similarly, a decrease in abundance of native insects was found when hives of Africanized honeybees were placed in forests in French Guiana. Native bumblebee (*B. occidentalis*) nests placed near honeybee hives in California brought back less food to the nest and produced fewer offspring than those that were not near honeybee hives.

To summarize, it seems almost certain that abundant and widespread exotic organisms that singlehandedly

use a large proportion of the available floral resources do impact the local flower-visiting fauna. Consider, for example, the Australian native bee community. Australia has over 1,500 known bee species, and many more probably exist. Nowadays, by far the most abundant flower-visiting insects throughout most of Australia are honeybees, often outnumbering all other flower-visiting insects by a factor of ten or more. In Tasmania, the second most abundant flower visitor is usually the bumblebee *B. terrestris*. The majority of floral resources are gathered by these bees, often during the morning before native bees have become active. It is hard to imagine how the introduction of these exotic species could not have substantially altered the diversity and abundance of native bees. Unfortunately, we will never know what the abundance and diversity of the Australian bee fauna was like before the introduction of the honeybee. The same applies to most other regions such as North America, where the honeybee has now been established for nearly 400 years. It is quite possible that some, perhaps many, native bee species were driven to extinction by the introduction of this numerically dominant species or by exotic pathogens that arrived with it. Even if it were practical or considered desirable to eradicate honeybees from certain areas, it would be too late for such species.

Introgression with Native Species

The global trade in bumblebees poses a threat to genetic diversity that has received very little attention. The trade is largely in *B. terrestris dalmatinus* from southeastern Europe, which are shipped throughout the range of *B. terrestris*, which consists of a number of distinct subspecies: *B. terrestris terrestris* in much of Western Europe, *B. t. audax* in Great Britain and Ireland, *B. lusitanicus* in Iberia, and various named subspecies on different islands in the Mediterranean and Canary Islands. In a laboratory setting, the subspecies readily interbreed, but this does not necessarily mean that they will interbreed in a natural setting. The transport of *B. t. dalmatinus* throughout Europe poses the threat that the distinct local races will be lost through introgression, resulting in an overall loss of genetic diversity within the species. However, there has been no attempt to ascertain whether this is happening.

Nonnative bees also pose a different threat through interspecific matings. In 2007, 30 percent of queens of the native Japanese bumblebee *B. hypocrita* were found to have mated with *B. terrestris* males, matings that result in no viable offspring and so effectively sterilize the queens. Such interspecific mating is to be expected among closely related species and is probably contributing to the decline of *B. hypocrita*.

Transmission of Parasites or Pathogens to Native Organisms

Bees and their nests support a diverse array of predatory, parasitic, and commensal organisms, including viruses, bacteria, protozoans, mites, nematodes, fungi, and parasitoid wasps and flies. There is no doubt that many bee parasites have been transported to new regions with their hosts, particularly where introductions were made many years ago when awareness of bee natural enemies was low. Thus, for example, the honeybee fungal disease chalkbrood, foulbrood (a bacteria disease), the microsporidian *Nosema apis*, and the mite *Varroa destructor* now occur throughout much of the world. Similarly, bumblebees in New Zealand are host to a parasitic nematode and three mite species, all of which are thought to have come from the United Kingdom with the original introduction of bees. Studies in Japan have demonstrated that *B. terrestris* imported from Europe are frequently infested with tracheal mites. Exposure of hosts to novel strains of mite can have dramatic consequences, as demonstrated by the recent spread of *V. destructor* in honeybees. There is strong circumstantial evidence that the most dramatic declines that have been observed in any bumblebee species are the result of exposure to a nonnative pathogen. In the 1990s, queens of various North American species were taken from North America to Europe and reared in factories alongside the European *B. terrestris*. The established nests were then returned to North America. Shortly afterward, *B. occidentalis*, *B. terricola*, and *B. affinis*, all widespread and abundant species, disappeared from much of their range. These three species, which are all closely related, belong to the subgenus *Bombus*. The only other North American member of this subgenus, *B. franklini*, was always very rare but has recently disappeared from former localities and may be extinct. Thus, an entire subgenus has been devastated across a continent in the space of a few short years. It is hard to conceive of an explanation for this decline that does not invoke a disease outbreak. Anecdotal evidence suggests that a nonnative strain of the disease organism *Nosema bombi* was transported to North America with the commercial colonies, but in truth we shall probably never know.

It is hard to exaggerate our ignorance of the natural enemies of most bee species, particularly their pathogens. We do not know what species infect them or what the host ranges of these pathogens are. The natural geographic range of bee pathogens is almost wholly unknown. Given the current collapse of honeybee populations in North America and perhaps also in Europe, thought to be driven by one or more viral diseases perhaps interacting

with parasitic mites, there is an urgent need to improve our understanding of the biology of bee diseases. In the meantime, legislation to enforce strict quarantine of all bees prior to transportation would seem to be sensible.

Pollination of Exotic Weeds

As we have seen, both honeybees and invasive bumblebees visit a broad range of flowers. They appear to prefer to visit nonnative flowers; for example, in New Zealand, *B. terrestris* has been recorded visiting only 19 native species but 400 exotic plants, almost all from the natural range of *B. terrestris* in Europe. These preferences presumably occur because the bees tend to gain more rewards by visiting flowers with which they are coadapted.

Do visits by exotic bees improve seed set of weeds? By virtue of their abundance and foraging preferences, they often make up a very large proportion of insect visits to weeds. In a site dominated by European weeds in Tasmania, honeybees and bumblebees were found to comprise 98 percent of all insect visits to the problematic weed-creeping thistle (*Cirsium arvense*). In North America, honeybees increase seed set of the yellow star thistle (*Centaurea solstitialis*) and are the main pollinators of the invasive weed purple loosestrife (*Lythrum salicaria*). Of the 33 worst environmental weeds in New Zealand, 16 require pollination and are visited by honeybees, and



FIGURE 2 A nonnative bumblebee *B. terrestris* worker pollinating nonnative lupins in New Zealand.

one is pollinated more or less exclusively by them (the barberry shrub, *Berberis darwinii*). In addition, the tree lupin (*Lupinus arboreus*), broom (*Cytisus scoparius*), and gorse (*Ulex europaeus*) are self-incompatible and rely on pollination by bumblebees (Fig. 2).

The tree lupin is currently a minor weed in Tasmania. However, seed set in areas recently colonized by *B. terrestris* has increased, and it is likely that *L. arboreus* may become as problematic in Tasmania as it is in New Zealand, now that it has an effective pollinator. And *L. arboreus* is only one of many weeds in Tasmania, New Zealand, and southern Australia that originated in the temperate northern hemisphere and that is coadapted for pollination by bumblebees.

At present Australia alone has 2,700 exotic weed species, and the costs of control and loss of yields due to these weeds is an estimated 3 billion Australian dollars per year. The environmental costs are harder to quantify but are certainly large. The majority of these 2,700 exotic weeds are, at present, scarce and are of trivial ecological and economic importance. The recent arrival of bumblebees in Tasmania may awaken some of these “sleepers” weeds, particularly if they are adapted for bumblebee pollination. Positive feedback between abundance of weeds and abundance of bumblebees is probable, because an increase in weed populations will encourage more bumblebees, and visa versa. If even one new major weed occurs in Australia owing to the presence of bumblebees, the economic and environmental costs could be substantial.

CONCLUSION

It must be remembered that introduced bees provide substantial benefits to humans in terms of pollination of crops, and in providing honey. These quantifiable benefits need to be weighed against the likely costs. In areas where weeds pollinated by exotic bees are a serious threat or where native communities of flora and fauna are particularly valued, it may be that the benefits provided by introduced bees are outweighed by the costs. Further investigation of the potential of native bees to provide adequate crop pollination is needed. A ban on the import of *B. terrestris* to North America led to the swift development of the native *B. impatiens* as an alternative pollinator for tomatoes. Most parts of the world probably have native bee species that could be exploited. For example, there are native Australian bee species that are able to pollinate tomatoes, but adequate means of rearing these bees for glasshouse use have not yet been developed.

The precautionary principle argues that, in the meantime, we should prevent further deliberate release of exotic

bee species. Unlike many of the other human activities that have an impact on the environment, introduction of exotic species is usually irreversible, and this is almost certainly true of bees. Similarly, if an exotic pathogen escapes into wild bee populations, there is no way it can be eradicated. If bees are to be moved between countries (regardless of whether or not they are native to the country of importation), rigorous screening should be used to ensure that they are not carrying parasites or pathogens.

Given the many potential interactions between alien bees and their pathogens, on one hand, and native flower visitors, native plants, and nonnative weeds, on the other, it seems almost certain that introducing new bee species has had serious impacts on natural ecosystems that we have not yet begun to appreciate.

SEE ALSO THE FOLLOWING ARTICLES

Competition, Animal / Hybridization and Introgression / Pollination / Wasps / Weeds

FURTHER READING

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BELOWGROUND PHENOMENA

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All terrestrial ecosystems consist of primary producers (plants), aboveground consumers (herbivores and their predators), and belowground consumers (bacteria, fungi, and soil animals). These organisms are all directly or

indirectly interlinked: plants determine the amount and quality of food resources for both the aboveground and belowground consumers, aboveground consumers affect the availability of resources to belowground consumers, and belowground consumers regulate decomposition and nutrient cycling processes that affect plants and aboveground consumers. Because of the degree of linkage between the aboveground and belowground ecosystem components, invasive plant and aboveground consumer species have the potential to greatly alter the belowground subsystem, while invasive belowground organisms can greatly influence what we see aboveground. The many spectacular examples of invasive organisms influencing biota on the other side of the aboveground–belowground interface include plants such as legumes, C₄ grasses, and coniferous trees; aboveground consumers such as deer, rats, and ants; and belowground consumers such as earthworms, flatworms, and fungal pathogens. The effects of these invaders in turn alter ecosystem properties such as ecosystem production, nutrient cycling, and soil fertility, and can thus greatly transform the functioning of the ecosystem.

INVASIVE PLANTS

Invasive plant species exert their most dramatic effects on the belowground subsystem when they differ in some fundamental way from the native species present. Classic studies on the island of Hawai'i have shown that the invasive shrub faya (*Morella [Myrica] faya*), native to the Azores and Canary Islands, can greatly transform native montane forest ecosystems. This is because faya differs from all the native species present, in being able to form root nodules that convert atmospheric nitrogen to potentially biologically available forms. As a consequence of invasion by this shrub, ecosystem nitrogen input is increased by over fourfold, greatly transforming the fertility of the soil. Another example involves the invasion of northern hemisphere pine (*Pinus*) tree species in many southern hemisphere ecosystems (Fig. 1). In New Zealand grasslands and forests, invasion by North American lodgepole pine (*Pinus contorta*) results in large reductions of soil animals such as nematodes that are responsible for regulating nutrient cycling and decomposition processes. This situation likely arises because of the low quality, highly acidic litter produced by the invader. Invasive plants also have important belowground effects when they alter the ecosystem's disturbance regime. For example, invasive C₄ grasses in forests in Australia and Hawai'i are highly flammable and greatly increase the fuel load for fires at the ground level. This switches the ecosystem to a new stable state, which