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Review article

Ecological impacts of invasive alien species on bees*

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Abstract – We review direct and indirect impacts of invasive alien species (focussing on plants and insects) on native bees worldwide. Although there is a rapidly growing body of research into the effects of invasive alien plants on native plant pollination via disruption of native mutualisms, there has been little research on the impacts of invasive alien plants directly on bees. Such impacts are likely to vary according to the taxon of plant, the functional specificity of the native bees, and ecosystem context. Conversely, there have been more attempts to document impacts of invasive alien social bees on native bees. Most of these studies only indirectly evaluate competition for resources, have focused on a few native species and findings are sometimes contradictory. However, some studies showed strong negative impacts, suggesting that effects might be species-specific. Additionally, pathogen spillover and reproductive disruption due to interspecific mating has been demonstrated among some closely related taxa. Where we lack unequivocal evidence for impacts however, this should not be interpreted as lack of effect. We recommend that future studies are robustly designed and consider impacts on genetic, species (particularly solitary bees) and ecosystem biodiversity.

***Apis mellifera* / *Bombus* / non-native species / pollinator / plant invasion**

1. INTRODUCTION

Alien species (exotic/non-native species introduced accidentally or intentionally by humans) that become invasive (i.e. recruit reproductive offspring, often in large numbers and at considerable distances from parents, and thus can spread at a considerable rate, Traveset and Richardson, 2006) are recognised as important drivers of global environmental change (Sala et al., 2000; Levine and D'Antonio, 2003). Although only a small proportion of alien species become invasive (Williamson, 1996), the massive increase in the rate of biological invasions due to rapid globalization of economies in the last decade, accelerating both the rate and geographic pattern of the trade and transport of species, has led to a corresponding increase in research into the impacts of invasive alien species (Lockwood et al., 2007). In addition to damage to human health and economies (Pimentel et al., 2005), invasive alien species can in some cases disrupt evolutionary process, and the composition and functioning of local ecosystems (Parker et al., 1999; Mooney and Cleland, 2001). Invasive alien species can have direct and indirect impacts on native biodiversity (Parker et al., 1999). The former occur when invasive aliens consume or otherwise physically affect native species, and the latter when the invasion affects interactions among native species in the ecosystem, for example via competition for biotic resources, or via alteration of abiotic resource availability, either by competition or when invasive aliens perform a novel ecosystem function (Simberloff, 1991; White et al., 2006). In many cases, a combination of both

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direct and indirect processes affect native biodiversity and the services it provides.

A key ecosystem service that has the potential to be interrupted by the arrival of novel species is pollination. This area has received a lot of recent research attention for several reasons. Firstly, there is widespread concern about loss of pollination services, both for wild plants and crops (Biesmeijer et al., 2006; Klein et al., 2007); but see (Ghazoul, 2005), and investigations into the drivers of pollinator loss are regarded as high priority (Steffan-Dewenter and Westphal, 2008). Secondly, some high-profile invasions have received considerable media and research attention, for example the spread of Africanized honeybees in the Americas (Schneider et al., 2004; Moritz et al., 2005). Thirdly, because pollinators perform a vital ecosystem function, impacts of alien species invasion can have knock-on effects on entire communities.

Bees are arguably the most important pollinator group and threats to wild bees have been more widely studied than impacts on other pollinator taxa (Kenis et al., 2009; Murray et al., 2009). Native (often referred to as "wild" bees, although this term strictly includes non-native domesticated species that have "escaped" into the wild) are very important for wild plant and crop pollination (Losey and Vaughan, 2006). Klein et al. (2007) estimated that 35% of global crop production relies on animal pollinators and 87/115 of the leading food crops worldwide require animal pollination. Many producers rely on domesticated bees, but with worldwide declines in the most important domesticated bee (*Apis mellifera*), the importance of native wild bees is becoming increasingly recognised. In the northeastern United States of America (New Jersey and Pennsylvania), it has been predicted that native bees provide sufficient pollination for watermelon crops in the absence of domesticated honeybees (Winfree et al., 2007), confirming the important role that native bees perform in modern agro-ecosystems.

Habitat change, loss and fragmentation associated with agricultural intensification are thought to pose the main risks to native bees (Kremen et al., 2002; Goulson et al., 2008; Steffan-Dewenter and Westphal, 2008; Murray et al., 2009) and the impacts of these processes on native bees have been studied on a range of scales. For example, recent research has suggested that landscape structure and land use management have important impacts on native bees (Brosi et al., 2008; Osborne et al., 2008) and that organic farming can improve bee species abundance (Tscharntke et al., 2005; Holzschuh et al., 2007). However, the impacts of invasive alien species on native bees are far from clear (Traveset and Richardson, 2006). We lack knowledge as to the extent at which alien invasions affect population density of bee species, and about how alien invasions affect composition of pollinator communities at different spatial and temporal scales (Bjerknes et al., 2007).

In this review, we aim to provide critical assessment of hypotheses and evidence for impacts of invasive alien species that directly or indirectly affect native bees in order to identify threats and to determine research and conservation priorities in this area. Specifically, we will consider impacts of invasive alien plants, bees and parasites on native bee behaviour, reproduction, populations and communities and the ecological services they provide.

2. IMPACTS OF INVASIVE ALIEN PLANTS

Alien plant invasions are common in virtually every terrestrial ecosystem on earth. The number of plant introductions has climbed steadily since the late eighteenth century (Pyšek et al., 2003), and in Europe, established alien plants are most common in nutrient-rich and/or man-made habitats (including urban and agricultural ones) (Lambdon et al., 2008). A large proportion of alien plants have been introduced as ornamental species, for example in Australia (Groves, 1998; Reichard and White, 2001) and Europe (Lambdon et al., 2008), and thus many produce showy, eye-catching flowers, which also often makes them attractive to animal visitors.

Many invasive alien plants are visited (Valentine, 1978; Butz Huryn and Moller, 1995; Chittka and Schurkens, 2001; Moragues and Traveset, 2005; Jesse et al., 2006; Stokes

et al., 2006; Stout et al., 2006; Totland et al., 2006; Lopezaraiza-Mikel et al., 2007; Bartomeus et al., 2008a; Tepedino et al., 2008) and pollinated (Parker, 1997; Richardson et al., 2000; Stout, 2007) by native bees. These plants are attractive to native bees for many reasons: some produce a massive floral display, have prolific nectar production, and often appear at high density or dominate the flower community in invaded sites (Ghazoul, 2002; Bjerknes et al., 2007). In addition, many invasive alien plants fill a phenological gap of flower resources for bees, extending their foraging season. As a result, invasive alien plants have the potential to impact not only on individual foraging behaviour, but also on colony success of social species, population size and distribution of native bees, bee community structure and entire plant-pollinator networks (Aizen et al., 2008). In addition, by affecting the native plant communities, invasive alien plants are likely to have indirect effects on native pollinator communities.

2.1. Indirect impacts via effects on plant communities

Invasive alien plants can cause a reduction in native plant abundance and/or diversity within a community (Pyšek and Pyšek, 1995; Martin, 1999), although the mechanisms for impacts are not always clear (Levine et al., 2003). Invasive alien plants affect native plants via physical mechanisms (e.g. allelopathy, smothering, strangling) or competition for abiotic resources (e.g. nutrients, light, space, water) (Lodge, 1993; Levine et al., 2003; Vilà and Weiner, 2004). In addition, competition for biotic resources, such as pollination services, can cause changes to community composition in invaded habitats.

Much of the research on the impacts of invasive alien plants on plant-pollinator interactions has focussed on the indirect impacts of alien plants on native plant pollination (Bjerknes et al., 2007). Impacts can be positive (alien plants facilitate pollination of native species by acting as "magnets" and drawing pollinators into a plant community), negative (alien plants compete with native plants and reduce visitation and hence their pollination success) or non-existent (alien plants have no impacts on native ones). Indeed, studies so far have found a range of results (Tab. I), even for the same invasive alien plant species interacting with native taxa in different geographic localities. For example, *Carpobrotus* spp. in California (Aigner, 2004), the Balearic Islands (Moragues and Traveset, 2005), and north-eastern Spain (Bartomeus et al., 2008b) have varying impacts on different taxa of native plants (Tab. I). In addition, interactions between the same alien and native plant species at different locations have found contradictory results. For example, the presence of *Impatiens glandulifera* decreased visitation to and seed set of *Stachys palustris* in Central Europe (Chittka and Schurkens, 2001) whilst Lopezaraiza Mikel (2006) found a facilitative effect on insect visitation in the UK, which varied with native plant density. Nienhuis et al. (unpubl. data), on the other hand, found no impact of varying *I. glandulifera* density on visitation, pollen deposition or seed set in *S. palustris* in a heavily invaded site in Ireland. Indeed, spatio-temporal variation in findings may well be due to not only plant (alien and native) but also pollinator density (Muñoz and Cavieres, 2008), which has not been fully addressed in field studies so far.

What is surprising, however, is that few studies have investigated the impacts of invasion by alien plants on the structure of pollinator communities, instead focussing on the impacts on native plant pollination (but see Aizen et al., 2008). Knock-on effects of changes in plant community composition could have dramatic implications for native pollinators, particularly specialist species which are not able to utilize the invasive alien plant because of temporal, morphological or nutritional restrictions (Fig. 1). For them, loss of their native host plants (assuming this occurs due to alien plant invasion) may severely reduce their fitness. A negative feedback would then operate whereby the decline of these specialist pollinator species may result in pollination limitation of the specialised native plants they pollinate, although so few plant-pollinator interactions are so tightly specialised that this is unlikely to present widespread problems

Table I. Impacts of alien plants on native plant pollination. In all cases the main pollinators of the native plants are bees, except * where Diptera are the main pollinators.

Alien plant species	Native plant species	Location	Impacts on native plant	Authors
Impatiens glandulifera	*Stachys palustris*	Central Europe	Negative on visitation and seed set	Chittka and Schurkens, 2001
Impatiens glandulifera	Several	Britain	Facilitation for visitation, possible competition for pollen deposition	Lopezaraiza-Mikel et al., 2007
Impatiens glandulifera	*Stachys palustris*	Britain	Facilitation for visitation, depending on native plant density	Lopezaraiza Mikel, 2006
Lythrum salicaria	*Impatiens capensis*, *Eupatorium perfoliatum*, *Eupatorium maculatum*	Ontario, Canada	Negative on seed and fruit set	Grabas and Laverty, 1999
Lythrum salicaria	*Lythrum alatum*	USA	Negative on seed set	Brown B.J. et al., 2002
Carpobrotus acinaciformis	*Lotus cytisoides*, *Cistus salviifolius*, *Anthyllis cytisoides*, *Cistus monspeliensis*	Balearic islands	competitive effect (*Lotus*), facilitative effect (*C. salviifolius* and *Anthyllis*), no effect (*C. monspeliensis*) – effects not consistent over time	Moragues and Traveset, 2005
Carpobrotus acinaciformis	*Dithyrea maritima*, *Cakile maritima*	California, North America	No impact	Aigner, 2004
Carpobrotus edulis and *C. affine acinaciformis*	*Asphodelus aestivus*, *Dorycnium hirsutum*, *Helichrysum stoechas*	Majorca, Spain	Low levels of pollen deposition on stigmas, negative impact on seed set of *H. stoechas*	Jakobsson et al. 2007
Carpobrotus affine acinaciformis and *Opuntia stricta*	Several	Spain	Facilitation (Carpobrotus) and competition (Opuntia)	Bartomeus et al., 2008b
Rhododendron ponticum	Several	Ireland	Varied on visitation across locations and within flowering season	Dietzsch and Stout unpubl. data
Heracleum mantegazzianum	Non-native *Mimulus guttatus*	Denmark	Enhanced visitation to native when close to alien but not seed set	Nielsen et al., 2008
Phacelia tanacetifolia	*Melampyrum pratense*	Norway	Visitation reduced, no impact on seed set	Totland et al., 2006
*Euphorbia esula**	*Linum lewisii* ssp. *lewisii*, *Oxytropis lambertii* ssp. *lambertii*	USA, N America	Variation in impacts on pollinator visitation, reduced pollen deposition	Larson et al., 2006
Chromolaena odorata	*Dipterocarpus obtusifolius*	Thailand	decreased visitation by butterflies but compensated by increased bird/moth pollination – no impact on seed set	Ghazoul, 2004
Solanum elaeagnifolium	*Glaucium flavum*	Lesvos, Greece	Reduced visitation	Petanidou et al., unpubl. data

(Waser et al., 1996). Generalist native pollinators that are able to utilize the resources of invasive alien plants may support native plant communities (Memmott and Waser, 2002) and promote further invasion of the alien plant species (Stout, 2007) (Fig. 1). Due to asymmetry in most plant-pollinator networks (Vázquez and Aizen, 2004), plus other drivers of environmental change (e.g. habitat loss, pollution, climate change), the impacts of invasive alien plants on native pollinator communities are difficult to detect.

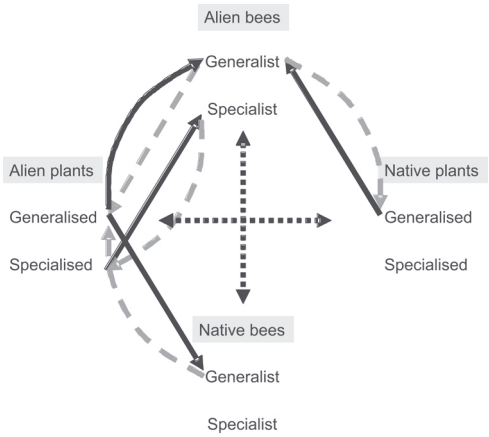

Figure 1. Potential interactions between native and alien plants and bees in invaded ecosystems. (Interactions among native species are not shown for clarity.) Note that native specialist bees (those which forage on one or a few host plants) and specialised plants (that can only be pollinated by one or a few pollinators) do not benefit from alien invasion, whereas alien generalist bees and generalised plants benefit the most. Interactions among alien bees and plants may result in the formation of invasion complexes. Black lines indicate direct impacts of plants on bees (by providing a forage resource) and broken grey lines indicate direct impacts of bees on pants (through pollination service). The broken black lines represent resource competition among native and alien species.

2.2. Direct impacts on bees

Very little research has focussed on the direct impacts of invasive alien plants on native pollinators, including bees. In order for native bees to utilise invasive alien plants successfully as a forage resource, alien flowers need to (i) be morphologically accessible, (ii) contain rewards of nutritional value, and (iii) be spatially and temporally available to native bees. Some alien plant species display flowers specialised for pollination by animals other than bees, and so nectar and/or pollen rewards may not be accessible to native bee taxa. For example, although *Salvia splendens* flowers produce copious nectar, nectar is concealed deep within long corolla tubes (Corbet et al., 2001), making it difficult for native bees to access nectar where this species is grown in the British Isles. Alternatively, invasive alien flowers could require some specific handling skills that native bees do not possess. For example, native bees in Tasmania are unable to manipulate the flowers of invasive alien *Lupinus arboreus* because the latter require large, powerful bees to expose stamens and stigma (Goulson, 2003), and native halictid bees in Florida are unable to buzz pollinate the flowers of invasive alien *Solanum torvum* because of their inability to sonicate anthers (Liu and Pemberton, 2008). In these cases, the invasive alien plant species are avoided by native bees and so do not act as a useful food resource.

It is more likely that generalist native bee taxa are able to include invasive alien plant species in their diet, either by legitimate visits to flowers, or via robbing (Inouye, 1980). Indeed, research has indicated that generalist bees are more common foraging on invasive alien plants than specialists (Lopezaraiza-Mikel et al., 2007; Tepedino et al., 2008). Although concern has been expressed over the loss of specialist bee taxa (Biesmeijer et al., 2006; Fitzpatrick et al., 2007), the loss of generalist bees could be far more detrimental to plant communities (Memmott et al., 2004). This is because pollination networks are asymmetrical and therefore have ecological tolerance to extinction of specialists (Memmott et al., 2004). Hence, if invasive alien plants support native generalist pollinators, they act as resource reservoirs in largely degraded landscapes (cf. Westphal et al., 2003). In turn, if generalist pollinators are well supported, then native plants that are specialised for pollination by one or a few generalist species may benefit (Ashworth et al., 2004), and their pollination positively facilitated (Aizen et al., 2008).

In terms of the nutritional value of invasive alien plant species for native bees, there has been very little direct research. The quantity and quality of nectar and pollen produced by any plant is affected by resource availability in the habitat, resource allocation by the plant, the pollination syndrome to which the plant belongs and, of course, genotypic constraints. Numerous studies have quantified nectar quantity and quality (in terms of sugar content) in a huge range of plant taxa, but it is pollen that

provides most of the dietary nutrition of bees. Pollen varies in protein content among species (Roulston et al., 2000) and this affects the pollen foraging behaviour of honeybees (Cook et al., 2003; Keller et al., 2005). If invasive alien plants produce nectar and pollen of sufficiently high quantity and quality, they could act as important foraging resources, particularly in forage-depleted agri-environments.

On the other hand, if invasive alien plant rewards are not beneficial to native bees, but even detrimental to them, they can have the opposite impact. For example, the nectar and pollen of the invasive alien *Rhododendron ponticum* contain grayanotoxins which cause poisoning in humans (Koca and Koca, 2007). Although *R. ponticum* nectar apparently contains relatively high levels of these toxins (Koca and Koca, 2007), they have no impact on individual workers of native bumblebees from Ireland (*Bombus lucorum*, Dietzsch et al., unpubl. data). This is probably due to the bumblebees' ability to metabolize or excrete the toxins (cf. *B. consobrinus* and others which are tolerant to aconitine in *Acotinum* (monkshood) across Europe (Ponchau et al., 2006)), or they may have sub-lethal effects. Interestingly, honeybees rarely visit *R. ponticum* flowers in the British Isles, which may indicate that they are deterred by these toxins. Indeed, other *Rhododendron* species contain nectar that is toxic to honeybees (Carey et al., 1959). Furthermore, there has been no study of the impact of invasive alien plant pollen on larval growth and survival, either in the lab or the field.

The impacts of invasive alien plants on native bees are relatively simple to study at the individual level (changes in foraging behaviour, survival etc.), but more difficult to study at the population and community levels. Populations of social bees may be studied using molecular techniques to determine sistership and estimate colony abundance (Darvill et al., 2004; Knight et al., 2005) in invaded landscapes. Recent studies have shown that mass flowering crops such as oil seed rape (*Brassica napus*) may positively influence the number of *B. pascuorum* colonies in agricultural landscapes (Westphal et al., 2006; Herrmann et al., 2007). Invasive alien plants with large, short-lived floral displays can be considered as ecological equivalents to mass-flowering crops. For example, *R. ponticum*, which produces a massive, short-term floral display with copious nectar rewards (Stout, 2007), facilitates the number of *B. lucorum* and *B. pascuorum* colonies in invaded sites in Ireland by providing floral resources to founding colonies (Dietzsch et al., unpubl. data). These latter two studies illustrate that generalist bees benefit from the forage resources provided by invasive alien mass-flowering plants, but both highlight the short-term nature of these floral resources in the context of the entire colony cycle. In addition, no studies have yet estimated the impacts of invasive alien plants as potential forage resources on populations of specialised and solitary bees. As well as the impacts that invasive alien plants could have on forage resources, we must also consider impacts on native bee nesting sites. For example, invasion by *R. ponticum* and replacement of the native vegetation in *Vaccinium*-dominated heathlands in the north western British Isles eliminates the microhabitats that form the nesting sites of declining heathland specialist species such as *B. monticola* (Edwards and Jenner, 2005).

In general, studies of impacts of invasive alien plants on bee communities are much harder to perform. Experimental manipulations of plants in order to assess impacts on bee communities would require huge areas to take account of large bee foraging ranges (Beekman and Ratnieks, 2000; Cresswell et al., 2000; Goulson and Stout, 2001; Knight et al., 2005; Westphal et al., 2006; Osborne et al., 2008). Alternatively, natural sites (invaded and uninvaded) can be used, but it is difficult (and sometimes impossible) to find appropriate independent replicates for study. A particular problem is finding un-invaded or pre-invaded control sites without confounding the experimental design with large-scale biogeochemical variation. For example, Lopezaraiza-Mikel et al. (2007) could find no suitable un-invaded control sites for comparison with their invaded and experimentally cleared sites. Bartomeus et al. (2008b) found similar pollinator community richness in invaded and uninvaded plots, but these were only separated by around 300 m. Hence

conclusions about the impacts of the invader on the native community are difficult to draw since it is difficult to measure the true native community. In addition, if displacement of native forage resources causes native specialist bees to disappear, there may be a time-lag during which this loss occurs, which may be difficult to detect via short-term alien removal experiments.

Invasive alien plants may have additional indirect impacts on native bees if they promote the successful establishment and spread of super-generalist invasive alien pollinators (Aizen et al., 2008). Associations between introduced pollinators and plants can have positive effects on both parties and form invader complexes, for example such as those between *A. mellifera* and *Centaurea solstitialis* in western USA (Barthell et al., 2001), *B. terrestris* and *Lupinus arboreus* in Tasmania and New Zealand (Stout et al., 2002), and *A. mellifera*, *B. ruderatus*, *Vespula germanica* and alien plants in the southern Andes, Argentina (Morales and Aizen, 2006). Super-generalist invasive alien bees can in turn have their own impacts on native bees.

3. IMPACTS OF INVASIVE ALIEN INSECTS

Invasive alien insects have the potential to exert considerable direct and indirect impacts on native bees. Recent reviews vary considerably in their conclusions on whether existing evidence does (Sudgen et al., 1996; Goulson, 2003; Morales, 2007) or does not (Donovan, 1980; Butz Huryn, 1997; Paini, 2004) support negative impacts of invasive alien bees. Previous reviews proposed that major ecological impacts are mediated by (i) competition for resources and nesting sites, (ii) transmission of pathogens, and (iii) reproductive disruption via interspecific mating with native congeners (Goulson, 2003; Traveset and Richardson, 2006; Morales, 2007). In addition, invasive insects which cause a change in the native plant community structure could cause further indirect impacts on native bees.

To date, ca. 20 species of solitary (*Nomia*, *Osmia* and *Megachile*) and social bees (*Apis* and *Bombus*) have been introduced outside their native range, as a consequence of intentional releases and the trade of colonies, and at least 18 have become established (Donovan, 1980; Goulson, 2003; Morales, 2007). *A. mellifera* and *Bombus* spp. have been introduced most widely, frequently and in higher numbers than any other taxon. Currently, *A. mellifera* is the most widely distributed alien pollinator in the world (Kearns et al., 1998), being present in all continents except Antarctica. However, bumblebees are increasingly viewed as valuable pollinators of many crops, with more than one million colonies produced annually (Velthuis and van Doorn, 2006). Since the start of commercial rearing of bumblebees in 1987, they have been introduced to more than 11 countries in South and North America, Australasia and Asia and they have further invaded other countries in South America and Australasia (Morales, 2007). Although most studies on invasive alien bees have focused on these two genera, and hereafter much of our discussion is on them, other invasive alien insects (especially other flower users, such as ants) might also potentially impact native bees, and they deserve further research attention. For example, studies have shown that invasive alien Argentine ants, *Linepithema humile*, can reduce the amount of time native bees spend foraging on flowers and can displace them altogether (Altshuler, 1999; Lach, 2008). As is the case with invasive alien plants, invasive alien social bees have been introduced intentionally for pollination purposes and are associated strongly with anthropized and highly disturbed habitats (Aizen and Feinsinger, 1994, 2003; Stout and Goulson, 2000; Morales and Aizen, 2002; Inari et al., 2005). This not only facilitates their invasion, but makes the assessment of their ecological impact difficult, because disturbance per se and invasion of alien bees are frequently considered as confounding factors (Aizen and Feinsinger, 1994; Paini, 2004).

Since *Apis*, *Bombus* and ants are social insects, their invasive potential is increased by the possibility of a single inseminated queen founding a new colony which is then capable of producing a high number of reproductive individuals (Moller, 1996). This could then lead to the invasion of an entire island or continent

(Chapman and Bourke, 2001). For instance, 236, 214, and 1–5 queens founded the current populations of alien bumblebees invading New Zealand (MacFarlane and Gurr, 1995), Chile and Argentina (Arretz and MacFarlane, 1986; Roig Alsina and Aizen, 1996; Ruz, 2002) and Tasmania (Semmens et al., 1993; Buttermore et al., 1998), respectively. Social bees can also communicate the availability and location of resources to nest mates, which improves their foraging efficiency (Dornhaus and Chittka, 1999, 2001). As resource acquisition is closely related to reproductive performance (Thomson, 2006), this efficiency might contribute to their invasive success. In addition, invasive alien bee species that have more successfully colonized new habitats have done so because they are generalists (Goulson, 2003). These traits are expected to increase their chances of survival and establishment in invaded regions.

3.1. Competition for resources

Invasive alien insects and native bees might compete for resources, if (1) they experience a substantial floral resource overlap, (2) resources are limiting, and (3) decreases in resource acquisition translate to a reduction of fitness of the less competitive or both competing species (usually expressed as a reduction in fecundity, survival, or population size). Experimental tests of the effect of invasive alien insects on any of these fitness measures provide the most direct and conclusive evidence of competitive impacts of alien on native bees (e.g. Thomson, 2004). However, the difficulty in carrying out well designed manipulated experiments has precluded such studies in most situations (Goulson, 2003; Thorp, 2003; Thomson, 2006; Velthuis and van Doorn, 2006; Morales, 2007). Rather, most studies on the impact of invasive alien insects on natives bees have inferred competitive impacts on the population dynamics or fitness of native species from one or more of the following indirect measures (reviewed in Goulson, 2003 for bees in general; Butz Huryn, 1997; Paini, 2004 for honeybees; and Morales, 2007; for bumblebees): floral resource overlap, comparative efficiency in gathering resources, resource depletion, spatial or temporal correlations between native and invasive alien bees, and, finally, changes in the patterns of abundance, activity, resource gathering, or diversity of native species, in relation to the natural or manipulated presence of invasive alien bees. All these variables are easier to measure in the field (Goulson, 2003; Thorp, 2003), but do not provide conclusive evidence on the existence of competition (Goulson, 2003; Paini, 2004; Thomson, 2004; Velthuis and van Doorn, 2006). However, they are valuable because they suggest a scenario of potential competition. Here we summarize the main conclusions of these studies, grouped by response variable and experimental approach.

3.1.1. Resource niche breadth and overlap

Honeybees and bumblebees are generalist species, thus they can interact indirectly via plant-pollinator interactions with a significant proportion of the local bee fauna (Goulson, 2003). Indeed, studies have shown that both honeybees and bumblebees' foraging niches overlap substantially with native visitors (Goulson, 2003), and most of them suggested that the impact on native bees was either negative or unnoticeable (reviewed in Paini, 2004; Morales, 2007). For example, Paini and Roberts (2005) found considerable resource overlap between native oligolectic bees and invasive alien honeybees in Australia, which led to a reduction in native bee fecundity. The use of resource overlap measures seems justified because some studies have found that the chances of having a detrimental impact increased with the degree of resource overlap. For instance, Goodell (2000) found that the performance of the native generalist megachilid *Osmia pumilia*, which had a higher resource overlap with honeybees, was more detrimentally affected than other native *Osmia* species. In addition, potential for competition suggested by the observed similarity in visitation patterns between invasive alien *A. mellifera* and native *B. occidentalis* was further experimentally confirmed by a reduction in *B. occidentalis* colony reproductive success at decreasing distances of *A. mellifera* hives

(Thomson, 2004). The proboscis length of *A. mellifera* and worker *B. occidentalis* is very similar, which probably leads to similarities in flower visitation patterns (Inouye, 1977). Nevertheless, as Thomson (2006) warns, substantial temporal variability in niche estimates might seriously compromise conclusions based on these measures.

3.1.2. Comparative efficiency in resource acquisition

Invasive alien bees are more efficient in the acquisition of resources than many native counterparts. For instance, in Chile *B. terrestris* spends less time per flower than native *B. dahlbomii* (Ruz and Herrera, 2001). Since most observations were performed on flowers with short corollas, where short tongued bees visit flowers faster than long tongued bees (Inouye, 1980), this difference might reflect the differences in tongue length between the alien (short tongue) and the native (long tongue length). In another study, alien subspecies of *B. terrestris* collected relatively more nectar per unit time than native subspecies (Ings et al., 2005b), which in turn translated into a better reproductive performance (Ings et al., 2006). It is not clear whether this is a result of long-term commercial breeding or due to inherent differences between the two subspecies. If resource overlap is substantial and alien bees gather resources more efficiently, they have the potential to displace native bees due to depleting common nectar sources (Ings et al., 2005b), which could be additionally exacerbated by their comparatively large numbers, particularly in the case of *A. mellifera*.

3.1.3. Resource depletion

Honeybees and bumblebees might deplete nectar and pollen. In Arizona, Schaffer et al. (1983) experimentally demonstrated that honeybees reduced the standing crop of nectar of *Agave schottii* to the detriment of native bees. In New South Wales, Gross (2001) attributed fewer visits by native bees recorded in *Dillwynia juniperina* to honeybees depleting the standing crop of nectar. Similarly, in the Canary Islands, Dupont et al. (2004) found that honeybees stayed longer and visited more flowers per inflorescence than native bees, depleting nectar in *Echium wildpretii*, suppressing visitation by native animals due to exploitative competition. In the Bonin (Ogasawara) Islands, Kato et al. (1999) found a negative relationship between the occurrence of honeybees and native bees, partly attributable to pollen depletion in native plants by honeybees, but also partly due to disturbance and invasion by alien flora. Resource depletion has been argued to result in a significant asymmetry in competition in favor of invasive alien bees (Goulson, 2003 and references therein). This effect varies among native plant species and the abundance of alien bees. Indeed, Horskins and Turner (1999) did not find that honeybees depleted resources of a native plant.

3.1.4. Spatial and temporal association between native and alien bees

Correlational studies have found mostly negative (Aizen and Feinsinger, 1994; Goulson et al., 2002; Inari et al., 2005; Yang, 2005; Thomson, 2006; Tepedino et al., 2007), but also null (Goulson et al., 2002; Thomson, 2006; Nagamitsu et al., 2007; Tepedino et al., 2007) and to a lesser extent positive (Nagamitsu et al., 2007) spatial associations between native and invasive alien bees. Interestingly, even within the same system, different studies (eg. Inari et al., 2005; Nagamitsu et al., 2007) or experimental approaches (e.g. Thomson, 2006; Tepedino et al., 2007) have provided contrasting evidence, illustrating the risks in drawing conclusions from a single correlational study. For instance, despite experimental data for both bumblebee foragers and colonies suggesting significant competitive impacts (Thomson, 2004), Thomson (2006) found that only one of seven analyses of correlational data showed a significant negative relationship between *A. mellifera* and native *Bombus* abundance. This apparent incongruence seems to be the result of substantial temporal variability of correlational data (Thomson, 2006). Competition might be absent or undetectable if resources are not limited (Paini, 2004),

a condition that varies from year to year. For instance, Pleasants (1981) found that native bumblebees in Colorado, USA, expanded their diet breadth to include honeybee-flowers in a year of honeybee scarcity.

Consistent temporal trends revealed by long-term studies can provide a much more reliable insight into the existence of competition (Roubik, 2001). Monitoring over many years did not show any clear declines in abundance or local extinction of native *Melipona* spp. since the arrival of the Africanized honeybees (Wolda and Roubik, 1986; Roubik, 1991; Roubik and Wolda, 2001). Conversely, in South Argentina, ongoing yearly monitoring of visitation frequency showed that since invasion of *B. ruderatus* in 1994 to 2006, the visits by native *B. dahlbomii* steeply declined simultaneously to an increase in visits by the invasive species in a mainly undisturbed forest (Morales, 2007; Morales and Aizen, in preparation).

Correlations do not reveal causation, and might indicate competitive exclusion only if other potentially confounding factors have been taken in account (Paini, 2004; e.g. Aizen and Feinsinger, 2003). For instance, positive spatial correlations suggest similar resource or habitat preferences; in turn, negative spatial correlations may reflect different habitat preferences or competitive exclusion. Increasing invasive alien bee abundances are often associated with increasing anthropogenic habitat disturbance, which may in turn explain declines in native bees (Aizen and Feinsinger, 1994; Butz Huryn, 1997; Goulson, 2003; Steffan-Dewenter and Kuhn, 2003; Paini, 2004). Nevertheless, it is also possible, that habitat disturbance synergistically exacerbates the negative impact of invasive alien on native bees, through asymmetric competition in a habitat favoring aliens, to the detriment of native bees.

3.1.5. Experimental manipulation of alien bees

Only a handful of studies have measured changes in fecundity, survival or population densities of native bees after densities of *A. mellifera* had been manipulated (e.g. Roubik, 1978, 1982, 1983; Roubik and Wolda, 2001; Thomson, 2004, 2006). In French Guiana, a decrease in the abundance of native bees was found in sites where Africanized bees were experimentally placed (Roubik, 1978), but no evidence was found that the addition of Africanized *A. mellifera* colonies affected the fecundity in two *Megachile* spp. (Roubik, 1983). Similarly, in Australia, large forage resource overlap was found between *A. mellifera* and a native *Megachile* sp., but no change in reproductive success in the native bee was detected (Paini et al., 2005). Also in Australia, increased brood rearing success but also changes in sex ratios were found in the semi-social *Exoneura asimillima* placed in the vicinity of honeybee hives (Sugden and Pyke, 1991). In a three-year study on four different sites, Thomson (2004) found striking evidence of competitive suppression of native *B. occidentalis* by *A. mellifera*, as reflected by decreased worker foraging activity, rate of pollen acquisition, and reproductive success of colonies experimentally placed close to *A. mellifera* hives. Furthermore, colonies with greater foraging success had higher reproductive success, emphasizing the importance of resource limitation in determining fitness (Thomson, 2004). However, since measures of colony resource intake explained a relatively low amount of the observed variance in reproductive success, caution should be taken in utilizing foraging behaviour alone to predict the importance of competitive effects (Thomson, 2004).

Thomson (2006) went a step further, and found that competitive effects on colony reproductive success were accurately estimated by experimental data on forager abundances, but the latter did not estimate competitive effects as strongly as those actually observed for reproductive success. Since correlational data mostly failed to predict the detrimental effects observed in the experimental study (see above), this suggests that the actual impact of invasive alien on native bees is stronger than inferred from estimations of niche overlap, spatial and temporal correlations, or changes in native bees foraging activities, and highlights how misleading a picture observational measures may paint of invasion impacts, particularly over short time scales.

Given the low number of experimental studies that directly measured individual fitness, it is difficult to make any definite conclusion until more research is conducted. This situation is further complicated by the fact that in regions where *A. mellifera* has invaded many decades or even centuries ago, displacement or extinction of most vulnerable native species may have occurred before the experiments took place (Paini, 2004). Thus, so far, we rely mostly on indirect evidence to draw conclusions about such situations.

Overall, there is no indisputable evidence that invasive alien bees have a substantial and consistent competitive impact on native bees. This lack of unequivocal evidence should not be interpreted as a lack of effect. Most indirect evidence to date suggests negative impacts, and the scarce direct evidence shows that in some cases, these negative impacts might be rather strong.

3.2. Competition for nesting sites

With the exception of Barthell et al. (1998), who found invasive alien insects (two Megachilid bees, *Megachile apicalis* and *M. rotundata*, and the European earwig *Forficula auricularia*), occupying more trap-nests than native bees in California, studies on competition between invasive alien and native bees for nesting sites are even scarcer than studies on competition for resources. Often, the best we can do is to infer potential competition on the basis of niche overlap. *B. terrestris* queens use nest sites that are similar to those used by native *Bombus* species in different invaded regions (e.g. *B. hypocrita* in Japan (Velthuis and van Doorn, 2006); *B. dahlbomii* in Argentina (Morales, 2007)) and by native *B. terrestris* subspecies in Europe, and so there is huge potential for nest site competition. However, no study has addressed whether nest sites limit bumblebee populations in their native ranges. In New Zealand, the availability of nest sites seems to be an important constraint to bee population levels; nevertheless, wide differences in nest site requirements among almost all species suggest that there is little or no competition between native and introduced species for this resource (Donovan, 1980). Interspecific nest usurpation is characteristic of many bumblebee species (Sakagami, 1976) but we are not aware of any studies that specifically address nest competition among invasive alien and native species in the wild. *B. terrestris* queens experimentally introduced into nest boxes containing incipient colonies of native *B. ignitus* and *B. hypocrita*, usurped the *B. ignitus* nest and killed its queen, whereas this behavior was not observed with *B. hypocrita* nests (Ono, 1997). However, this is clearly an area where further research is required.

3.3. Transmission of pathogens

One of the biggest threats associated with the invasion by alien bees is the spread of disease to native species. Invasive alien bees can act as vectors of novel pathogens that can infect native con-specifics and other closely related species (Tab. II). The importation of commercial bee colonies is thought to be the source of exotic parasites and pathogens. Because honeybee health is extensively dealt with in numerous publications (including a forthcoming Special Issue in Apidologie in 2010), we limit our discussion to the impacts of commercially imported bumblebees and their associated parasites.

A diverse array of pathogens affect *Bombus* spp. (Macfarlane et al., 1995; Schmid-Hempel, 1998; Schmid Hempel and Loosli, 1998), some of them with devastating effects on infected colonies (e.g. the tripanosomatid *Crithidia bombi* (Brown M.J.F. et al., 2000, 2003); the acarine *Locustacarus buchneri* (Goka et al., 2001); the microsporidian *Nosema bombi* (Otti and Schmid-Hempel, 2007), and the hymenopteran *Melittobia acasta* (Estay, 2007)). These pathogens are among the most important threats from introduction of commercial colonies to native species because they thrive in conditions of artificial rearing. Studies have demonstrated that commercial bumblebee colonies can hold higher levels of infection than wild colonies (Colla et al., 2006). Thus the escape of workers, and potentially the establishment of feral bumblebee colonies from commercial

Table II. Evidence of pathogen/parasite transmission from non-native *Bombus* and *Apis* species imported for commercial crop pollination.

From	To	Pathogen	Location	Reference
B. terrestris	Native conspecifics & congenerics	*Nosema bombi*	Europe	Schmid-Hempel, 1998
B. terrestris & *B. ignitus*	Native conspecifics & congenerics	*Locustacarus buchneri*	Japan	Goka et al., 2001; Goka, 2006
B. impatiens	Native conspecifics & congenerics	*Crithidia bombi*	Canada	Colla et al., 2006; Otterstatter and Thomson, 2008
A. mellifera	*B. terrestris and B. pascuorum*	Deformed wing virus	Europe	Genersch et al., 2006
A. mellifera	*B. impatiens*	*Aethina tumida*	North America	Hoffmann et al., 2008*
A. mellifera	*B. impatiens* **	*Aethina tumida*	Florida, USA	Spiewok and Neumann, 2006
A. cerana	*A. mellifera*	*Nosema ceranae*	Spain, Europe	Higes et al., 2006
A. cerana	*A. mellifera*	*Nosema ceranae*	Taiwan	Huang et al., 2007
A. cerana	*A. mellifera*	*Varroa destructor*	Asia	Akratanakul and Burgett, 1975; de Jong et al., 1982

* Potential for transmission demonstrated, no evidence of host switch in the wild.
** Commercial colonies.

colonies, or the infiltration of glasshouses by wild bees, could introduce pathogens to native conspecifics and congeners while foraging on the same flowers (Durrer and Schmid-Hempel, 1994). Indeed, in Ontario, Canada, native bumblebees in the proximity of greenhouses hosting commercial colonies of bumblebees were infected by *C. bombi*, whereas there was no incidence of this pathogen in bumblebees collected at other sites in the region (Colla et al., 2006). Furthermore, the former had concentrations of the microsporidia *N. bombi* three times higher than the latter (Colla et al., 2006). Recently, Otterstatter and Thomson (2008) constructed a spatially explicit model of *C. bombi* infection spreading from commercial to wild bumblebees, and found that although the forecasted "wavefront" of infection was not detected, the prevalence of *C. bombi* near greenhouses was consistent with their predictions.

Detection of microorganisms and endoparasites is very difficult in living bees (Thorp, 2003). Therefore, in spite of quarantine controls, infested commercial colonies have been introduced to some countries (Goka et al., 2001). Following interspecific transmission of parasites, virulence on new hosts could be higher or lower, although more noticeable in the former case (Bull, 1994). Furthermore, it is postulated that the sudden decline of five North American bumblebee species might be related to *N. bombi* outbreak in bumblebee facilities that decimated the commercial colonies of *B. occidentalis* (Thorp and Shepherd, 2005; Winter et al., 2006; Williams and Osborne, 2009).

There is a serious gap in our knowledge about the reproductive effects, geographical distribution, epidemiology and evolutionary ecology of most pathogens associated with *Bombus* (Schmid-Hempel, 1998), and to a

lesser extent with *Apis*. In light of the existing evidence, the improvement of methods for preventing commercial bee escape (through mesh screens in commercial greenhouses) and for detecting pathogens in living specimens, and the standardization of inspection protocols for importing and exporting colonies should be high priorities (Morales, 2007).

3.4. Reproductive disruption and hybridization

The rupture of biogeographical barriers that maintained isolated related species will have genetic consequences for both the invasive alien and native species and/or subspecies. For example, commercial importation of *A. mellifera ligustica* and *A. m. carnica* around Europe has caused introgression of alleles into the native *A. m. mellifera*, completely replacing the native sub-species in some areas, notably Germany (De La Rúa et al., 2002, 2009; Jensen et al., 2005). Similarly, in Europe, commercial use of colonies of various *B. terrestris* subspecies (mostly *B. terrestris dalmatinus* (Velthuis and van Doorn, 2006)), could result in interbreeding between commercial and native bees, and introgression into local subspecies such as *B. terrestris audax* in Britain and Ireland and other subspecies elsewhere in Europe (Ings et al., 2005a). Until recently, suitable molecular markers have not been available to test whether this is indeed occurring, but recent research has found evidence for introgression in the wild between commercial and native *B. terrestris* in Poland (Rohde, unpubl. data).

In addition to hybridization and introgression among subspecific bees, there may also be hybridization among species. For example, there is evidence of mating between invasive alien and native bumblebees belonging to the same subgenus: *B. terrestris* mates with its Japanese consubgenerics *B. hypocrita* and *B. ignitus* (Ono, 1997; Goka et al., 2001), and *B.* (*Pyrobombus*) *impatiens* with its consubgeneric *B. ephippiatus* (Vergara, 2008). For instance, 30% of native *Bombus hypocrita* queens copulate with *B. terrestris* males in the field (Kanbe et al., 2008 and references therein); nevertheless interspecifc mating between *B. terrestris* and *B. hypocrita sapporoensis* in the laboratory results in the production of inviable hybrids (Kanbe et al., 2008). Thus, despite the potential failure to produce hybrid progeny, interspecific mating negatively affects the reproductive rate of native species due to a reduction of intraspecific matings, and in turn, of viable progeny (Kanbe et al., 2008). In addition queen mortality has been observed to increase after interspecific matings (e.g. Cuadriello et al., unpubl. data).

3.5. Modification of native plant community structure

Invasive alien insects can mediate changes in native plant communities via disruption of native- and promotion of alien-plant pollination, with knock-on impacts on native plant seed set, succession and community structure (Roubik, 1996; Yang, 2005; Kenta et al., 2007), which can facilitate further impacts on native bees. For example, although *A. mellifera* do not deplete the resources collected by native pollinators of *Clusia arrudae*, a tropical tree pollinated by resin-collecting *Euffriesea nigrohirta*, honeybees do affect the pollination of the species by removing virtually all pollen from flowers (Mendes do Carmo et al., 2004). Similarly, Gross and Mackay (1998) found that honeybees negatively affected pollination of *Melastoma affine*, a pioneer species in tropical Australian rainforests. In both cases, suppression of native plant pollination has the potential to alter plant community structure, which could have dramatic impacts on native bees and pollinator communities.

4. RESEARCH PRIORITIES

In order to prevent, assess and/or manage impacts on native bees, further research is required. Whilst it will not be possible to investigate all impacts in all systems, we suggest some priorities for study. Firstly, studies on impacts of invasive alien plants and pollinators should be extended to the landscape scale and should be long-term and observations should

be carried out at the species and community level (Walther-Hellwig et al., 2006). Implicit within this, is to examine the impacts on solitary bees, particularly rare/specialist bee species, as well as on generalist and common social species. Secondly, these studies need to be properly replicated in time and/or space (e.g. Thomson, 2004). Systems are naturally variable and in order to generate useful conclusions, rigorous experimental design is required. Thirdly, the rapid rate of new introductions, in particular by the exponential expansion of the bumblebee market (Velthuis and van Doorn, 2006), means that conducting detailed experimental studies of each alien species, in each native area may be impractical. For this reason, determining measures to identify quickly the likely impacts of new introductions is a key step to improve decision making, monitoring and rapid response (Thomson, 2006). Fourthly, it is important to understand the pathology, virulence and cross-infectivity of disease organisms like *N. bombi*, *L. buchnerii*, *C. bombi* and others (Thorp and Shepherd, 2005), and to adjust the mechanisms of detection of these pathogens in live bees in order to improve the quarantine measures. Finally, there is an urgent need to consider the impacts of climate change on spatial and temporal shifts in invasive alien and native plants and pollinators and their interactions (Schweiger et al., unpubl. data).

5. CONSERVATION NEEDS

Whilst research is still required, conservation measures should be put in place as a precaution in the intervening time. For example, mass flowering invasive plants and simplification of agricultural landscapes may increase competition among pollinators (Bronstein, 1995; Steffan-Dewenter and Kuhn, 2003). Thus, habitats rich in native flowering species, which provide plentiful pollen and nectar resources during the whole foraging season should be protected and promoted in restoration projects. These can support a larger diversity of native bees, which benefits agriculture (Hoehn et al., 2008) and the pollination of native wild plants.

Invasive alien flowering plants are often introduced intentionally as ornamentals (Dehnen-Schmutz and Williamson, 2006; Milbau and Stout, 2008). Many nations need tighter restrictions ("biosecurity") on the importation, sale and planting of certain flowering invaders. In this regard, some countries (e.g. New Zealand) are far ahead of others (e.g. many countries in the European Community lack border restrictions with other EU countries). Educational programs aimed at promoting gardening with native flowering plants would help to reduce alien importations and at the same time increase public awareness of the value of local biota.

With regards to imported commercial bees, all efforts should be made to license importation and minimise bee escape and the subsequent spread of disease to native species and populations. Bees do escape from commercial colonies used in the field and in glasshouses and so the potential for spread of disease, and hybridization is substantial. In addition, from the point of view of safety and nature protection, local production, preferably of a locally pollinating species, should be encouraged. If there is concern about dangers of introducing alien species, both the government and the farmers should invest in research (Velthuis and van Doorn, 2006). Finally, the most effective, economical, and ecologically sound approach to managing invasive species is to prevent them from arriving (Windle and Chavarría, 2005).

6. CONCLUSIONS

Some invasive species provide benefits (including the economic and environmental benefits of increased pollination services) but others have negative impacts on native bees. Impacts of invasive alien species on specialist and generalist bee taxa may differ, and probably vary according to landscape context, and although it is difficult to test impacts experimentally in well designed and replicated experiments, this is what we should strive to achieve. More research is required on all native bees (Committee on the Status of Pollinators in North America, National Research Council,

2007), but especially on solitary species and specialists. Unfortunately, in many parts of the world, these studies are limited by taxonomic expertise, an issue which may be overcome to some extent by DNA barcoding (www.bee-bol.org). Finally, we need predictions of impacts not just on species, but on entire plant-pollinator-parasite communities, ecosystem services and ecosystem functioning.

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Impacts écologiques d'espèces invasives étrangères sur les abeilles.

***Apis mellifera* / *Bombus* / pollinisateur / espèce non indigène / espèce invasive / plante / parasite / protection / conservation**

Zusammenfassung – Ökologische Folgen invasiver fremder Arten auf Bienen. Invasive fremde Arten sind wichtige Antreiber globaler Umweltveränderungen, indem sie direkt oder indirekt auf die einheimische Biodiversität und die Ökosystemprozesse Einfluss nehmen. Die durch einheimische Bienen erbrachten Bestäubungsleistungen werden allgemein durch einen weiten Bereich menschlicher Aktivitäten als gefährdet angesehen, im Blickpunkt dieser zusammenfassenden Untersuchung stehen potentielle Gefährdungen durch invasive Arten. Ziel des Artikels ist, den möglichen Einfluss invasiver fremder Arten auf die einheimischen Bienen abzuschätzen, um Gefährdungen bestimmen und Forschungsprioritäten in diesem Gebiet festlegen zu können. Wir berücksichtigten die Auswirkungen invasiver fremder Pflanzen, Bienen und Parasiten auf das Verhalten, die Populationen und Gesellschaften einheimischer Bienen und die Leistungen, die sie für das Ökosystem erbringen.

Invasive fremde Pflanzen können direkt oder indirekt auf die einheimischen Bienen Einfluss nehmen (Abb. 1). Direkter Einfluss beinhaltet die Bereitstellung von Blütenressourcen, wobei deren Wert entsprechend ihrer morphologischen Zugänglichkeit, Nährwert und der zeitlichen und räumlichen Verfügbarkeit der Belohnungen variiert. Ein indirekter Einfluss liegt vor, wenn invasive fremde Pflanzen die einheimische Pflanzengemeinschaft beeinflussen (entweder durch Wettbewerb um abiotische Ressourcen oder um biotische Ressourcen einschließlich der Bestäubung) (Tab. I). Insgesamt können Beeinflussungen des individuellen Verhaltens und Überlebens relativ leicht bestimmt werden, während dagegen Einflüsse auf Populationen oder Gesellschaften wesentlich schwerer vorauszusehen sind und bislang nur wenig untersucht wurden.

Der überwiegende Teil der Forschungen über die Auswirkung fremder invasiver Insekten auf die einheimischen Bienen hat sich auf die Auswirkungen von eingeführten sozialen Arten von Honigbienen oder Hummeln bezogen, die um Ressourcen oder Nistplätze in Konkurrenz stehen, die Verbreitung von Pathogenen und Krankheiten verursachen oder die Populationsstruktur durch Hybridisation oder Introgression beeinflussen. Trotz erheblicher Aufmerksamkeit der Forschung gibt es wenig schlüssige Nachweise für eine Kompetition zwischen fremden und einheimischen Bienen um Futterressourcen, hauptsächlich weil Untersuchungen zur Kompetition schwierig durchzuführen und zu interpretieren sind. Allerdings haben einige Untersuchungen eine Verminderung der Fitness einheimischer Bienen bei Anwesenheit invasiver fremder Bienen nachgewiesen. Es gibt allerdings so gut wie keine Untersuchungen zur Kompetition um andere Ressourcen als Futterressourcen, dies schließt Nistplätze trotz ihres offensichtlichen kompetitiven Potentials ein. Kürzlich wurde offensichtlich, dass insbesondere in Nordamerika eine der größten von eingeführten Bestäubern ausgehenden Gefährdungen ist, dass sie möglicherweise neuartige Pathogene und Krankheiten auf die einheimischen Bienen übertragen (Tab. II). Die Fähigkeit eingeführter Arten mit einheimischen Arten zu hybridisieren ist gut bekannt, und mit der Entwicklung molekularere Marker zur Erkennung einer Introgression dürfte das Ausmaß des Problems klarer werden.

Wir schlagen verschiedene Forschungsschwerpunkte vor, nämlich dass (1) Untersuchungen des Ausmaßes der Auswirkungen sollten sowohl in zeitliches als auch räumlicher Hinsicht erweitert werden, in einem robusten Versuchsdesign strukturiert sein und repliziert werden, (2) besondere Aufmerksamkeit sollte den Auswirkungen auf solitäre und spezialisierte Bienenarten zukommen, (3) eine schnelle Erfassung potentieller Auswirkungen neuer Eindringlinge sollte zu einer raschen Entscheidungsfindung, Überwachung und Entschärfung des Problems führen, (4) die Pathologie, Virulenz und Kreuzinfektiösität von Pathogenen und Parasiten muss besser verstanden werden, und (5) die Auswirkungen weiterer Umweltänderungen auf Grund des Klimawandels müssen wegen der potentiellen räumlichen und zeitlichen Verlagerungen bei invasiven und einheimischen Pflanzen und Bestäubern sowie ihrer Interaktionen

in Betracht gezogen werden. Wir empfehlen, dass Erhaltungsmaßnahmen einheimischer Bestäuber eine hohe Priorität zukommen sollte und dass diese Angelegenheit auf der Ebene des gesamten Ökosystems betrachtet werden sollte und nicht anhand eines nur artbasierten Ansatzes.

***Apis mellifera* / *Bombus* / nicht einheimische Bestäuber / Pflanzeninvasion**

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