

Chapter 2

The Diversity and Impacts of Alien Species

2.1 Introduction: The Diversity of Alien Species

The numbers and impacts, both actual and potential, of alien species in any area are hard to estimate, and only clear ideas of what constitutes ‘an alien’ can aid this. Distinction between (1) aliens that have arrived in a new geographically discrete area from other geographical regions separated by sea or other clear barrier that has been transcended and (2) those that have not had to overcome any such marked boundary or discontinuity in extending their range is useful. Thus, considering alien Hymenoptera in Europe, Rasplus et al. (2010) separated ‘species alien to Europe’ (those clearly from other parts of the world) from ‘species alien in Europe’, for which expansions into neighbouring contiguous countries have not included any sea or other such barrier. In this example, the great majority of the first category represent biological control introductions, most of them to restricted anthropogenic areas such as cropping systems, and many of the species have remained localised in occurrence. In contrast, ‘aliens in Europe’ are more commonly associated with more natural forest or woodland habitats. Whilst many of the former group are parasitoids, many of the latter are phytophagous species that have accompanied spread of their host plants to increase their range. For many, however, it remains uncertain whether documented spread to neighbouring contiguous countries represents gradual movement or independent colonisation events or, even, lack of historical information on their long-term incidence. One important implication of the difference between these two categories is that transfers ‘in’ an area are more likely to encounter other taxa with more in common with those of their area of origin, rather than the predominantly more novel taxa resulting from introductions from afar ‘to’ that area. Some ambiguities remain, reflecting incomplete knowledge and surveys. Whilst both movement patterns are common, the transfer of species across biogeographical boundaries is acknowledged widely as the greater potential concern, and measures to prevent such occurrences are the foundation of many biosecurity programmes.

Table 2.1 Groups of Lepidoptera in Europe which were excluded from the major categories of ‘aliens’ (namely, naturalised alien species originating from outside Europe, and European species spreading through the continent as a result of human activity) (Lopez-Vaamonde et al. 2010)

- | |
|--|
| 1. Species that show clear range expansions/colonisation at a country level, which are known to follow global climate change trends |
| 2. Naturally expanding species known as migrants which have established without clear human assistance |
| 3. New records of species probably overlooked in particular countries, and for which there is no clear evidence of range expansion |
| 4. Deliberate introductions of species between European countries |
| 5. Species once apparently established but now extinct |
| 6. The large number of living ‘display species (as in butterfly houses) unless these are either establishing in the wild or have become greenhouse pests |

For the better-documented Lepidoptera in Europe, Lopez-Vaamonde et al. (2010) also recognised two major categories of aliens, paralleling those for Hymenoptera, above. The species originating from continents beyond Europe were largely outcomes of deliberate or indirect (accidental) human activity, and this category included species introduced into greenhouses and similar environments with their host plants and regarded as having potential to spread through horticultural trade or expansion. The second category was of European species spreading within the continent, again largely from human activity. However, a number of contexts were excluded from their defined scope of ‘aliens’. Table 2.1 summarises these, each of which may need independent evaluation in considering the definition (and, hence, richness) of alien species for any particular study. In addition, introductions of alien host plants have undoubtedly facilitated range expansions of some Lepidoptera that have tracked these resources in some way. The Geranium bronze butterfly (*Cacyreus marshalli*, Lycaenidae), native to southern Africa, has progressively colonised much of southern Europe since it was initially recorded in Mallorca (in 1991), and is a potential pest of native and ornamental *Pelargonium* and *Geranium* species (Quacchia et al. 2008) whenever these are encountered.

Difficulties of generalisation from the European data were highlighted by a parallel study of alien Hymenoptera in New Zealand, demonstrating that inferences from one part of the world may indeed differ markedly elsewhere (Ward and Edney-Browne 2015). The families with highest numbers of alien species were broadly similar, but major differences from Europe included (1) a lower proportion (70 of 334) of intentionally released species and (2) a greater proportion of parasitoids amongst the unintentionally introduced taxa, together with (3) a considerably larger proportion of alien species occurring in urban areas. Differences in place of origin were also evident (Fig. 2.1), with increasing predominance by alien species from Australia evident over recent decades. Australia is the source of 98 alien Hymenoptera species (and many other alien insects) in New Zealand, spanning many taxonomic groups and acting as a secondary source for some (such as the Argentine ant, *Linepithema humile*), so further aiding spread of some invasive alien species. Importation of live plants is a significant entry path for these.

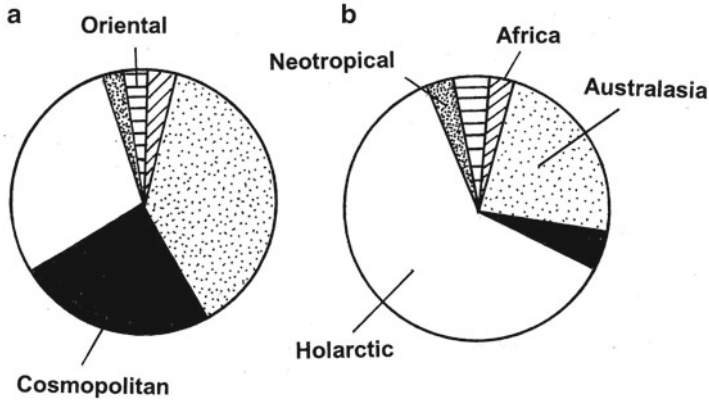


Fig. 2.1 The origins of alien species of Hymenoptera established in New Zealand, indicating differences between (a) unintentional introductions and (b) intentionally released species (Ward and Edney-Browne 2015)

Especially beyond Europe, many invertebrate taxa cannot be allocated reliably to either native or alien status because of incomplete taxonomic knowledge and species inventory; many orders of insects are amongst the most problematic groups for which to redress this. Nevertheless, even very conservative figures of alien species richness tend to be impressive. The Hawai’ian archipelago, for example, was assessed to have 5246 native insect species by 2000, with a further 2583 alien insect species including 98% of the state’s pest insects (Pimentel et al. 2005). For the United States (including Hawai’i), Pimentel et al. cited ‘approximately 50,000’ non-native species (all taxa). These include many introduced deliberately as crops or ornamentals and for a variety of more specific purposes, such as classical biological control of pests and landscape restoration. They included approximately 4500 arthropod species (Pimentel 2011), of which more than 95% were accidental introductions. Of these, about half are crop pests. General ecological concerns from this substantial pool of invaders included (1) lack of natural enemies controlling invasive populations; (2) development of new ecological associations; (3) artificial or disturbed habitats that facilitate invasions; (4) ecological characteristics such as being successful generalist predators in the new environment; and (5) more general ecological adaptability.

These concerns collectively encapsulate many of the ecological correlates and mechanisms associated with invaders, and also much of the wider fear of conservationists for the fate of invaded ecosystems and the endemic or other native species there: they are central and recurring themes in insect conservation. Acknowledging the difficulties of determining the full range and extent of environmental damage and native species extinctions flowing from invasive alien species, Pimentel et al. (2005) also noted that about 400 of the 958 species (all taxa combined) then listed as threatened or endangered under the United States Endangered Species Act were so primarily because of competitive or predation impacts of alien species. Similar,

Table 2.2 Comparison and composition of non-native insect species (total, and percentage composition of some predominant orders) in mainland North America and Japan, and associated islands of Hawaii, Ogasawara and Okinawa (Abstracted from Yamanaka et al. 2015)

Taxon	Locality				
	N. America	Hawaii	Japan	Ogasawara	Okinawa
Total spp.	3540	2651	471	168	349
Coleoptera	26.8	21.5	35.5	28	31.8
Hymenoptera	22.5	25.5	11	13.7	12
Hemiptera	27.3	16.4	22.5	26.8	22.6
Diptera	8.1	16.3	8.3	6.5	5.7
Lepidoptera	8.2	7.9	9.6	7.1	15.8
Thysanoptera	2.5	4.3	4.2	5.4	4

No other order has any entry above 4%

if less severe or less obvious, impacts must extend to numerous non-listed taxa. Pimentel et al. (2005) also emphasised the distinction between plant and vertebrate introductions (most of which have been intentional) and invertebrate introductions (most of which have been accidental or unplanned). Most insect invaders are not detected until they are already established and, in many cases, spreading. For many, the earlier phases of arrival and initial establishment can only be inferred. Relative attention to major taxa of invasive species was highlighted by Pysek et al. (2009), who analysed 2670 published papers collectively dealing with studies on 892 invasive species. These were dominated by plants (48.3% of papers, 395 species) and insects (18%, 157 species). Most species were treated in rather few papers – but the most intensively studied invasive insect (the Argentine ant, *Linepithema humile*, p. 159) was the subject of 61 studies.

Numbers of alien insect species in different places, although commonly high, pose some intriguing questions of their genesis and similarity. Thus, Yamanaka et al. (2015) pondered whether (1) a single pool of species, originating from the same areas and following similar invasion pathways, is the source of most insect invasions worldwide, or (2) insect invasions in each region are unique, and reflect an individualistic set of origins and pathways. They approached this dilemma by comparing established insects of North America and mainland Japan and their key island groups (as Hawai'i, Ogasawara and Okinawa). The native area of each identified invasive insect was assessed, and deliberately introduced species were distinguished from accidental arrivals. Outcomes, not wholly unexpectedly, showed high numbers of non-native species, with those on Hawai'i and Okinawa approaching totals for the mainland areas (Table 2.2). Far more insects have been introduced deliberately to Hawai'i than to the Japanese islands, reflecting its long history of classical biological control (Chap. 6). Comparison of each fauna showed clear differences in origins across the five regions, with each attaining a unique suite of species and pathways moulded by opportunity, propagule pressure and habitat/climate compatibility.

2.2 Alien Species in Invaded Ecosystems

In extreme cases, becoming all too commonly found on some isolated island groups in particular, the dominance of local faunas by alien colonists causes severe ecological disruption and loss. Some examples have been reported in which the entire current fauna of particular insect groups is of alien species. Ants on the Hawai'ian and Juan Fernandez (Chile) archipelagos represent this scenario. Thus, the only three ant species found on the latter island group are invasive species (Ingram et al. 2006). Most bees found on islands of the south west Pacific are also very recent introductions with probable anthropogenic origins, and with many of the species likely to be from Australia or south east Asia (Groom et al. 2014, assessing bees of Fiji, Vanuatu and Samoa). Some species have become abundant in this otherwise depauperate bee fauna, and Groom et al. discussed two major ecological implications of these pervasive recent introductions, as (1) awakening of sleeper weeds, the impacts of which on many islands are likely to have been inhibited by lack of suitable pollinators; weeds that depend on buzz pollination or with long corolla tubes (necessitating long-tongued bees for pollination) may be particularly affected, as elsewhere (Goulson 2003); (2) displacing native pollinators is a theme of very wide concern amongst island biota in which endemic flora may have evolved pollination mechanisms with specialist native vectors that may be outnumbered and outcompeted by newer arrivals. An allied concern is that the introduced bees exploit flowers of native angiosperms, but do not pollinate them effectively. On many oceanic islands, a major outcome from human settlement has been loss and fragmentation of native vegetation, which becomes progressively confined to remote, topographically extreme, or upland areas that are not immediately suitable for urban or agricultural conversion. Alien pollinators and others invade these increasingly vulnerable areas/ecosystems, which have become the sole refuges for many endemic species that now occur in only small, circumscribed populations and areas. However, they are generally far richer and more abundant in areas disturbed and changed by people, often conditions under which invaders may become competitively superior (Borges et al. 2005) and, perhaps, leading to large populations enabling increased potential to disperse to more natural biotopes.

Predominance and functional dominance of alien insects in feeding guilds on remote islands is exemplified by the parasitoid wasp fauna in Hawai'ian ecosystems (Lockwood et al. 2001). Peck et al. (2008) used Malaise traps in native wet forests at three elevations to monitor parasitoid richness and abundance over 17 months. Aliens dominated the 18,996 individual Ichneumonoidea collected, comprising 44 of the 58 species. Most species were captured in very low numbers, with the bottom collective 34 species making up <1% of the total. Ichneumonidae was more diverse than Braconidae (69% of species, 67.5% of individuals), but a single alien braconid (*Meteorus laphygmae*) was the most abundant wasp, as 28.3% of the total catch. Collectively, alien species accounted for 75.9% of individuals. Their incidence was greatest on lowland areas, and declined from 98.8% there to 64% at the highest elevations sampled. Their impact on native Lepidoptera, the predominant host

group for the great majority of parasitoids obtained (many of them with broad host ranges within that order), appeared severe. As many earlier workers had noted, a broad host range was considered advantageous for species introduced during early biological control programmes on the archipelago. Their legacy has been strong implication in the reduction and extinctions of many native endemic hosts. Thus, *M. laphygmae* has been reported from hosts in six families of Lepidoptera, and whilst difficult to ascribe the dramatic losses of Hawai'ian Lepidoptera unambiguously to any single cause, increased parasitisation rates associated with proliferation of alien species have been widely considered the predominant single contributor (Gagné and Howarth 1985). Other factors involved include loss of native host plants, and predation by invasive ants and social wasps (notably *Vespula pensylvanica*).

Broad accusations that introduced biological control agents are a primary cause of endemic species losses in island environments may thus be tempered by demonstration that they are sometimes only a part of the processes involved. As one specific example, there is no doubt that the Hawai'ian species of *Omiodes* leaf-roller moths (Crambidae) have undergone considerable declines and local extirpations, with some species declared extinct, over the last century or so. Some species were targets for classical biological control by imported ichneumonoid wasps, with these agents moving to attack non-target species. King et al. (2010) deployed eggs and larvae of *Omiodes continualis* in field sites on Maui and Oahu and measured rates of parasitisation, in conjunction with extensive field surveys for wild larvae of this and four other *Omiodes* species, and including some of conservation concern. Some, indeed, had been believed to be extinct, included in considerations by Gagné and Howarth (1985) of alien agent impacts, but have since been rediscovered. Information accumulated by King et al. suggested a lesser role for introduced parasitoids, and impacts differing also on different islands. The species-specific and location-specific impacts revealed the need for impacts of invasive predators and habitat variability on native insects to be investigated in conjunction with those of alien parasitoids. Adventive parasitoids may be far more significant threats to native Hawai'ian insects than are deliberately introduced species. Investigation of the parasitoid spectrum of the endemic moth *Udea stellata* (Crambidae) revealed seven alien parasitoids, only two of which were deliberate introductions (Kaufman and Wright 2009). Examination of 'sentinel larvae' deployed in the field implied that simple disappearance (attributed to predation) was far higher (42.1%) than parasitoid (4.9%) mortality, but of the latter, 97% was due to adventive species. Without quantitative assessments of this kind, it is generally not clear whether, despite evidence of attack, introduced species contribute significantly to declines of native taxa. A complementary approach to parasitoid impacts, employing the wider perspective of impacts on food webs, involved plotting associations derived from the Lepidoptera species from 60 host plants in a remote forest site (Alakai, Kauai), where 83% of parasitoids recovered were introduced classical biological control agents, 14% were accidentally introduced species and only 3% were natives (Henneman and Memmot 2001). Simply assessing the diversity and impacts of alien parasitoids or predators as they exploit native biota is complex, and illustrated by further appraisal of the predators of the Alakai Lepidoptera (Sheppard et al.

2004). Predatory arthropods collected from different host plants were subjected to DNA analyses capable of detecting individual prey species in their gut contents. The proportion of alien predators was far lower (11%) than that for parasitoids (97%, above), but that even closely related species can be differentiated unambiguously by such investigations opens novel avenues for similar comparisons in the future.

Many workers, exemplified by Messing (2000), have considered the impacts of non-target effects on the conduct of biological control programmes (Chap. 6), emphasising the need to weigh these carefully in relation to the enormous benefits such programmes can bring. Messing suggested three intergrading categories of non-target effects to help display the range of putative problems, as (1) estimated risk of non-target impacts by a proposed natural enemy introduction so great that the project does not go ahead; (2) a perceived or potential non-target effect, perhaps based on casual observations or other non-quantitative information leads to abandonment of a project that might otherwise be beneficial – this category could include projects in which a real (but small) non-target impact blocks a potentially worthy programme; and (3) the apprehension mirroring what Messing called ‘a general fear of exotic organisms’, associated with strict regulatory controls that can preclude or severely deter the project through factors such as needs for more extensive and stringent screening and related slowing of obtaining the requisite permits to proceed. The second category broadly includes many of the most controversial examples, reflecting both lack of comprehensive evidence and the relative strengths of views advanced by different stakeholder groups. The approach resembles the philosophical stance sometimes advanced for biological control agents as being ‘guilty until proven innocent’ (Simberloff and Stiling 1996).

The third category effectively prevents introductions of any but the most intensively studied agents that are deemed ‘safe’, endorsing the views of Louda et al. (1998) that the best release strategy would be to use ‘the fewest and most effective agents with the lowest probability of non-target effects’. As Ehler (2000) commented, this assumes that such agents are actually available. It also displaces the previously widespread ‘lottery’ approach by which any likely agents were introduced and largely left to their own devices in the hope that one or more would succeed, and with little (if any) regard for non-target impacts or monitoring to detect these. That practice has led to much of the concern for conservation, from proliferation of generalised alien predators and parasitoids becoming widely distributed far from anthropogenic environments. However, Ehler discussed another potential problem – that the agents selected because of minimal non-target risk may not be the most effective natural enemies of the target pest, and might provide (at most) only moderate control. Occurrence of several such suboptimal species could lead to problems in establishing ‘better’ or additional agents later. Assessing candidate agents on their potential non-target effects might thus come at the expense of both short-term impacts on the target pest and chances of improving control in the future.

Entire groups of insects in some ecological groups have been lost from some islands, from a variety of causes but with alien species (including introduced biological control agents) often implicated as a major contributor. For Hawai’i, Cox

and Elmqvist (2000) noted that 52 reported endangered species of *Nesoprosopis* bees and 26 species of endemic moths are now extinct, severely impoverishing insect pollinator guilds to the detriment of native flora. Assessment of the impacts of individual alien species on individual native species, rather than more embracing statements of general losses from the invader, is often inferential - not least because the manipulative experiments needed to prove causative loss are usually impossible for most of the rare or threatened species over which such concerns arise. Thus, the major impacts of the invasive Argentine ant (*Linepithema humile*) on native ants and other arthropods are well-documented (for example, again in Hawai'i: Cole et al. 1992) but its impacts on individual threatened insect species are only rarely assessed. The same applies for many aliens regarded as aggressive generalist predators (p. 131).

The threatened Valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*, Cerambycidae) frequents riparian woodlands in California, where its sole host plant (Blue elderberry, *Sambucus mexicana*, Caprifoliaceae) grows. By sampling for the beetle (searching for current year emergence holes on plot samples of elderberries) and *L. humile* (bait traps and direct searching on elderberry plants), Huxel (2000) confirmed that the ant was spreading along permanent streams. His correlations suggested that links between habitat loss and fragmentation and the invasion of *L. humile* may increase risk to the beetle. Although the exact mechanism of ant impacts was unknown, it might include egg predation – but Huxel's model implied that long-term survival of *Desmocerus* might require control of the spread of Argentine ant.

Impacts on non-threatened species have been evaluated predominantly in agroecosystems, in which native 'natural enemies' of economically important pests may be active targets for conservation and increase as valued conservation biological control agents (Chap. 6). Alien ladybird beetles (Coccinellidae) in North America have been implicated in declines of native species, but confirmation has been hampered by the substantial natural variation in ladybird population size. Changes in the native ladybird community associated with potato crops in Maine over about 31 years implied that, before 1980, those communities were composed largely of native species. After this, the alien Palaearctic *Coccinella septempunctata* established permanently and progressively became dominant (Alyokhin and Sewell 2004). Two other aliens (*Harmonia axyridis*, *Propylea quatordecimpunctata*) became prominent in 1995 and 1996. Invasion of these aliens was followed by significant declines of the two major native species (*Coccinella transversoguttata*, *Hippodamia tredecimpunctata*) – but they persisted in low numbers, so that the net outcome has been increased species richness within the crop.

These predatory beetles illustrate that impacts of aliens can be appraised at the level of feeding guild or other functional group, as a possible guide to impacts on ecological functions, and involving comparisons of how effects of invasive and native species may differ. Extending from the commonly documented scenario of native ant species being displaced by invasive alien ants (Chap. 6), Ness and Bronstein (2004) noted that mutualisms involving ants (such as myrmecochory) may be disrupted. Their review compared impacts of seven key invasive species

Table 2.3 The seven key species of invasive ants discussed by Ness and Bronstein (2004), indicating the extent of their invasions at that time

Species	Preferred regime	Introduced (native) range
<i>Anoplolepis longipes</i>	Tropical	Africa, Asia, Australia, Caribbean (Africa, Asia)
<i>Linepithema humile</i>	Mediterranean	Africa, Asia, Australia, Mediterranean, North America (South America)
<i>Paratrechina longicornis</i>	Tropical	North America (Africa)
<i>Pheidole megacephala</i>	Tropical	Australia, North America, Caribbean, Mediterranean, South America (Africa)
<i>Solenopsis geminata</i>	Tropical, semitropical	Africa, Asia, Australia, Caribbean, (North America, South America, Central America)
<i>Solenopsis invicta</i>	Mild temperate, semitropical	Caribbean, North America, Australia (South America)
<i>Wasmannia auropunctata</i>	Wet tropical	Africa, Caribbean, North America (Central America, South America)

(Table 2.3) which were nominated as the most widespread and invasive ants (Holway et al. 2002). All were likely to eliminate native ants from invaded areas and, in many cases, to mediate their interactions with prospective mutualists.

Any key resource that benefits an invasive insect sufficiently to facilitate its spread and increase population growth may also correlate with increased impacts on native species. Carbohydrate resources for invasive ants are a well-studied context, whether those nutrients are from scale insects (p. 76) or from extrafloral nectary-bearing plants, as described for *Anoplolepis gracilipes* on Samoa (Savage et al. 2009), where high abundances of crazy ants at sites with abundant extrafloral nectary-bearing plants were associated with low richness of native ants visiting those plants. Outcomes of invasive species may include some form of facilitation for the wellbeing of native species, but the variety of such impacts and their likely occurrence has often been overlooked. Most commonly involving habitat modifications by the invading taxa, three functional categories have been distinguished amongst the varied mechanisms involved (Rodriguez 2006). These conceptual models (Fig. 2.2) are based on the changing population sizes of the interacting species over time, and are (1) novel facilitation, when the invader constitutes a new exploitable resource for the native species; (2) substitutive facilitation, when an invasive facilitator functionally replaces a native facilitating species because of superior competitive ability; and (3) indirect facilitation, that occurs if a native predator or competitor is reduced by the invasive species, so leading to increase of the native prey or native competitively inferior species.

Functional impacts are illustrated repeatedly by studies of the roles of alien pollinating insects, which may be key factors in conservation of endangered native plants whose native pollinators have succumbed to local environmental changes. The North American Western prairie fringed orchid (*Platanthera praeclara*) has become scarce due to destruction of tallgrass prairie, and is pollinated by hawkmoths

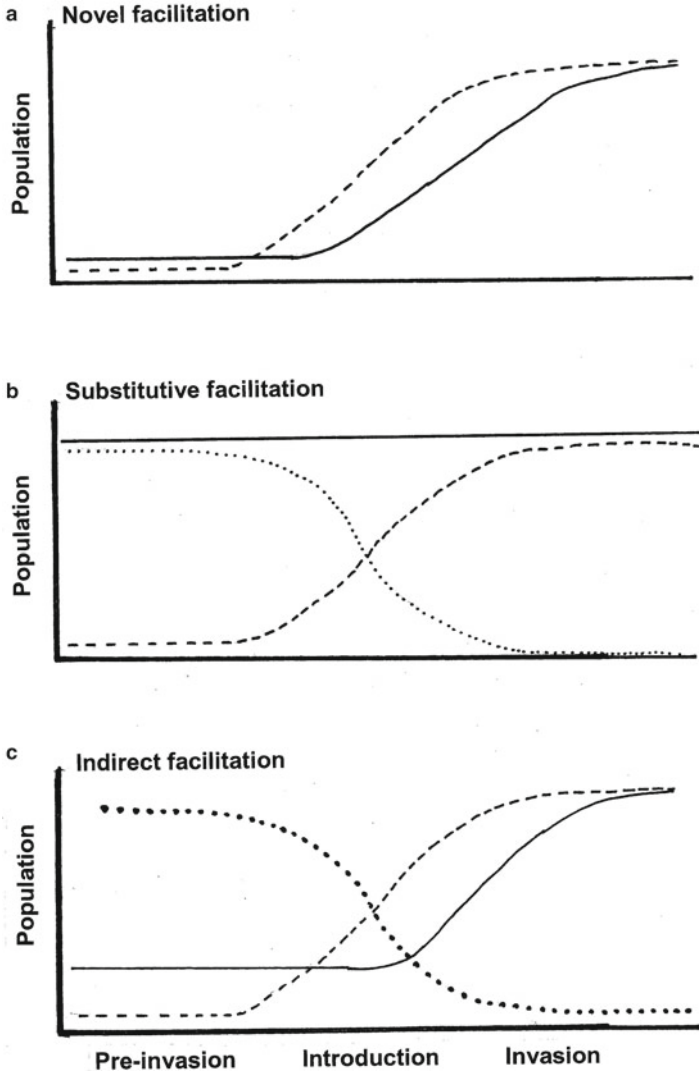


Fig. 2.2 Three conceptual models of different scenarios that define why invasive species can facilitate native species, shown along the timeline of successive invasion events. The scenarios are (a) novel facilitation, when no native facilitator existed; (b) substitutive facilitation, when an invader functionally replaces a native facilitator; and (c) indirect facilitation, occurring when reduction of a predator or dominant competitor indirectly results in facilitation of a native (Rodríguez 2006)

(dashed line: invasive facilitator, solid line: native facilitated, small-dotted line: native facilitator, large-dotted line: predator/competitor)

(Sphingidae) (Fox et al. 1997). Only three metapopulations of the orchid remain, and several species of Sphingidae have been found carrying its pollinia. One of five such species recorded in observations of visitation rates to flowers over 4 years is the introduced European Spurge hawk (*Hyles euphorbiae*), introduced from the late

1960s as a potential control agent for Leafy spurge (*Euphorbia escula*). Fox et al. believed that the orchid could only be conserved effectively if pollinator populations are maintained, so that larval food plants and additional nectar sources are needed, and also that *H. euphorbiae* was an important pollinator. It was the only sphingid found in all of the 9 years of their extended study, and the only bivoltine species – so that adult moths are present across the entire flowering period of the orchid. It is important also to conserve the native pollinators – not least because successful biological control of the spurge may eventually curtail presence of *H. euphorbiae* (Fox et al. 1997).

The endemic South American bumblebee *Bombus dahlbomii*, a generalist pollinator, was considered to be a keystone species in temperate forest environments in the south of the continent where many native flora rely on it for pollination. With progressive introductions of alien bees for manipulated pollination based on, initially, *Apis mellifera*, followed by *Bombus ruderatus* (from 1984 for red clover pollination) and *B. terrestris* (from 1998, for glasshouse tomatoes), all these bees expanded their range. *B. dahlbomii* contracted in distribution and its populations declined substantially (Sanguinetti and Singer 2014). The three aliens have become the major pollinating agents of two notable sympatric orchids (*Chlorea virescens*, *Brachystele unilateralis*). *B. dahlbomii* is rarely seen in the areas where the orchids grow, and accounts for less than 10 % of bee visits to flowers. Sanguinetti and Singer believed that the high reproductive success of the orchids was linked directly with abundance of alien bees, with *B. dahlbomii* no longer effective. Whilst *a priori* the introduction of alien bumblebees might have been anticipated as highly detrimental to these orchids, reflecting losses of *B. dahlbomii*, it now seems clear that they functionally substituted for, and enhanced, the role of that endemic species. The wider effects of *B. dahlbomii* declines as a key mutualist pollinator of *Alstroemeria aurea* (Alstroemeraceae) are still somewhat unclear. Aizen et al. (2008) noted its displacement by *B. ruderatus*, a less effective pollinator because of its small size, and that this might select for smaller flowers. Maintenance of native pollinator mutualisms poses intricate ecological problems as they become invaded by alien species, and native pollinators become vulnerable. Competitive interactions between native and alien bees have attracted considerable attention. Studies on the introduced *Apis mellifera* and its interactions with the native *Bombus occidentalis* in California (Thomson 2004, 2006) demonstrated the needs for experimental investigations, rather than solely observational information, to elucidate the invader's impacts. *B. occidentalis* colonies near introduced *A. mellifera* hives showed trends such as lower ratio of foraging trips for pollen relative to nectar, and of both male and female reproductive success. Those trends implied that this important native pollinator was indeed functionally suppressed when forced into competition with introduced honeybees, and such impacts might have further consequences for native flora if *A. mellifera* is a less efficient pollinator.

The invasive social wasp *Vespula pensylvanica* (p. 22) is both a predator and a nectar feeder in Hawai'i, adding considerable complex and unanticipated malfunctions in invaded communities. These include changing intricate plant-pollinator mutualisms. Experimental reduction of wasp populations in large plots containing

the insect-pollinated endemic tree *Metrosideros polymorpha* led to significantly increased visitation rates by bee pollinators (Hanna et al. 2013). As a further complexity, the alien *Apis mellifera*, itself preyed upon strongly by *Vespula*, also became a significant pollinator of *Metrosideros* once wasps had been removed. This case thereby involved management of one key invasive species, which had caused decreased fruit production of an endemic tree by disrupting pollination, enabling a different introduced species to facilitate that mutualism and increase fruit production. This positive attribute for *A. mellifera* (introduced to the archipelago in 1857) must be weighed in the context of its broader community impacts, considered widely to be harmful.

A somewhat different view of a social wasp's impact on native species, comparing arthropods on wasp-infested control plots and sites on which *Vespula germanica* had been substantially reduced by toxic baits in Patagonia (Sackmann et al. 2008), suggested that the wasp had very little effect – a considerable contrast to the dramatic restructuring of natural communities by the same species in New Zealand (Beggs 2001, p. 142). In Patagonia, no impact on abundance, richness or assemblage composition was detected, with the differences between poisoned and control sites attributed to the site differences present before wasps were reduced and evident at that earlier stage. Sackmann et al. suggested three possible explanations for lack of impact detected, each a relevant consideration in parallel studies. These were (1) the time span of wasp poisoning – the 3 years of bait deployments might not have been sufficient to allow the native community to respond; this was considered unlikely; (2) the level of wasp reduction (averaging 50%) may not have been sufficient to reduce the overall impact on the native community, as trials elsewhere have indicated that wasp reductions of the order of 80–90% might be necessary to protect vulnerable species; and (3) that overall, wasp abundance was quite low, again a contrast to the New Zealand surveys, so that any impact would be insufficient for detection. This last consideration links with substantial variations in wasp abundance in different years. Generalisations on the impacts of such invasive species may need verification in the context of the individual community structure.

Alien vespid wasps, as above, illustrate a considerable variety of ecological impacts, some of which may become of particular sectoral significance. *Vespa velutina* (p. 40) was the first predatory alien vespid introduced accidentally from Asia to Europe. The hornet preys on honeybees and contributes to loss of *A. mellifera* colonies, providing an additional stress on declining pollinator services (Monceau et al. 2014). The extent of this predation is not yet clear, but both hive destruction and hive weakening occur. Much of the current control of *V. velutina*, by nest destruction, is undertaken by apiculturists, and *V. velutina* is a declared noxious pest species in France, as a 'class 2 health hazard'. Of direct conservation concern, in France the hornet may also interfere with the European hornet, *Vespa crabro*, which is a protected species over much of its range. However, some reports indicate increased *V. crabro* predation on honeybees since *V. velutina* arrived – possibly benefiting from the reduced fitness and defensive capability of colonies resulting from the latter species' attack facilitating prey accessibility.

The commonly designated polarisation of alien species' impacts as either 'good' or 'bad' is often an oversimplification (Simberloff et al. 2012, 2013), with many such allocations subjective or depending on the point-of-view of particular interest groups. Public perception may view Australian *Eucalyptus* elsewhere as valuable shade, ornamental or timber trees, for example, or as invasive weeds that harm native taxa. The European Gypsy moth (*Lymantria dispar*) is more clearly a forestry pest, capable of inflicting large scale ecological changes in North America. It was formerly common in Britain, but became extinct there early in the twentieth century, since when it was sought (as a presumed occasional migrant) avidly by collectors. Small resident colonies now occur in southern England, presumed to originate from accidental transport of eggs.

Assessing impacts of any invasive alien species involves the duality of ecological and socioeconomic effects. These are often closely correlated, but terrestrial invertebrates commonly create greater concern for economic than for ecological effects (Vila et al. 2009). Of the total 2481 alien terrestrial invertebrates in Europe, based on the DAISIE database, 342 (13.8%) had ecological impacts, but 601 (24.2%) economic impacts – but Vila et al. also noted that this discrepancy may be related to the economic impacts being more easily perceived. Nevertheless, all four major groups of ecosystem services (namely supporting, provisioning, regulatory and cultural) are affected, together with impacts on human wellbeing. Ecological impacts, critical considerations for conservation, are indeed often very difficult to quantify or, even, detect. Many of the concerns arising from entry of species into new environments focus on the wellbeing of native insects and other biota, and are the major topics of the following chapters.

References

- Aizen MA, Morales CL, Morales JM (2008) Invasive mutualists erode native pollination webs. *PLoS Biol* 6(2):e31; 396–403
- Alyokhin A, Sewell G (2004) Changes in a lady beetle community following the establishment of three alien species. *Biol Invasions* 6:463–481
- Beggs JR (2001) The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biol Conserv* 99:17–28
- Borges PAV, Aguiar C, Amarel J, Amorin IR, Andre G (and nine other authors) (2005) Ranking protected areas in the Azores using standardized sampling of soil epigeal arthropods. *Biodiv Conserv* 14:2029–2060
- Cole FR, Medeiros AC, Loope LL, Zuehlke WW (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73:1313–1322
- Cox PA, Elmqvist T (2000) Pollinator extinction in the Pacific islands. *Conserv Biol* 14:1237–1239
- Ehler LE (2000) Critical issues related to nontarget effects in classical biological control of insects. In: Follett PA, Duan JJ (eds) *Nontarget effects of biological control*. Kluwer, Dordrecht, pp 3–13
- Fox CW, Nilsson JA, Mousseau TA (1997) The ecology of diet expansion in a seed-feeding beetle: pre-existing variation, rapid adaptation and maternal effects? *Evol Ecol* 11:183–194

- Gagné WC, Howarth FG (1985) Conservation status of Hawaiian endemic Lepidoptera. Proc 3rd Congress of European Lepidopterists, Cambridge, 1982:74–85
- Goulson D (2003) Effects of introduced bees on native ecosystems. *Annu Rev Ecol Evol Syst* 34:1–26
- Groom SVC, Ngo HT, Rehan SM, Skepton P, Stevens MI, Schwarz MP (2014) Multiple recent introductions of apid bees into Pacific archipelagos signify potentially large consequences for both agriculture and indigenous ecosystems. *Biol Invasions* 16:2293–2302
- Hanna C, Foote D, Kremen C (2013) Invasive species management restores a plant-pollinator mutualism in Hawaii. *J Appl Ecol* 50:147–155
- Henneman ML, Memmott J (2001) Infiltration of a Hawaiian community by introduced biological control agents. *Science* 293:1314–1316
- Holway DA, Suarez AV, Tsutsui ND, Case TD (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–133
- Huxel GR (2000) The effect of the Argentine ant on the threatened valley elderberry longhorn beetle. *Biol Invasions* 2:81–85
- Ingram KK, Bernadello G, Cover S, Wilson EO (2006) The ants of the Juan Fernandez Islands: genesis of an invasive fauna. *Biol Invasions* 8:383–387
- Kaufman LY, Wright MG (2009) The impact of exotic parasitoids on populations of a native Hawaiian moth assessed using life table studies. *Oecologia* 159:295–304
- King CBA, Haines WP, Rubinoff D (2010) Impacts of invasive parasitoids on declining endemic Hawaiian leafroller moths (*Omiodes*: Crambidae) vary among sites and species. *J Appl Ecol* 47:29–308
- Lockwood JA, Howarth FG, Purcell MF (eds) (2001) Balancing nature: assessing the impact of importing non-native biological control agents (an international perspective). Entomological Society of America, Lanham
- Lopez-Vaamonde C, Agassiz D, Augustin S, De Prins J, De Prins W, Gomboc S (and 18 other authors) (2010) Lepidoptera. *BioRisk* 4:603–668
- Louda SM, Kendall D, Connor J, Simberloff D (1998) Ecological effects of an insect introduced for the biological control of weeds. *Science* 277:1088–1090
- Messing RH (2000) The impacts of nontarget concerns on the practice of biological control. In: Follett PA, Duan JJ (eds) Nontarget effects of biological control. Kluwer, Dordrecht, pp 45–55
- Monceau K, Bonnard O, Thiery D (2014) *Vespa velutina*: a new invasive predator of honeybees in Europe. *J Pest Sci* 87:1–16
- Ness JH, Bronstein JL (2004) The effects of invasive ants on prospective ant mutualists. *Biol Invasions* 6:445–461
- Peck RW, Banko PC, Schwarzfeld M, Euaparadorn M, Brinck KW (2008) Alien dominance of the parasitoid wasp community along an elevational gradient on Hawai'i Island. *Biol Invasions* 10:1441–1455
- Pimentel D (ed) (2011) Biological invasions. Economic and environmental costs of alien plant, animal and microbe species, 2nd edn. CRC Press, Boca Raton
- Pimentel D, Zuniga T, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273–288
- Pysek P, Richardson DM, Pergl J, Jatosik V, Sixtova Z, Weber E (2009) Geographical and taxonomic biases in invasion ecology. *Trends Ecol Evol* 23:237–244
- Quacchia A, Ferracini C, Bonelli S, Balleto E, Alma A (2008) Can the Geranium Bronze, *Cacyreus marshalli*, become a threat for European biodiversity? *Biodiv Conserv* 17:1429–1437
- Rasplus J-Y, Villemant C, Paiva MR, Delvare G, Roques A (2010) Hymenoptera, Chapter 12. *BioRisk* 4:669–776
- Rodríguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol Invasions* 8:927–939
- Sackmann P, Farji-Brener A, Corley J (2008) The impact of an exotic social wasp (*Vespula germanica*) on the native arthropod community of North-West Patagonia, Argentina: an experimental study. *Ecol Entomol* 33:213–224

- Sanguinetti A, Singer RB (2014) Invasive bees promote high reproductive success in Andean orchids. *Biol Conserv* 175:10–20
- Savage AM, Rudgers JA, Whitney KD (2009) Elevated dominance of extrafloral nectary-bearing plants is associated with increased abundances of an invasive ant and reduced native ant richness. *Divers Distrib* 15:751–761
- Sheppard SK, Henneman ML, Memmott J, Symondson WOC (2004) Infiltration by alien predators into invertebrate food webs in Hawaii; a molecular approach. *Mol Ecol* 13:2077–2088
- Simberloff D, Stiling P (1996) How risky is biological control? *Ecology* 77:1965–1974
- Simberloff D, Souza L, Munez MA, Barrios-Garcia MN, Bun W (2012) The natives are restless, but not often, and mostly when disturbed. *Ecology* 93:598–607
- Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA (and nine other authors) (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66
- Thomson D (2004) Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85:458–470
- Thomson D (2006) Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–418
- Vila M, Basnou C, Pysek P, Josefsson M, Genovesi P (and six other named authors and 'DAISIE partners') (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Front Ecol Environ* 8:135–144
- Ward DF, Edney-Browne E (2015) Poles apart: comparing trends of alien Hymenoptera in New Zealand with Europe (DAISIE). *PLoS One* 10(7):e0132264
- Yamanaka T, Morimoto N, Nishida GM, Kiritani K, Moriya S, Liebhold AM (2015) Comparison of insect invasions in North America, Japan and their islands. *Biol Invasions* 17:3049–3061