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Risks to pollinators and pollination from invasive alien species

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Abstract

Invasive alien species modify pollinator biodiversity and the services they provide that underpin ecosystem function and human well-being. Building on the IPBES global assessment of pollinators and pollination, we synthesise current understanding of invasive alien impacts on pollinators and pollination. Invasive alien species create risks and opportunities for pollinator nutrition, re-organise species interactions to affect native pollination and community stability, and spread and select for virulent diseases. Risks are complex but substantial, and depend greatly on the ecological function and evolutionary history of both the invader and the recipient ecosystem. We highlight evolutionary implications for pollination from invasive alien species, and identify future research directions, key messages, and options for decision-making.

Introduction

Global anthropogenic drivers including land-use change, conventional intensive agriculture, pesticide use or misuse, pests and pathogens, and climate change threaten pollinators and pollination services[1,2]. Biological invasions are another major global change driver that can affect this natural capital[1,3]. The Convention on Biological Diversity (www.cbd.int/invasive/WhatareIAS.shtml) describes invasive alien species as those intentionally or accidentally introduced by human actions beyond natural ranges, which subsequently spread as vigorously growing populations that impact on biota, ecosystems and society. The global growth in economic wealth, trade, commerce, and transport efficiency facilitates this human-mediated spread of organisms into novel environments[4-6], with implications for the benefits that humans derive from nature[1].

Successful invaders have both ecological and evolutionary effects on native species and their interactions. Invasive alien species can alter the flow of energy and nutrients within an ecosystem[4], and disrupt mutualisms including those underpinning crop and wild plant reproduction[7-9]. Strongly interacting alien invaders can also establish novel selection pressures within a community that can modify evolutionary trajectories and adversely affect species with low genetic diversity and/or small effective population sizes[10-12].

Scientific and policy concern over various threats to pollinators and pollination led the Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES) to carry out a global evidence-based assessment on their values to humanity, their status and trends and drivers of change, and to identify policy response options to conserve them for the future[3,13]. In 2016, the Parties to the Convention on Biological Diversity (CBD-COP13) endorsed the findings of this IPBES assessment.

In this review, we build on the peer-reviewed IPBES evaluation[3,13] and earlier review papers[14-17] to synthesise the current understanding of impacts on pollinators and pollination from invasive alien species spanning different ecological functions (**Fig. 1**). We evaluate the negative, neutral or positive impacts of: 1) alien flowering plants on pollinator nutrition, community assembly and native pollination; 2) introduced alien pollinators on native plant-pollinator systems via competition, genetic exchange and pathogen and parasite transfer to new hosts; and 3) alien predators that consume pollinators and transform pollination systems. We outline potential risks to evolutionary dynamics from invasive aliens (**Box 1**) and conclude by identifying future research directions, key messages, and recommendations for decision-making.

Invasive alien plants

Global human-mediated dispersal of alien plants has increased, both accidentally (e.g. contamination of agricultural cargo) and deliberately (e.g. horticultural species)[4-6]. Introduced alien plants may prosper by escaping biological regulation of population size, by occupying a vacant ecological niche in the recipient ecosystem, or by possessing or evolving phenotypic traits (e.g. novel defences) that confer competitive advantage over native plant species[4,8,18]. Insect-pollinated species represent a large proportion of documented invasive alien plants; however, the capacity for self-pollination often aids initial establishment and spread[19]. Thereafter, invasive alien plant species that become abundant, and possess copious nectar and pollen rewards or large and enduring floral displays can lure and co-opt pollinators adapted to exploit such floral resources (**Fig. 2**)[19-22]. In this manner, invasive alien plant species can dominate species interactions and the diet and community structure of pollinators[19,23-25].

Impacts on pollinator nutrition

Whilst providing a substantial food resource for pollinators[19,24,26], a predominance of alien pollen and nectar in pollinator diets may produce risks for pollinator health. Pollinator species have particular physiological requirements for energy and a diversity of macronutrients[27-29], and they forage to balance these needs over time at both individual and colony levels[26,30-32]. Alien plant domination of floral communities can transform pollinator diet from a diverse suite of floral species to a largely monotypic diet comprising alien pollen and nectar (**Fig. 2**)[25]. Pollinating bees are highly sensitive to the specific dietary source and combination of nutrients, e.g. ratio of different essential amino acids (EAA) to carbohydrates, showing poor growth and survival when reared on monotypic or nutritionally sub-optimal diets[29,30,33,34]. Consequently, alien plant invasions may raise the risk of nutritional deficits for pollinators by eroding the ecosystem availability of combinations of essential nutrients provided by diverse floral resources. Alternatively, invasive alien plants can adequately supply carbohydrates or essential amino acids exploitable by pollinators with generalized foraging behaviour and diet[26]. However, the subtle nutrient requirements of pollinators, e.g. protein to lipid or EAA combinations, and a species' capacity to balance nutrition through flexible foraging[29,30] mean that the benefits of invasive pollen and nectar for native pollinators remain to be determined. Adverse impacts of alien pollen or nectar are more likely for relatively specialized pollinator species, either physiologically or morphologically ill adapted to exploit the alien food resource, or dependent on native plants outcompeted by the invader[34-36]. Secondary compounds in alien pollen and nectar can be differentially toxic to native pollinator species representing a further risk from plant invasions where they come to dominate diets[34,37,38].

Dominance of plant communities by invasive alien species (**Fig. 2**) could also restrict community-wide flowering phenology, truncating the period of floral resources' availability. Such curtailment could cause pollinator population declines and an overall decrease in pollinator diversity, as proposed for agricultural landscapes[39]. Surprisingly, there are comparatively few recorded examples of alien plant invasions consistently lowering overall pollinator diversity or abundance[40-42].

Although more research is definitively needed, this scarce evidence implies that pollinators may either physiologically or behaviourally trade-off or compensate for spatial and temporal changes in nutrient availability due to invasive alien plants[26], that effects are subtle, chronic and possibly undetected hitherto, or that they only adversely affect pollinators in combination with other stressors[2,43].

Modified interactions and community stability

The dynamic and flexible nature of pollinator foraging behaviour[30,44,45] means interaction networks are readily penetrated by flowering alien plants[23,46], where they often assume a key role in community organisation and function[7,8] (**Fig. 2**). Where the invasive alien plant species is highly abundant or possesses generalized floral traits that make it highly attractive to pollinators, it can rewire interspecific interactions to modify network architecture (**Fig. 2**)[44,45,47,48]. For example, they can usurp native interactions and operate as a hub that increases the size and connectivity of network modules (subsets of highly co-dependent species)[7], or weaken the co-dependency of mutualistic relationships in the network[49]. Such changes in modularity and interaction strength[7,49] can increase community stability by lowering the risk of co-extinction cascades arising from future environmental changes[50], unless the invasive alien performing the central role in the network is itself extirpated. Conversely, as seen with habitat structure, the high dominance of invasive alien plants could erode the co-phylogenetic structure of native plant-pollinator networks, reflecting poorer phenotypic matching between interacting partners and less-fitted mutualism, potentially introducing instability and reduced function of the pollination system[48,51].

Disrupted native pollination

The influential functional position of invasive alien plants once integrated into pollinator networks may have ramifications for native plant species reproduction. Invasive alien plants may affect co-flowering native plants by elevating pollinator activity to facilitate native pollination[22,52,53]. However, if an invasive alien plant reduces the abundance of native plants that become overly reliant on the invader for facilitation of pollination services, then there is a potential risk to the native species, should those connections become eroded or lost due to further environmental changes. Alternatively, invasive alien plants may simply outcompete native plants for pollinators (**Fig. 2**) and meta-analyses suggest native plant visitation rates do tend to decrease, indicating that competition prevails[48,54-57]. Whether regional facilitation or local competition predominates may depend on the spatial scale of the alien plant invasion, and the differing foraging ranges and ecology of pollinators in the species pool[53,58-60]. Overall, the impact of alien plant invasions on native plant pollination and reproductive success is greater if, relative to the native flora, the alien produces higher densities of flowers, they are phylogenetically related, or they possess similar phenology and anatomy of floral displays[9,19,59,61]. Aside from fundamental competition for pollinators, there may also be native pollen loss and pick up of foreign pollen during visits to alien flowers. This could either reduce conspecific native pollen transfer or increase deposition of heterospecific alien pollen that could cause stigma clogging or chemical inhibition of pollen germination[62]. This improper pollen transfer can translate into reduced native plant reproduction[55,57,63,64], yet the extent of this is complicated by plant compensatory mechanisms that can assure pollination and reproduction, such as the capacity for self-reproduction or recruitment of alternative pollinators[14,54,56,65].

Invasive alien pollinators

Competitive exclusion and co-existence

Humans have globally translocated many different bee species (e.g. species of *Apis, Bombus*, *Osmia*, *Megachile*) for apiculture and crop pollination services[13,66-68]. The principal managed pollinators, the western honeybee *Apis mellifera* and the bumblebee *Bombus terrestris,* possess traits such as sociality, generalist feeding habit and nesting flexibility, that coupled to recurrent introduction of managed colonies and frequent escape and establishment of feral populations, raise the risk of competition with native species[66,69-72] (**Fig. 1**). Direct competition from alien honeybees has altered the behaviour and reproductive success of native pollinators[69,73]. Given their long history of global spread, however, there are surprisingly few accounts of honeybee competition reducing survival or densities of native wild bee species and no reported extinctions[67,74-76]. One possibility is that the introduced super-generalist honeybee, by occupying a distinct ecological niche, becomes readily integrated into native pollinator networks, apparently with little competitive displacement of native pollinators[77,78]. Alternatively, the role of alien honeybees in historic declines of native pollinators, while noted in certain regions (e.g. decline of congener *Apis cerana* in China) may have contributed to declines in places like oceanic islands, but gone unrecorded[75,79]. In contrast, introduced alien bumblebee species, typically *B. terrestris*, often compete with native congeners that occupy very similar niches for nesting and floral resources, leading to the invader becoming dominant and excluding natives[66,70,71]. An example is the extirpation of the Patagonian giant bumblebee *Bombus dahlbomii* from most of its range following the introduction and subsequent establishment of feral populations of managed European bumblebee species (*B. terrestris* and *B. ruderatus*)[66] (**Fig. 1**).

Genetic effects and mating interference

Another potential risk from anthropogenic introductions of bee species is intra-generic hybridization and introgression, and reductions of native species fitness through mating interference[80-82]. Despite the history of global translocation of *A. mellifera*, overall evidence of hybridizations, introgression or mating interference with endemic sub-species is scant[67,83]. A notable exception was the movement of *A. mellifera capensis* into the range of *A. m. scutellata* as part of migratory beekeeping in South Africa, where it behaved as a social parasite, resulting in substantial *A. m. scutellata* colony losses[67,83]. Another example, from South America, was the introduction (>250 years ago), establishment of feral populations and spread of managed stocks of European *A. mellifera*, and more recently (1956) an African sub-species (*A. m. scutellata*) regarded as better suited to tropical environments. Debate continues about the extent that hybridization and introgression of the European type occurred, nonetheless there seems to be a latitudinal gradient in the extent of hybridization and the type possessing so-called ‘African’ traits came to dominate bee assemblages across the Neotropics and Southern USA[67,84].

Pollination disruption or rescue

Introduced pollinators can influence native pollination processes in complex ways, according to the identity of the pollinators and the nature of the recipient ecosystem[53]. There is evidence that the introduced honeybee’s foraging behaviour, i.e. social recruitment of numerous worker bees to a floral resource, can effectively maintain pollination function over great distances, particularly where the ecosystem and indigenous pollinators have been disrupted by anthropogenic habitat loss and species invasions[77,84,85]. Interactions between naturalized honeybees and native pollinators have been seen to enhance pollination of native plants and crops, additively or synergisitically[86,87]. However, alien pollinators are efficient pollen collectors and nectar robbers, so at high densities they can also behave as antagonists rather than mutualists, adversely affecting plant pollination[72,88], as seen in South America where frequent visits by abundant invasive bumblebees reduce crop yields[89]. A preponderance of invasive alien pollinators that either prefer or are able to exploit alien forage plants, may also produce less effective native mutualisms. To illustrate, removal of invasive plant species from a Seychelles island ecosystem decreased the domination by invasive *A. mellifera* of plant-pollinator networks; correspondingly increasing network flower visitation, interaction diversity and functional redundancy, which resulted in higher fruit production of native plants[48]. Alien pollinators, by altering mutualistic networks, can raise the likelihood of inbreeding depression via increased selfing within plant species, or outbreeding depression through hybridization between closely related alien and native plants[62,66,69,90]. Ultimately, such changes represent a risk to plant fitness, community structure and function.

Introduction of alien pests and pathogens

An outcome of the trans-continental transport of pollinating bees beyond their native ranges is the greater likelihood of pathogen and parasite transfer to new hosts, with the potential to elicit population declines of native pollinators[66,91,92] (**Fig. 1**). Introductions of *A. mellifera* to China in 1896 coincided with a drastic reduction in the range and population size of the Asian honeybee *A. cerana* with interspecific competition and pathogen transfer (e.g. Sacbrood viruses) implicated[75,93]. The sustained movement by humans of managed honeybee (*A. mellifera*) colonies into Asia ultimately resulted in the host shift of the ectoparasitic *Varroa* mite from sympatric *A. cerana* populations and its subsequent worldwide spread, along with a complex of viral pathogens (*Picornavirales*) it transmits among bee hosts, as part of trade in managed honey bees[94,95] (**Fig. 3**). Through vectoring viruses, possibly suppressing bee immune functions, and direct parasitic feeding the *Varroa* mite is among the major pressures impacting managed and feral honeybee colonies[1,2,96]. Indeed, the most recent analyses suggest that the *Varroa* host shift may have elicited eco-evolutionary changes in host-vector-pathogen dynamics resulting in selection for increased virulence of strains of

Deformed Wing Virus (DWV) infecting honeybees and implicated in colony losses[94-98] **(Fig. 3).** Moroever, there are also signs of pathogen transmission between managed bee populations and wild pollinators[91,95,99,100]. Possibly these pathogens are generalists infecting a broad spectrum of hosts and commonly shared across flower-visiting insects[100,101]. Alternatively, pathogens introduced along with alien pollinators, managed or feral, might represent a novel ecological and selective pressure with consequences for pollinator decline and the epidemiology of pollinator communities (**Fig. 3**).

Invasive alien predators

Invasive alien predators, such as cats, rats, and stoats, spread by humans often exert strong top-down pressure on plant pollination and fitness by consumption of pollinators such as birds, lizards, bats and other small mammals[13] (**Fig. 1**), especially in the specialised and simpler networks of island ecosystems[6]. A recent example of a direct threat to already stressed European honey bee populations is the accidental introduction (2004) of the predatory yellow-legged hornet (*Vespa velutina*) into Europe from Asia[102,103] (**Fig. 1**).

Alien predators can also indirectly shift the functioning of native pollination systems through networks of trophic and competitive interactions. For instance, in Africa, California and Mauritius, invasive ant species that are more aggressive or competitive than native ants, deter pollinators and seed dispersers thereby reducing plant fitness[104-106]. Alien insectivorous lizards transformed the pollination system of the Ogasawara archipelago of Japan by extirpating endemic bee species and leaving the alien honeybee (*A. mellifera*) that prefers flowers of invasive alien plants to dominate, thus completing the shift to an invasive-dominated pollination ecology[107].

A case that highlights the complex nature of interactions between predators, pollinators and plants is that of the invasive predatory wasp (*Vespula pensylvanica*) in Hawaii[72,77]. This generalist predator of arthropods also behaves as a nectar thief, competing with native *Hylaeus* bees and the alien honeybee *A. mellifera* that pollinate the native tree *Metrosideros polymorpha*, thereby lowering pollinator visitation and resultant fruit production[72,77] (**Fig. 4**). Experimental removal of the wasp revealed the alien *A. mellifera* was the most effective pollinator in this system, in all likelihood fulfilling a niche previously occupied by extinct or declining bird pollinators, themselves reduced by introduced vertebrate predators[77] (**Fig. 4**). These examples serve to illustrate the impact that alien predators can have on the community of interactions affecting pollination, but also how invasive alien pollinator species can maintain pollination in highly modified ecosystems in the absence of native pollinators.

Future research directions

Invasive alien species remain an ongoing threat to pollinator biodiversity and pollination function worldwide. Nonetheless, our ability to understand and forecast the risk to pollinators and pollination requires that we fill substantial gaps in knowledge by stimulating future biological, ecological and evolutionary research.

The impact of particular invasive alien species on native pollinators and pollination has been somewhat overlooked. The impact of introduced solitary bees on the ecology of native pollinators and pollination is a specific gap in knowledge and risk assessment, warranting further study to help forecast and prevent future invasions by alien pollinators. For instance, solitary bees such as species of *Osmia* or *Megachile*, introduced for crop pollination services, sometimes possess similar traits (e.g. dietary generalism) to the bee species *A. mellifera* and *B. terrestris*, which facilitated the invasion and modification of native mutualisms by these social bees[13,66-68]. There has also been little investigation of herbivory as an aspect of pollination invasion ecology, compared to other trophic interactions. Introduced mammalian herbivores can modify plant communities affecting the floral or nesting resources available to native pollinators and influencing native plant pollination[108,109]; given the global prevalence of livestock introductions, this is an understudied research area. Similarly, insect herbivory can influence plant physiological function and allocations of metabolites to floral displays, pollen and nectar, and emissions of volatile organic compounds that recruit pollinators[110] and affect pollination[111-113]. Yet, the impact of invasive insect herbivory on the chemical ecology of native pollination remains a significant knowledge gap with considerable research potential.

Much remains to be discovered about the impact of invasive alien species on the structure, function and stability of plant-pollinator networks. Henceforward, research should employ recent innovations in simulation modelling that capture greater biological realism and complexity of species interactions - such as temporal dynamics, interference competition, variable mutualism dependence - to obtain new insights on how invasive species re-organise pollinator network structure and affect key mechanisms or properties underpinning the stability of invaded networks facing future global change[45,48,50,114,115]. Furthermore, research on network structure and stability should be extended beyond impacts from alien plants and alien pollinators to other invasive groups occupying different trophic or parasitic roles and evaluate the overall consequences for interconnected mutualistic and antagonistic networks[116].

Research must continue to understand the community dynamics of invasions and their consequences for pollination processes. We know little about the consequences of massive plant species invasions for community-wide flowering phenology, and how such temporal changes in distribution of floral resources link to changes in the temporal dynamics, composition, and diversity of pollinator communities. The extent that co-flowering native plant species, through their influence on foraging behaviour of different pollinator groups (e.g. flies, bees, birds), facilitate alien plant establishment is a gap in understanding the dynamics of alien plant invasions[117]. Similarly, the impact on agricultural crop production of changes in pollinator foraging due to invasive alien plants has yet to be well studied[60]. Furthermore, by usurping native interactions[7,49], alien plant and pollinator species may increase the proportion of ill-matched interactions and, therefore, decrease pollination function, an untested hypothesis based on a relatively well-established assumption with important ecological and evolutionary consequences.

Evolutionary mechanisms facilitating or hindering invasions by mutualists are largely at a theoretical stage[10,118], but recent observations show how rapid adaptation in invading plant populations may aid their spread and establishment, and also the role of balancing selection at the sex locus of *A. cerana* enabling its recent establishment in Australia[11,119]. More empirical research is needed to test predictions such as understanding micro-evolutionary effects, shifting trait structure of plant-pollinator networks, or the role of genetic diversity in shaping invasion probabilities and dynamics in an ecosystem (see **Box 1**). We need to understand better the eco-evolutionary constraints to invasion of pollinator communities and their effects on evolutionary trajectories post- invasion to predict future risk. For instance, community permeability to an invasive species may be limited by the genetic diversity or the effective population size of the invading populations, governing their ability to adapt to novel environments. Genetic variability in the native populations with which the invader will interact may contribute to the success or failure of the invasions, depending of the type of interaction (e.g. competitive, mutualistic) established with the invasive species. Once established, an invader has the potential to affect the evolvability of native species, since introductions can affect the (effective) population sizes, the genetic diversity and the fitness of native populations (**Box 1**).

There is considerable scope for increasing our knowledge about the disease risks for native pollinators and pollination from exposure to invasive alien species. The epidemiology of pollinator communities is in its infancy with recent detection of pathogen sharing and potential asymmetric interspecific transmission and virulence[91,95,99,100]. There is an opportunity to unify network theory, evolution, disease biology and ecology to understand how novel host-vector-pathogen shifts involving alien organisms affect the evolution of pathogen virulence within hosts; competition and coexistence among assemblages of ecotoparasites, viral, fungal and bacterial pathogens; and transmission processes and disease frequency among multiple pollinator hosts[2,96]. Related to this, there is a need to study the underlying mechanisms for pathogen resistance/tolerance among bee species in their native and invaded ranges, including those living wild and those reared commercially (e.g. *B. terrestris*)[120]. Furthermore, global trade in agricultural commodities or the human-mediated translocation of alien plant species increase the risk of spreading alien plant pathogens[121]. There is some evidence that plant pathogens in native systems may modify plant physiology and flowering to affect plant-pollinator interactions and plant reproduction[122,123], but this possibility during invasion of pollination systems has been hitherto ignored. Moreover, a single study provides some evidence that a plant pathogenic RNA virus (TRSV) due to its evolutionary history may infect bees via *Varroa* mite vectors, albeit without apparent effects on bee colony health, intriguingly pointing to the potential for viruses to transcend kingdoms[124]. Overall, the biological and evolutionary complexity and phylogenetic breadth of potential plant-pollinator-pathogen epidemiology arising from species invasions is considerable and warrants investigation.

Conclusions and policy responses

The effects of invasive alien species on pollinators and pollination are complex and substantial, particularly under the biogeographical circumstances of oceanic islands[6,13], but depend greatly on the functional ecology and phylogenetic history of the invader and the recipient ecosystem. For example, invasive alien species possessing generalised ecological traits or evolutionarily close to natives are readily incorporated into species networks and ecosystems, and when attaining great abundance, they substantially modify structure and function of pollination systems, often negatively for native species. Alien predators exert considerable top-down pressure on native pollination systems through direct and more subtle indirect trophic interactions that can transform the pollination ecology into a state dominated by alien interactions. Global trade in managed bees and horticultural or agricultural plants increases disease risks through the interspecific spread and selection of novel pathogens with the potential to impact pollinators and pollination in unforseen ways. Invasive alien species thus tend to represent a significant biological risk to pollinators and pollination, albeit one that varies with species identity, abundance and environmental context.

In the globalised economy, there is considerable scope for interactions among drivers of biodiversity change, thus the impact of invasive alien species on pollinators and pollination is exacerbated or complicated when it occurs in combination with other threats such as diseases, climate or land-use change[2,6,43]. Policies that minimize impacts on pollinators from stresses such as conventional intensive agricultural management and climate change, for example by diversifying agricultural landscapes and building ecological infrastructure[1,2,13,125], are likely to relieve some of this overall multifactorial pressure on pollinators. In principal, this could increase the resilience of native plant-pollinator communities to alien species invasions. Current and future research focused on the interplay between invasive species and other global change drivers affecting pollinator biodiversity in different ecosystems will enable subsequent refinement of intergovernmental policy (e.g. CBD) tackling invasive alien species.

Eradication or control of established invasive aliens is often prohibitively expensive and rarely successful beyond oceanic islands and vertebrate species. Consequently, the most effective policy response is a tiered approach to mitigate the risk. Crucial to forestalling invasions is horizon scanning for emerging threats and forecasting likely impacts, which allows for timely scientific, technical and policy responses[3,103,126,127]. Thereafter, actions leading to improving regulation, e.g. of trade in managed pollinators or horticultural plants, maintaining surveillance and establishing rigorous monitoring[3,126,128], and once detected, rapid assertive management to avoid establishment by the alien species are expected to prevent new invasions or limit their impacts[3,126]. If invasive alien species go unchecked, the risk to pollinators and pollination is elevated, ultimately with unpredictable but mostly negative consequences for ecosystem health and human well-being[1].

Competing interests

There are no competing interests.

Author Contributions

In the cited IPBES report AJV and AE authored the section in Chapter 2 on invasive species impacts on pollinators and pollination. AJV conceived and led this article, AE & MAA provided insight, co-wrote the review and all authors performed revisions following peer review.

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Box 1. Evolutionary perspectives on impacts of invasive alien species on pollinators. Evolution is driven by four processes: mutation, gene flow, drift and selection. Anthropogenic changes to a pollination system that modify these processes have the capacity to affect the evolutionary outcomes for species, co-evolutionary dynamics and community structure and function. Several eco-evolutionary characteristics of the interacting communities can modulate these evolutionary processes, such as the extent of mutual dependence between the interacting species, the probability of encounter, the demography of the invasion, and the phylogenetic histories of the plants and pollinators[10,129-131].

Species invading a pollination community create and are exposed to novel selective pressures have the ability to modify ongoing evolutionary trajectories[10-12]. Indeed, the newly interacting species compete for resources (e.g. floral rewards, pollination service), and asymmetric interactions will allow some to dominate the community. This is one of the reasons why mathematical models predicted that the widespread introduction of the super-generalist and very competitive honeybee *A. mellifera* is expected to select for convergence in flower traits across many wild plant species, affecting plant-pollinator community function and structure in the longer term[118]. The relative changes of both the census and effective population sizes of the invasive and native species[131] can also have a direct impact on the evolutionary paths of the interacting species. Because invasive species usually reach large population sizes, they can affect the populations of co-occurring natives negatively through either interference or exploitative competition. Ultimately, this can, on the one hand, decrease the native population's chances of demographic recovery, and on the other hand, reduce the native's effective population size increasing the effects of genetic drift. Likewise, the effects of genetic drift are also expected to be amplified in species that already have low effective population sizes, such as is usually the case in endangered or rare species[132]. Further, organisms with small effective population sizes are less responsive to selection, which negatively affects the ability of natives to adapt to the new conditions created by the arrival and establishment of the invasive species.

Through its effect on the population sizes of co-occurring native species, invasive species can also affect connectivity among native populations. Loss of connectivity decreases gene flow and in some cases genetic diversity and evolvability, rending native species less able to adapt to new conditions or to recover from the effects of drift[132-134]. Impoverished genetic diversity may affect adaptive processes contributing to the success or failure of invasions, depending of the type of interaction the native has with the invasive species. On this point, modelling approaches indicated that an alien species with high genetic diversity (usually associated with a higher ability to adapt) is expected to establish in the community. Further, higher genetic diversity in the resident (native) species than in the invasive species can lead to exclusion of the invasive in predator-prey interactions, and may allow adaptation to the invasive and survival of both species in other types of interactions (e.g., mutualistic, competition)[10].

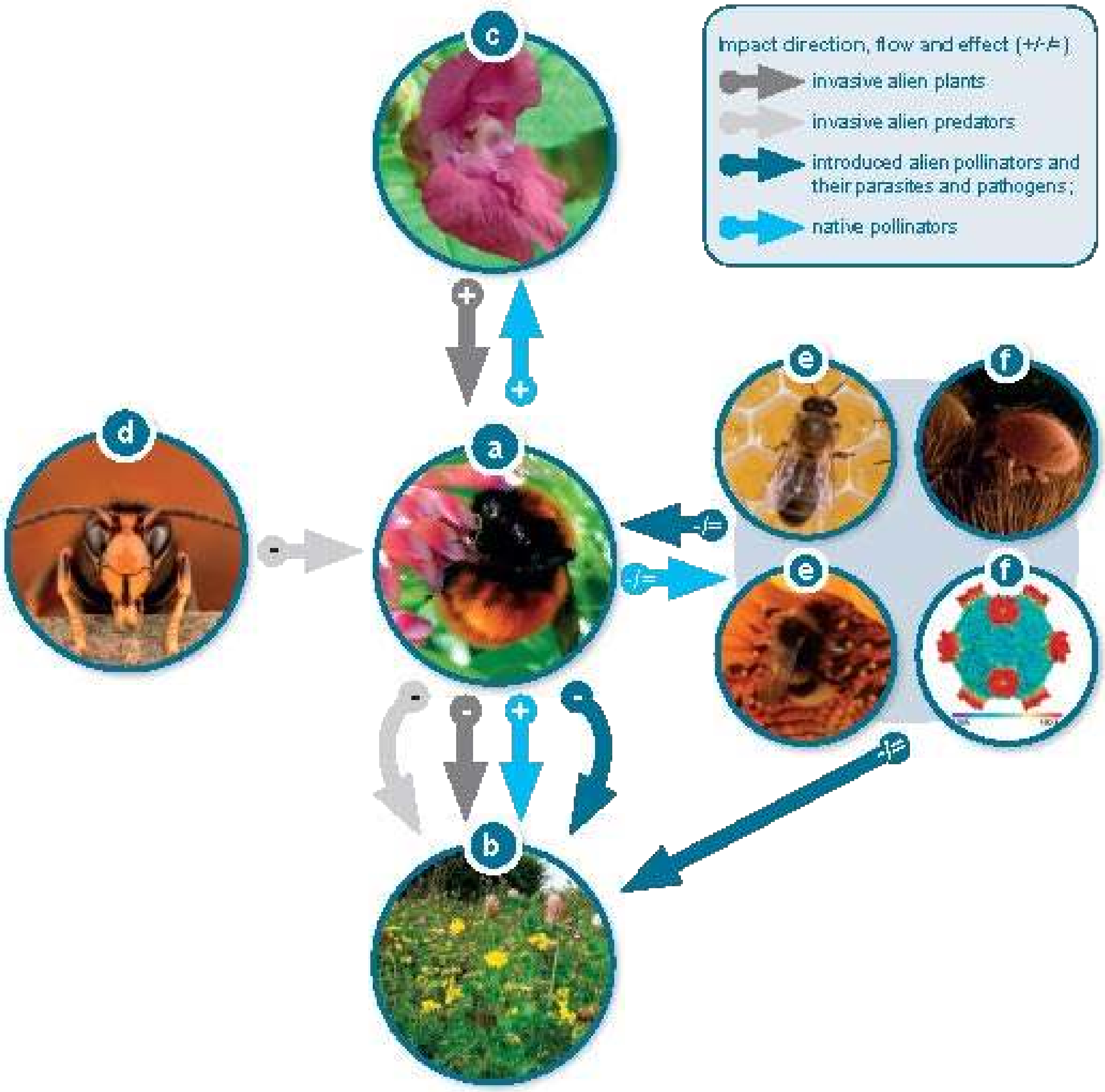
Figure 1. Conceptual synthesis of the direct and indirect impacts on (A) native pollinators and (B) native plant pollination from invasive alien species of (C) plants, (D) predators, (E) introduced pollinators and their (F) pests and pathogens. Images are representative examples of native and invasive alien species and do not portray a particular ecological system: (A) native Patagonian giant bumblebee *Bombus dahlbomii* (source Carolina Morales); (B) native British wildflowers (source Claire Carvell); (C) Himalayan balsam *Impatiens glandulifera* invasive in Europe (source Dan Chapman); (D) Asian hornet *Vespa velutina* invasive in Europe (source Gilles San Martin) (E) managed pollinators translocated worldwide include the western honeybee *Apis mellifera* (source Eugene Ryabov) and *Bombus terrestris* (source Adam Vanbergen), which has spread (F) pests and pathogens e.g. *Varroa* mite (source USDA); Deformed Wing Virus (source Pavel Plevka).

Figure 2. Invasive alien plant impact on pollinator visitation and network structure. An example of an alien plant species (A) Himalayan balsam, *Impatiens glandulifera* native to Asia and invasive in Europe. This plant attains high densities, produces copious nectar and pollen and possesses a large, enduring floral display, all of which enables it to readily penetrate and dominate plant-pollinator networks by co-opting pollinators, such as (B) the honeybee and (C) syrphid hoverflies. In turn, alien plant invasions can alter the composition and structure of native plant-pollinator networks from (D) to (E). This raises the risk of (E) pollinator nutritional deficits due to reductions in availability of essential nutrients from diverse floral resources, poorly matched mutualisms and impaired native plant pollination (but see[59] for an exception). Source of images: Dan Chapman, Claire Carvell and Adam Vanbergen.

Figure 3. Global movement of managed pollinators and risk of altered host-vector-pathogen dynamics. The historic and current human-assisted translocation of (A) the western honey bee *Apis mellifera* for apiculture and pollination services led to its range extending from its native range (vertical lines) to a near global distribution (shaded green area) that overlapped with other *Apis* species including the Asian honey bee *A. cerana* (horizontal lines). This led to (B) the *Varroa* mite, a parasite of *A. cerana*, infecting sympatric colonies of *A. mellifera* and subsequently spreading worldwide in association with the new host bee. *Varroa* is now the major worldwide pest of managed honeybees between which it transmits many viruses[2,13]. Recent

evidence suggests that (C) the novel eco-evolutionary interaction between *Varroa*, *A. mellifera* and the Deformed Wing Virus (DWV) has increased viral virulence and that DWV (D) co-infects bumblebee species with (E) unknown implications for pollinator community epidemiology. Image sources: *Apis mellifera* (Eugene Ryabov); *Apis cerana* (Dino Martins); *Varroa* mite (USDA); Deformed Wing Virus (Pavel Plevka).

Figure 4. Complex interactions between alien predators, alien and native pollinators and native plants transform and maintain pollination in highly modified ecosystems. Within the Hawaiian archipelago (map outline), historic introductions of (A) mammalian predators (e.g. cats and rats) led to (B) extinctions and declines of birds, particularly of the charismatic Hawaiian honeycreepers, that (C) pollinated the tree *Metrosideros polymorpha* among many other native plant species. More recently, the invasion by (D) *Vespula pensylvanica* the predatory wasp and nectar thief has increased competition for floral resources, deterred flower visitation by (E) native *Hylaeus* bees and the (F) alien honeybee *A. mellifera* and thereby (C) reduced *M. polymorpha* pollination and fruit production. Experimental exclusion of the wasp showed the alien honeybee (F) is now the most effective pollinator in this system with the decline or loss of bird pollinators. Double-headed arrows indicate mutualisms. Single headed arrows show impacts. Grey arrows = alien interactions; Blue arrows = native interactions. Dashed arrow = declining or extinct interactions. Image sources: *V. pensylvanica* (J. Gallacher CC-BY-2.0); *Hylaeus* spp. Forrest & Kim Starr; feral cat (Batty CC-BY-2.0); rat (US-NPS).



c
Impact direction, flow and effect (+/-/≠)
invasive alien plants
invasive alien predators
introduced alien pollinators and their parasites and pathogens;
native pollinators
+
+
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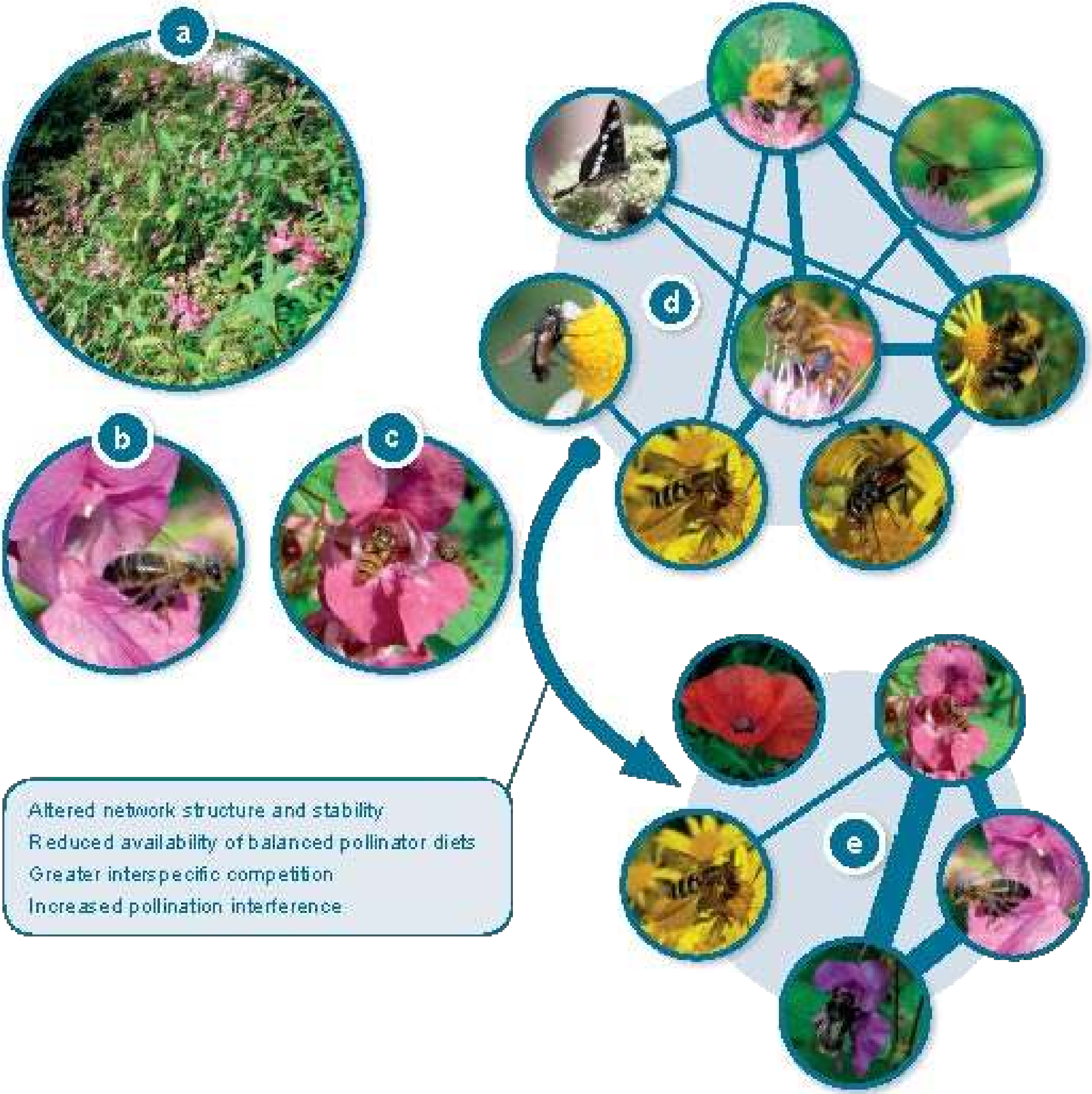

a
b
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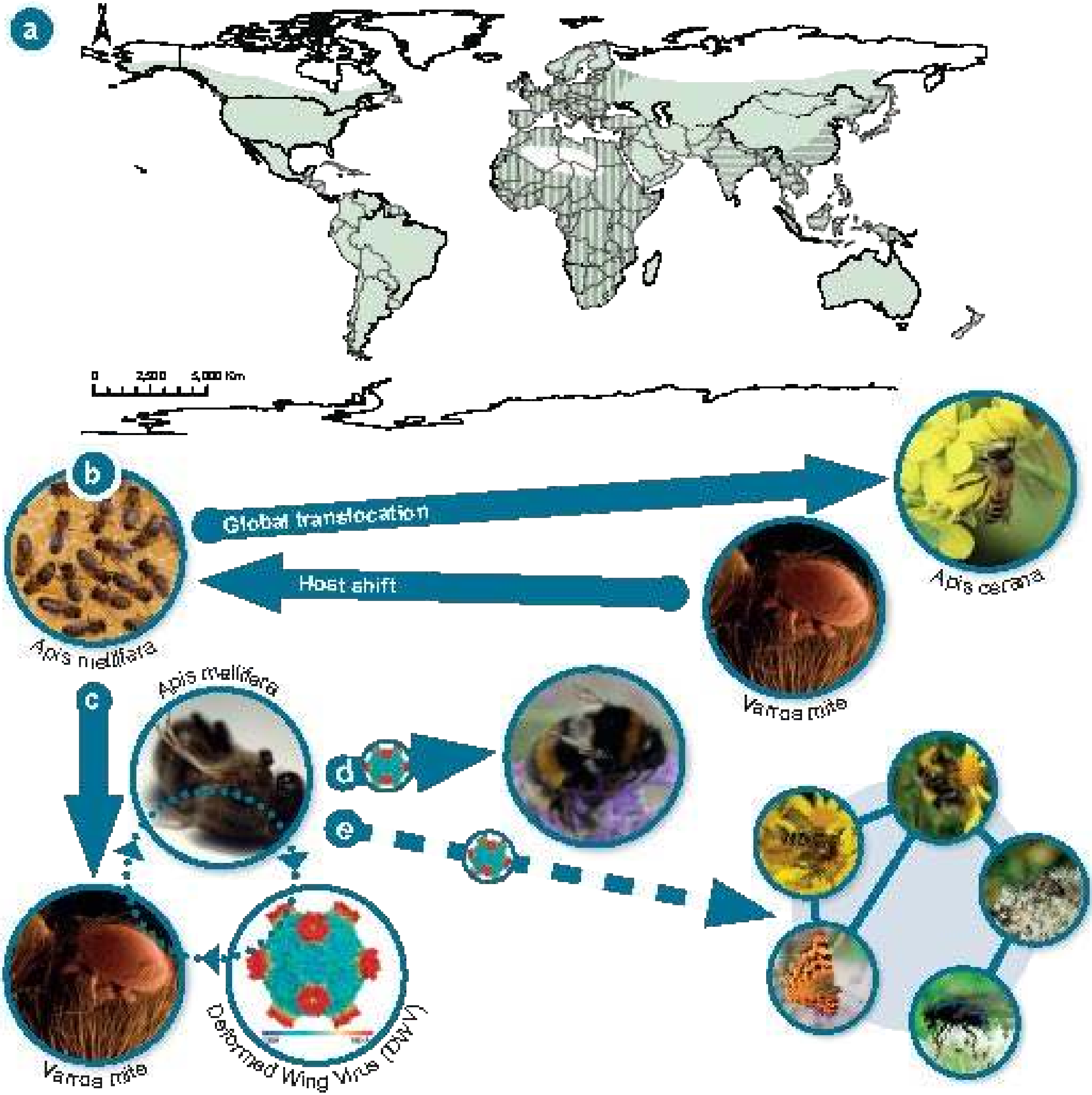
d
e
Altered network structure and stability
Reduced availability of balanced pollinator diets
Greater interspecific competition
Increased pollination interference


a
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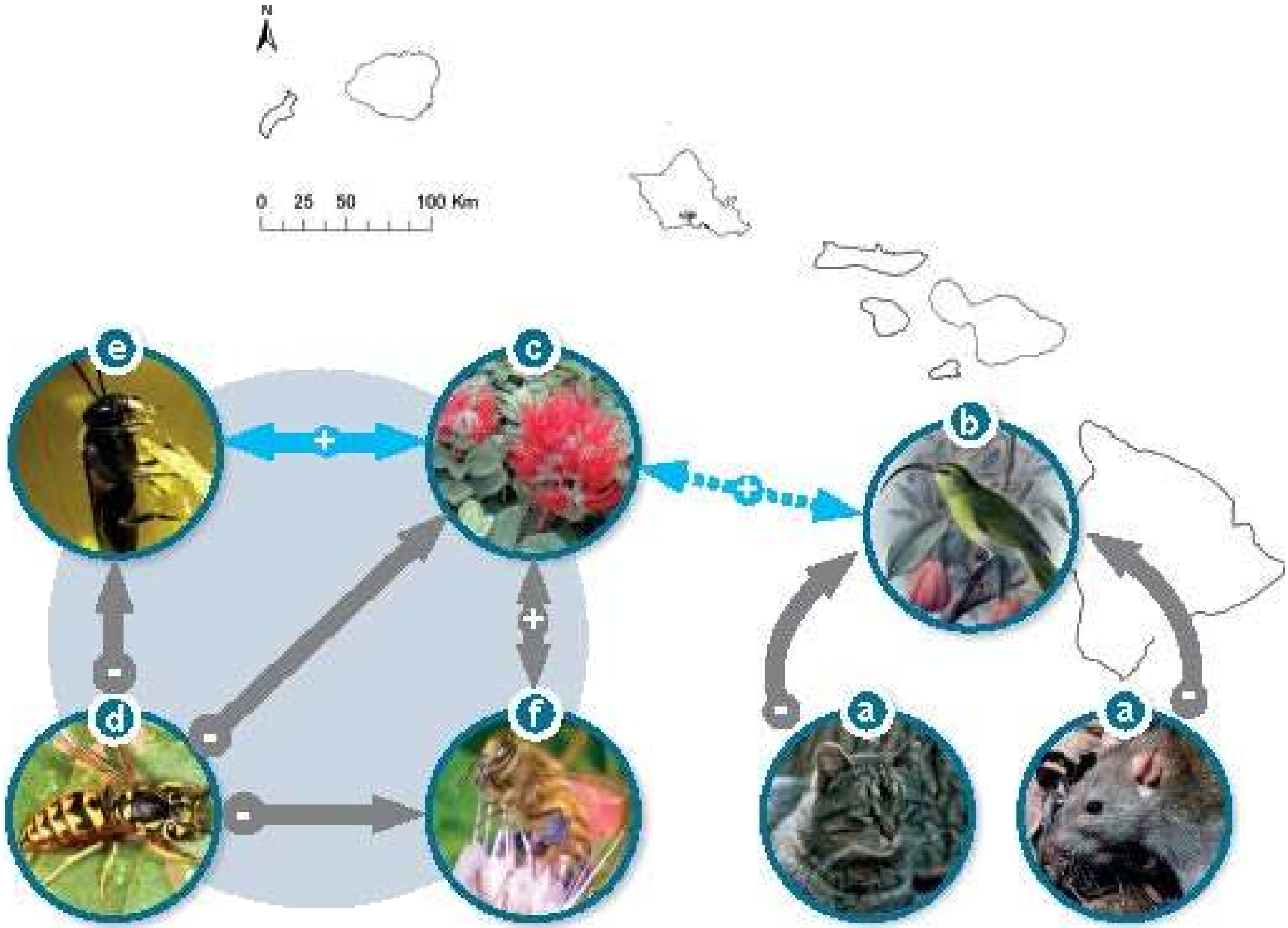
b
Global translocation
Host shift
Apis mellifera
Apis cerana
Varroa mite
c
Apis mellifera
d
e
Varroa mite
Deformed Wing Virus (DWV)



N
0 25 50 100 Km
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