

# Chapter 4

## The Ecological and Evolutionary Consequences of Alien Invasive Species

### 4.1 Introduction: New Associations and New Impacts

Invasive species have almost innumerable potential interactions with native biodiversity, and these include potential to reduce local distinctiveness of biota at three main levels. Of these, the taxonomic level of change is that most frequently noted, as local endemic species decline or are lost and replaced by invasive species. They are followed by functional changes flowing from changed assemblages and novel interactions. Least heeded, but likely to be widespread, genetic distinctiveness and impoverishment must also be included. For understanding the last theme, and in contexts such as seeking natural enemies for biological control (p. 135), tracing origins of invasive stocks by genetic characterisation is increasingly relevant, with a comment that ‘novel molecular techniques are under-utilised in studies of invertebrate pest invasions’ (Cesari et al. 2015) exemplified by analyses of the Brown marmorated stink bug (*Halyomorpha halys*, Pentatomidae). Those investigated showed that two different populations were present in Europe, and that recent invasions to Italy occurred through two different pathways.

Rapid evolutionary changes are common amongst invasive species – for plants, Buswell et al. (2011) discussed the widespread changes in morphological features that can occur within relatively short times after introductions. More generally, Whitney and Gabler (2008) noted contexts of rapid adaptation to new environments, evolution within new communities, and hybridisation. Such changes are considered only relatively rarely: only 3 of the 29 releases they reviewed included any consideration of adaptive potential of the invaders, and none acknowledged that evolution in the recipient communities might alter impacts or success of an invader. Greater consideration of these effects in predicting outcomes seemed necessary. More commonly, schemes for predicting invasiveness include four major categories of criteria as bases for formal modelling or devising some form of ‘index’ that guides assessment of risk. These categories (summarised by Whitney and Gabler) are (1) the biological features of the species involved; (2) its distribution and any history of

pest status in other places, sometimes also with consideration of trends among close relatives; (3) climate matching and considering other abiotic conditions of the receiving environment; and (4) potential ecological and economic impacts. Evolutionary diversification resulting from invasive species may offset or counter losses to biodiversity attributed to them (Vellend et al. 2007). The initial stage is the almost inevitable reduction of genetic diversity in small founder populations relative to that in the native source population, as the basis for adaptive responses to the novel environment. Three main mechanisms for subsequent diversification were distinguished (Vellend et al. 2007), as (1) bottlenecks and genetic drift in the new population might lead to divergence from the native range populations; (2) directional selection from the novel environment might have the same result; and (3) if the new environmental conditions are sufficiently varied, disruptive selection might lead to diversification there. In parallel, alien species may promote diversification among native species, a process to which at least two contexts contribute, as (1) invaders might impose disruptive selection within local populations of native insects, and (2) only some populations of the native species may be affected, so genetic differentiation between affected and unaffected populations may occur. The shifts of native insect herbivores onto novel alien host plants (p. 109) are the most frequently reported examples, and are sometimes obvious scenarios for evolutionary diversifications. Occasionally, such shifts may be associated with hybridisation and speciation – as in the *Rhagoletis* fruit flies (Tephritidae) discussed by Schwarz et al. (2005), and associated with host shifts to an alien honeysuckle (*Lonicera*). Two native flies (*Rhagoletis zephyria*, *R. mendax*) formerly specialising on different host plants were thus brought together in a situation that enabled hybrid speciation between them. The closely related parental species belong to the *R. pomonella* complex in the north-eastern United States, and the invasive *Lonicera* spp. are originally from Asia and have been introduced over the last 250 years. This case exemplified how invasive weeds may influence evolution of native fauna, and the difficulty of detecting hybridisation amongst such morphologically cryptic herbivore species may mask the frequency with which it occurs. It was detected in this example largely through the availability of extensive genetic information on this economically important species group, and the generation of new phenotypes might lead to increasing the range of host plants that can be exploited.

Occasional cases of hybridisation between alien and closely related native species occur. The European Winter moth (*Operophtera brumata*, Geometridae) in the north eastern United States can hybridise with the native *O. bruceata* (Elkinton et al. 2014), and may have (as yet unexplored) implications for the spread of the invader. Hybridisation even between distinct subspecies can also be a concern. The international trade in bumblebees for pollination (p. 63) includes both species and subspecies, the latter of species that may be native to the receiving environment and so susceptible to hybridisation and alteration of the native gene pool. Hybridisation of any deliberately introduced non-native species with closely related native taxa is a conservation concern, and any such cases in a context of classical biological control (p. 135) might also affect the control outcome and change impacts on local species. Such cases have been investigated sporadically under laboratory condi-

tions, but only more rarely in field environments. Two reported examples involving introduced predatory insects are (1) laboratory crosses between the green lacewing *Chrysoperla carnea* (Chrysopidae, native to Europe) and the native Japanese *C. nipponensis* (Naka et al. 2005, 2006), for which ramifications were expected to be low because hybrid fertility was low and the different courtship songs of the parental species rendered mixed mating unlikely to be common; and (2) hybridisation between two predatory beetles (Derodontidae) feeding on woolly aphid (Adelgidae). One of these (*Laricobius nigrinus*) is native to the western United States, but was introduced to the eastern states as an aphid predator, and where it encountered the eastern *L. rubidus* (Havill et al. 2012). The relative fitness of the ensuing hybrids, which are fertile, remains to be clarified, and Havill et al. recommended further study to ascertain this and likely impacts on the biological control programme against Hemlock woolly aphid, *Adelges tsugae*. They recommended that the potential for introduced biological control agents to hybridise with any close relatives in the area of introduction should be evaluated, and the consequences considered. Two parallel examples involving parasitoids were also noted by Havill et al. (2012). One comprised only laboratory crossings, between two wasp parasitoids of the Diamondback moth (*Plutella xylostella*, Plutellidae), namely the alien *Diadegma semiclausum* (Ichneumonidae) hybridising with the native Japanese *D. fenestrata* (Davies et al. 2009), and for which field observations were not reported. The second example included both laboratory and field hybridisation between the Chinese *Torymus sinensis* (Torymidae) and the native *T. beneficus* in Japan (Yara et al. 2010) as natural enemies of the Asian Chestnut gall wasp, *Dryocosmus kuriphilus* (Cynipidae). Simply that a few such cases have been detected and reported, and represent different trophic groups, suggests that alien-native hybridisation might be a more frequent occurrence.

Fears over negative impacts from competition and the possibility of these being enhanced through hybridisation are well-documented for alien subspecies of *Bombus terrestris*, in particular, as the most thoroughly studied, widely distributed and traded bumblebee species. Ings et al. (2006) wrote that ‘a closer examination of the dangers posed by importation of non-native subspecies of bumblebees is urgently required’. Their concerns flowed from comparison of the biology of native and commercially imported subspecies of *B. terrestris* in the United Kingdom, where the introduced *B. t. dalmatinus* and the native *B. t. audax*, very similar in appearance, both occur in the wild. Comparison revealed that *B. t. dalmatinus* had considerably higher foraging rates and reproductive outputs, leading to larger colony size and likelihood of out-competing the native bee. Although, as elsewhere, the imported bees were intended mainly for glasshouse crop pollination in enclosed environments, it is almost inevitable that ‘escapes’ occur, here of potentially hybridising subspecies. Ings et al. feared that feral commercial bees and/or their hybrids may displace native *B. t. audax* and other locally threatened bumblebees.

The essence of many novel associations arising from alien incursions is evolutionary novelty in bringing together taxa that have never co-evolved or competed. Mutual adaptation may not occur, reflect newly initiated compatibility, or gradually develop over some extended period, with many of the mechanisms determining the

outcomes of any new juxtaposition still not well understood (Verhoeven et al. 2009). The roles of novel natural enemies, for example, may help to explain the success of some invaders and the failure of others – with the overall effect of the frequently-cited ‘Enemy Release’ principle (p. 117) being a balance between losing ancestral enemies and gaining new ones after invasion. The latter can have complex consequences, as those predators or parasites/parasitoids may be diverted from their more usual targets. Aquatic water boatman bugs (Corixidae) are parasitised by larvae of ectoparasitic water mites, whose incidence in Spain was compared on two native host species of *Sigara* and the North American invasive bug *Trichocorixa verticalis verticalis* (Sanchez et al. 2015). Distribution of the two mite species involved was related to water salinity levels, and part of the success of *T. v. verticalis* was attributed to its presence in saline waterbodies where mites were absent. In lower salinity level wetlands, all three hosts were affected - but both parasite presence and abundance was higher on the invasive host than on either native bug, despite the latter being larger than *Trichocorixa*. The latter’s susceptibility to the mites might help to explain its low abundance there. One of the mites (*Eylais infundibulifera*) occurred as one or two individuals on native hosts but up to seven on *Trichocorixa*, and the other (*Hydrachna skorikowi*) was usually present as single individuals on native bugs and up to six on the invasive host. Such different infestation and susceptibility rates may restrict invasion success of *Trichocorixa* in low salinity wetlands, and concentrating parasites on the alien host might reduce their pressures on the native bugs. Parasite incidences on a wide range of (mostly non-insect) hosts commonly imply that parasites encountering novel hosts may show impacts. Whilst this is most commonly observed for alien parasites, some of which are non-pathogenic in their natural range but cause mass mortality in new hosts, as the ‘naïve host syndrome’ (Mastitsky et al. 2010), the converse may also occur, as the above case shows.

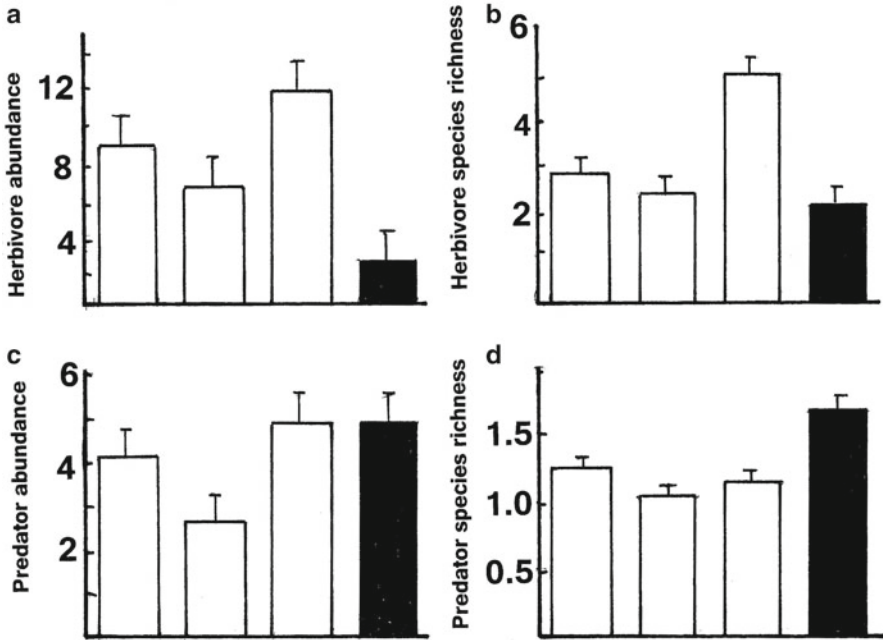
## 4.2 Novel Trophic Associations

As discussed for alien plants by Verhoeven et al. the toxic (defensive) chemical compounds they produce may differ from those of native plants, so allowing aliens to invade whilst less hampered by herbivore pressures. A somewhat different viewpoint (after Parker et al. 2006) is that an alien plant may be equally susceptible to native generalist herbivores that have not been selected to resist – so that the evolutionary novelty then causes the alien plant to fail to establish or spread. High levels of plant endemism might help to confer resistance to invasive herbivores, as explored for New Zealand by Brockerhoff et al. (2010). Many native New Zealand plants are phylogenetically distinct from the normal host plants of many specialised invaders, whilst more generalised taxa may overcome this evolutionary barrier. This constraint may be related to only relatively few invasive herbivore insects having invaded New Zealand’s natural ecosystems. Species from other former Gondwanan land components with historically shared plant families and genera may be more likely to invade than those from the more evolutionarily distant northern

hemisphere. However, and despite feeding trials with a number of polyphagous herbivores indicating that they can indeed exploit a wide range of native plants, the concept has important implications, these becoming more so if specialised natural enemies of the excluded herbivores are also affected. Many of New Zealand's indigenous trees were less palatable to larvae of the alien Gypsy moth (*Lymantria dispar*, Lymantriidae [or Erebidae: Lymantriinae]) (Matsuki et al. 2001), representing a moth (sub)family naturally absent from the New Zealand fauna, so that even markedly polyphagous defoliators may be constrained by unfamiliar available host plants. The idea led to the 'Island Resource Allocation' hypothesis (IRA: Kay and Wratten 2006), implying that plants in specialised restricted habitats and which do not support complex food webs in comparison to continental species must limit herbivore impacts through plant defences, reflecting the lack of potential for 'top-down' regulation by predators and parasitoids. The latter option increases with more complex food webs. Brockerhoff et al. noted the wider tendency amongst New Zealand indigenous plants to acquire inherent defences against invertebrate herbivores.

Direct interactions between invasive plants and insect herbivores have dominated discussions on mechanisms of change, but wider recognition of the roles of the natural enemies of the herbivores has been advocated increasingly (Harvey et al. 2010). These, by feeding on herbivores, obtain their nutrition indirectly from the plants, with evidence that impacts of plant quality can extend to this third trophic level, or even higher. The twin effects, paralleling those applicable directly to herbivores, are (1) the direct impacts of defensive plant chemicals on the development of predators or parasitoids, and (2) an extension of herbivore performance on the plant, which may induce a parallel change in performance of natural enemies. Several studies noted by Harvey et al. suggested that alien plants that contain novel chemical compounds may generate effects felt one or more levels higher up the food chain. The conservation consequences include that native herbivores may be threatened by alien plants through either 'bottom-up' (plant) or 'top-down' (natural enemy) influences, or by a combination of these. The patterns are exemplified by the *Alliaria-Pieris-Cotesia* association discussed on p. 81, with modelling exercises implying that loss of native host plants (through loss of forest understorey and invasion by Garlic mustard) are the most significant factors that drive decline of *P. napi oleracea*. Whilst parasitisation by *Cotesia glomerata* may interact and reduce *Pieris* populations more rapidly, this is insufficient to alone cause local extinctions (Keeler et al. 2006): 'bottom-up' influences here drive the butterfly's decline.

Following initial effective release from herbivory by invading plants, herbivore species can accumulate to reach diversity levels comparable to those on native plant species in the invaded area – so that an initial facilitating situation of 'freedom from attack' gives way to greater 'equalisation' between invasive and native plant interactions. Siemann et al. (2006) referred to this process as 'naturalisation', and exemplified it by study of herbivory levels on the Chinese tallow tree (*Triadica sebifera* [or *Sapium sebiferum*], Euphorbiaceae). Seedlings were planted in common garden prairie-like vegetation in four of the United States, forming a chronosequence along a gradient of time since the tree was first introduced to each and so potentially



**Fig. 4.1** Abundance and species richness of arthropod herbivores and predators, shown as average numbers of individuals and species collected/plot/sampling event, from four focal tree species in Texas: three native tree species (open bars, from left to right Silver maple [*Acer saccharinum*], Sycamore [*Platanus occidentalis*], Sweetgum [*Liquidambar styraciflua*]) are compared with the invasive Chinese tallow tree, *Triadica sebifera*, black bars (Hartley et al. 2010)

capturing herbivores from local species pools that differed in their period of association with this host – from approximately 230 years (Georgia), or 140 years (Florida) to about 100 years (Louisiana, Texas). Herbivory was highest, and tree performance (seedling height) poorest where the tree had been present for longer, and this example implied that slow accumulation of herbivores may aid naturalisation over time. Many comparisons of insect fauna on alien versus native plants have not incorporated this axis of ‘time since establishment’ but have still emphasised herbivores – although community composition reflects also the incidence of higher trophic levels. In Texas, species richness and overall arthropod abundance were similar on the invasive tallow tree and three native trees, but tallow tree communities had relatively lower herbivore abundances and relatively more predator species (Hartley et al. 2010). Whilst each tree species differed in richness of trophic groups, the high predator richness on tallow (Fig. 4.1) accompanied the lowest herbivore abundance of the tree species sampled – with implication that predator levels might be quite high, as a trend that might increase loss of arthropod diversity when such trees are planted as monocultures that replace native taxa.

Novel species interactions between alien and native taxa develop from the basis of ‘compatibility’, and generally cannot directly reflect any prolonged

**Table 4.1** Performance of the endemic *Lycaena salustius* on different host plants in New Zealand (Gillespie and Wratten 2011)

Criterion	Optimal plant species
Relative growth rate	<i>Muehlenbeckia astonii</i>
Larval duration	<i>Rumex flexuosus</i>
Pupal mass	<i>M. astonii</i>
Adult mass	<i>Fagopyron esculentum</i> <sup>b</sup>
Eggs on emergence <sup>a</sup>	<i>F. esculentum</i> <sup>b</sup>
Survival	<i>Muehlenbeckia australis</i>

<sup>a</sup>No significant effect of plant species

<sup>b</sup>Alien plant host

co-evolutionary history other than that which could be implied from phylogenetic relatedness, a situation that has been termed ‘ecological fitting’ (Chupp and Battaglia 2014). The mechanism has been applied to explain the process whereby organisms colonise novel environments and/or form novel associations with other species as a consequence of the traits they possess at the time of encounter (Janzen 1985). It is thus an additional mechanism to the more commonly invoked themes of coevolution and in situ evolution in inducing, for example, novel host shifts by invasive insect herbivores (Agosta 2006). Its functional equivalence to longer term evolutionary relationships can sometimes furnish resilience to disturbance and even mask the losses of local species and their functional roles. In most studies on insect herbivore host selection, evolutionary ‘explanations’ of host shift or preferences almost always gain preference over ecological fitting, and are largely based on the principle that the female insect should choose to lay eggs on the host plant that gives greatest fitness to the offspring. The endemic New Zealand lycaenid butterfly *Lycaena salustius* studied by Gillespie and Wratten (2011) illustrated some of the variations that can occur in performance on endemic Polygonaceae and the introduced related *Fagopyrum esculentum*. The latter is favoured by viticulturists because it is a nectar source for insect parasitoids used in local biological control. In comparative field cage assays, *F. esculentum* was markedly preferred over endemic plant hosts for oviposition. However, as indicated in Table 4.1, optimal larval performance was not always mirrored in this female choice, leading to different inferences on the preference-performance relativity involving *F. esculentum*. Gillespie and Wratten suggested that ovipositing *L. salustius* females may thus apply a ‘risk-spreading’ strategy and that the native host plants (namely all *Muehlenbeckia* spp. including the rare, and preferred, *M. astonii*) should be considered when managing the butterfly’s habitat.

Novel interactions involving invasive species arise fundamentally by their planned or unplanned association with species with which they either have no previous co-evolutionary history, or with which they are now reunited in a new environment in which one has in part adapted to a new ecological context. The latter is the foundation of much classical biological control, in which an invasive plant or animal has thrived over time in part because of its freedom from the ‘natural enemies’

of its native environment: it has gained ‘enemy-free space’. It has thus been ‘released’ from native consumers, and deliberate introductions of biological control agents seek to re-impose that consumer pressure to reduce incidence of the alien target species. The central condition of enemy release is, clearly, that the invader is displaced from its usual natural enemies, and their negative impacts are removed. However, such presumptions do not investigate the accompanying key need – the extent to which those enemies actually affect the species in its native range. Prior et al. (2015) noted that if such enemies are ineffective or have little impact, any later ‘release’ has little meaning, and alternative explanations for invasion success are needed. By contrast, species that suffer strong natural enemy impacts in their native range have high potential for enemy release elsewhere. An augmentary approach, discussed by Gandhi and Herms (2010) suggested that amongst the advantages of enemy-free space for herbivores attacking native host plants, the lack of coevolutionary history also leaves the host plants without any specific defences against the invader(s), so that the success of the herbivores occurs also because of ‘defence-free space’. Invasion success, as apparently in some major alien insect forest pests in North America may flow from the novel hosts being more susceptible than co-evolved congeneric hosts in the insect’s native range. The roles of enemy-free space for herbivores have been studied only rarely in non-agricultural environments, but selection might be expected to benefit herbivores that can avoid their natural enemies in this way. Although not involving alien species, a series of trials on the Alaskan swallowtail butterfly (*Papilio machaon aliaska*, Papilionidae) feeding on an ancestral and two more recently acquired host plants is an instructive analogy (Murphy 2004). In the presence of predators, larval survival was higher on the novel hosts than on the ancestral host, but when predators were absent survival and growth rate were greater on the ancestral host. The host shift, presumed natural, was thus demonstrably linked with enemy-free space.

Absence of herbivores and pathogens can help invasive plants to establish, as documented for the Neotropical shrub *Clidemia hirta* (Melastomaceae) in Hawai’ian forests by DeWalt et al. (2004), when they compared planted *Clidemia* in its native Costa Rica with Hawai’i, with pesticides applied to some plants to eliminate herbivores. In Costa Rica, survival of *Clidemia* increased markedly on sites where the understorey was sprayed, and its absence in sites with strong forest understorey was attributed to pressures from natural enemies. Its expansion in Hawai’ian forests then apparently reflected release from comparable natural enemies there.

Prospective agents are usually sought initially from amongst candidates revealed in the target’s native range, particularly in places most similar climatically to the proposed introduction area. Success of an introduced biological control agent may itself depend on it not being exploited by native parasitoids and predators in its receiving environment. Maintaining enemy-free space in combination with lack of competition for hosts (in this context, pests) aids chances of success. A review of the native parasitoids attacking introduced biological control agents in New Zealand (Paynter et al. 2010) showed that native parasitoid richness there correlated well with parasitoid richness in the agent’s home areas, and that high parasitisation was associated with failures of agents to suppress pest weeds. Susceptible agents rapidly



accumulated parasitoids after release. New associations between native natural enemies and invasive hosts or prey imply features such as host-switching or facultative incidence – so that the enemies are essentially either ‘entirely new’ or reassociated as accompanying or independent arrivals to the areas that the host has invaded. Details of individual cases can sometime be elucidated by genetic studies, as undertaken for a eulophid parasitoid wasp, *Pnigalio mediterraneus*, in Europe (Gebiola et al. 2014). Such studies, involving patterns of haplotype incidence across different populations, implied that association of this parasitoid with the recently invasive Horse chestnut leafminer moth, *Cameraria ohridella* (Gracillariidae) arose from initial host-switching in the Balkans area, and later tracking of this host as it gradually spread through much of Europe.

### 4.3 Wider Ecological Impacts

Invasive predators or parasitoids affect not only the prey/hosts they encounter, but also interact with the existing natural enemies of those, so that competitive displacement may occur. This important effect is often overlooked as a conservation concern but, as Parry (2009) pointed out ‘for highly polyphagous species such as *Compsilura concinnata*, negative interactions could conceivably extend to hundreds of native parasitoids’. This tachinid fly is most notorious for widespread non-target impacts on native Lepidoptera in North America (p. 134).

However, relatively little is known of how introduced biological control agents influence local food webs based on the target species in the novel environment. For weed control agents, comparison of the structure of food webs in the native environment (where the agent and target co-occur naturally) with post-introduction structure in the new region might indicate agents of conservation risk more realistically than from monitoring the two central interacting species alone. Few such investigations have been made, but the approach is exemplified by study of two biological control agents from Australia (the pteromalid wasp *Trichilogaster acaciaelongifoliae* and the fungus *Uromycladium tepperianum*) introduced to South Africa as agents to combat invasive Australian acacias (Veldtman et al. 2011). *T. acaciaelongifoliae* is largely specific to *Acacia longifolia*, and has spread throughout the South African range of its host over more than two decades. It forms spherical galls on the developing flower buds, and these may be invaded by a range of other insects. Associations with other community members were assessed by collecting 3270 wasp galls on 218 host trees at 19 widely spaced localities in South Africa, and comparing the emerging insects with those from published Australian surveys. Similar appraisal with *Uromycladium* involved a smaller sample (232 galls) from the more restricted primary host, *Acacia saligna*. ‘Novel’ and ‘native’ food webs showed substantial similarities but, unsurprisingly across two such very different regional faunas, these were mostly at higher taxonomic levels, and genus or species overlap was very low. Veldtman et al. suggested that the approach of examining the numbers and kinds of food web linkages in the native area might have some promise for predicting the

establishment of parallel feeding links in a novel environment: even if newly formed links could be predicted only at the ‘order level’, that information might highlight potential associations or relationships with parasitoids and inquilines similar to those associated with an agent in the native range.

Some such introductions are not deliberate, but some fortuitous ‘accidental’ cases are both informative and successful. The potential complexity is illustrated well by a recent example in which a New Zealand native shrub (*Myoporum laetum*, Myoporaceae) has become an invasive woody weed in parts of coastal California, following its earlier desirability as an ornamental plant there. Recently it has undergone massive decline in California from attack by a *Myoporum*-specific thrips (*Klambothrips myopori*, Phlaeothripidae), which was described from Californian specimens and initially known only from California, and suspected to be invasive from New Zealand (but not known there) and found in 2011 in Tasmania. Over only about 5 years the thrips had killed about half the *M. laetum* in California, and most surviving plants were also being defoliated. This example, discussed fully by Sullivan (2014), therefore brings together an Australian insect feeding on an invasive New Zealand plant in the United States. Such very rapid suppression as occurred in this case, and mirrored in some deliberate introductions, has been referred to as the ‘New Associations Hypothesis’ (after Hokkanen and Pimentel 1989, p. 153). As above, the combination of a genus-specific enemy with a naïve host congener of the usual native host may lead to particularly strong host suppression with little or no lag time before enemy numbers build up.

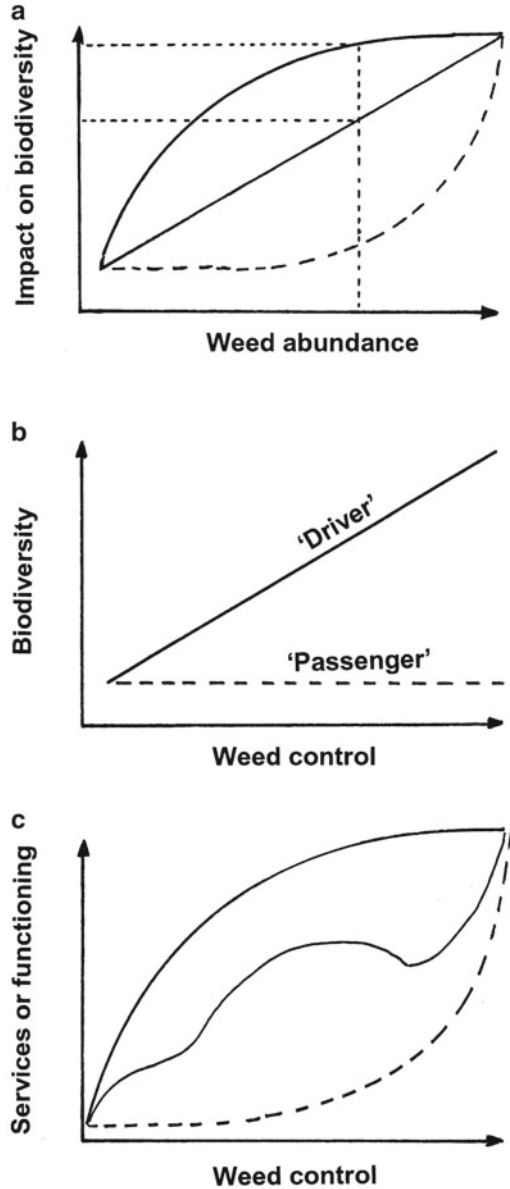
Native insects can be affected negatively by alien plant invasions, both because of the aliens outcompeting natives – reducing insect food resources – and changing environmental features rendering areas unsuitable for the native food plants. Such changes in floristic structure may induce wider effects. Impacts of the introduced Goldenrod (*Solidago* sp., Asteraceae) on ants in abandoned grasslands in Poland were severe (Lenda et al. 2013), as shown by comparisons of ants on five heavily invaded sites and five non-invaded parallels. Ant colonies were assessed by direct searching, with collection of workers for later identification. *Solidago*-invaded grasslands were clearly impoverished, with the four ant species found a subset of the eight on non-invaded sites, and only 58 colonies, compared with 169 on the latter. Average ant colony size was also lower on the invaded grasslands, and ants foraged over larger distances to collect food. The three most common species on the invaded sites (*Myrmica scabrinodis*, *M. rubra*, *Lasius niger*) are all recognised as ecologically tolerant.

Many ecologists and conservationists have posited direct cascade links between species invasions into new environments and the extinctions of native species. However, as noted by Gurevitch and Padilla (2004), many such correlations are based on anecdotal or very limited field information. They urged the need for more critical examination of the roles of many invasive aliens, commenting that severe habitat changes commonly co-occur with proliferation of alien plant species, so that the twin impacts may be synergistic and their separate impacts indistinct. One possible consequence of this confusion is that efforts to remove alien species might be unnecessary, and the resources involved be deployed more usefully elsewhere. This

'driver versus passenger' dilemma in deciding roles of invasive species was explored for invasive plant weeds by Thomas and Reid (2007), to demonstrate considerable gaps in understanding over mechanisms of invasive species impacts in relation to needs for biological control and the benefits this might confer. They noted the idealised scenario summarised in Fig. 4.2. Impact on biodiversity (Fig. 4.2a) can be related to weed abundance, and result in different benefits to biodiversity from a given level of control. Thus, if impact is related to weed abundance, the change in impact is intermediate between scenarios in which low weed abundance causes high impacts and the converse, in which high impact occurs only at high weed abundance – each assumes a causative association between biodiversity and weed abundance. Figure 4.2b contrasts the biodiversity benefit by control for a weed that is a 'driver' of biodiversity change, and one which is a 'passenger' for which even complete control may not confer any change to biodiversity benefit. The trends of Fig. 4.2c exemplify rates at which control may associate with functional change – where function might return at a higher or lower rate than biodiversity, or with some intermediate vagaries.

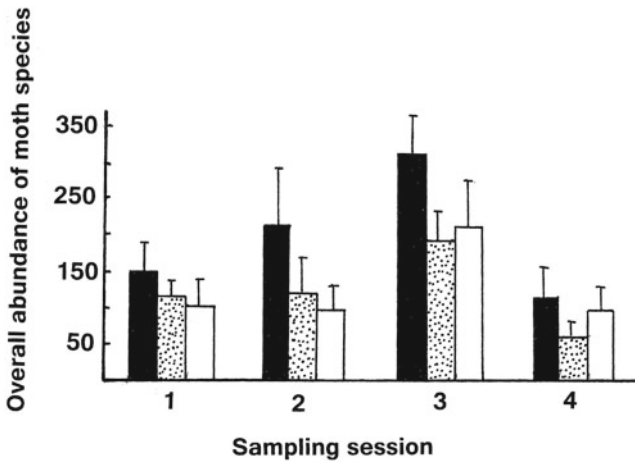
Possible outcomes when an invasive species encounters a resident competitor may be competitive displacement or extinction of the resident, or some form of coexistence – always presupposing that the invader has, by definition, successfully established and is itself unlikely to be displaced unless conditions change. Many conservation concerns relate to the first scenario, in which the resident species becomes disadvantaged by the invader. These concerns emphasise understanding the ways in which the resident may resist those impacts, or in which the invader becomes dominant. Distinction is not always made between 'invasion success', the ability of the invading species to increase from low to high density, and 'invasion impact', the effect of the invader on the receiving community. Exploring the latter can be complex. The severe forest defoliations caused by outbreaks of Gypsy moth in North America occur in areas that support large numbers of native Lepidoptera, whose fate may be influenced by (1) the direct loss of foliage food and (2) indirect trends such as plant host defences induced by Gypsy moth feeding, so that the available foliage becomes less nutritious (Manderino et al. 2014). Light trap sampling of moths in the Shenandoah National Park, Virginia, examined their richness and abundance 3 years after an outbreak between (1) sites that were defoliated but not treated with the pathogen *Bacillus thuringiensis kurstaki*, (2) defoliated and pathogen-treated sites, and (3) unaffected sites that were both undefoliated and unsprayed, in an effort to clarify the relative effects of defoliation and microbial pesticides on the forest moth communities. Fourteen families of moths included a collective 284 species, of which almost half (137 species) were represented by 7 or fewer individuals and 52 were singletons. The most diverse family, Geometridae, included 88 species, followed by Erebidae (74), Noctuidae (66) and Notodontidae (23). Four separate trapping sessions showed significantly different abundance, with undisturbed sites yielding more moths than treated sites (Fig. 4.3). Defoliation and *B. thuringiensis* application had little effect on overall moth diversity, but Geometridae in late summer after early season defoliation by *L. dispar* might reflect lowered survival of larvae because of lack of food. Adding to the complexity, it also appeared

**Fig. 4.2** Three aspects of the benefits of biological control for an environmental weed: (a) impact of the weed on biodiversity can be saturating, be more-or-less linear in relation to its abundance, or be negligible until weed abundance becomes high, so that quantitatively different benefits for biodiversity can occur for a given level of control (*dotted lines*); (b) if the weed is a 'driver' of biodiversity change, control will give a biodiversity benefit, here shown for the linear function; if it is a 'passenger', and biodiversity loss is due to other factors, even complete control may not yield a biodiversity benefit; (c) even with a benefit, the return of ecosystem function and services can be complex, returning at a higher rate than biodiversity (*upper line*), at a slower rate (*lower line*), or follow some intermediate idiosyncratic pattern reflecting local characteristics and differences within the biota (Thomas and Reid 2007)



that *B. thuringiensis* application following defoliation might protect Geometridae from that loss of diversity. That scenario was discussed earlier by Scriber (2004), in arguing that a decision to not spray may have more severe impacts on non-target Lepidoptera than going ahead with carefully planned spraying of the biopesticide.

Likewise, interactions between Gypsy moth and the native Northern tiger swallowtail (*Papilio canadensis*) where they overlap in range and host range are intri-



**Fig. 4.3** Overall abundance of moth species across four light-trapping seasons and three categories of site history (undisturbed controls [black], defoliated [dotted], *B. thuringiensis* treated [open]) in Shenandoah National Park, in relation to *Bacillus thuringiensis* controls for Gypsy moth (Manderino et al. 2014)

cate, and the swallowtail is negatively affected in several ways (Redman and Scriber 2000). Laboratory comparisons of the species' preferences on leaves from moth-defoliated and unattacked trees, and of pathogen-treated and sterilised leaves, suggested strongly that indirect competition can occur, inferring the likely incidence of similar mechanisms amongst other native herbivores sharing host trees with the invasive moth. Thus (1) defoliation by Gypsy moth lowered swallowtail survival and growth rate, whether or not the leaves were sterilised; (2) sterilisation reduced the effects of defoliation; (3) contamination by Gypsy moth body fluids was lethal to swallowtails; and (4) swallowtail larvae were substantially more heavily parasitised when in the field near gypsy moth infestations. Non-target effects of pest populations, paralleling those listed above, are clearly complex and often overlooked. Perhaps integrating the above examples, the diversity of native Lepidoptera can be reduced severely by Gypsy moth outbreaks (Sample et al. 1996). Abundance and species richness of non-target Lepidoptera were reduced in *B. thuringiensis*-treated plots in relation to untreated plots. Repeated biopesticide applications could offset the benefits obtained by reduced competition with gypsy moth larvae and also delay recovery of native species.

Ecological impacts of most alien insect species are not fully understood, and are difficult to predict. For the Galapagos Islands, Causton et al. (2006) noted likely impacts as 'still unknown', especially when only other invertebrates are affected. As a step toward redressing this, Causton et al. developed a 'scoring system' for alien insects to appraise and prioritise impacts. Criteria (Table 4.2) included the number of individual islands occupied, whether the species is naturalised, documented as invasive elsewhere, its dispersal and feeding habits, and whether known or suggested to have impacts. The seven ranking scores range from no perceived threats

**Table 4.2** Criteria of a 'scoring system' for predicting the invasiveness of insects introduced to the Galapagos Islands (after Causton et al. 2006)

Invasiveness ranking	Criteria
7	Species (or species belonging to a genus) that a. Seriously impacts species of high conservation value or communities (or is suspected to do so), or b. Is invasive in similar ecosystems elsewhere, or c. Kills or directly damages its food source and aside from the host upon which it was introduced, is principally restricted to feeding on taxa of high conservation value, or d. Is a vector or potential vector of a disease that is transmittable to native species, or e. Is a social predator and is a strong disperser and coloniser
6	Species that kills or directly damages living animals or plants, and has: a. An extensive distribution in the Galapagos (three or more uninhabited islands), or b. Spread rapidly on inhabited islands since its known recent (<20 years) introduction, or c. A high ability to disperse and colonise.
5	Species that kills or directly damages living animals and plants and was introduced >30 years ago and is naturalised on two or fewer uninhabited islands in addition to the inhabited islands
4	Species that does not kill or directly damage living animals and plants and has: a. An extensive distribution in Galapagos (three or more uninhabited islands, or b. Spread rapidly on inhabited islands since its known recent (<20 years) introduction, or c. A high ability to disperse and colonise
3	Species that kills or directly damages living animals or plants and is: a. Naturalised only on inhabited islands and was introduced >30 years ago, or b. A poor disperser or coloniser, and/or c. More likely to be associated with humans or introduced species
2	Species that does not kill or directly damage living animals and plants and was introduced >30 years ago and is naturalised on two or fewer uninhabited islands in addition to the inhabited islands
1	Species that does not kill or directly damage living animals or plants and is: a. Naturalised only on inhabited islands and was introduced >30 years ago, or b. A poor disperser or coloniser, or c. More likely to be associated with humans or introduced species
0	a. Species only found in urban zones or agricultural zones and was introduced >30 years ago, or b. No recent records (past 30 years), or c. Feeding restricted to introduced taxa or typically only associated with humans, or d. Intentionally introduced as a biological control agent following rigorous risk assessment

(level 0) to high potential invasiveness (levels 6, 7), with increasing levels between these extremes. Several themes used in this scheme have much wider importance in assessing invasiveness than to this single example. Three of especial note are: (1) insects high on food chains and that can cause direct damage to native species (as herbivores, predators or parasitoids) have potential to induce cascade effects, and are ranked higher than scavengers or decomposers; (2) species that are known disease vectors for endemic/native species or known to cause environmental damage elsewhere were given increased scores; and (3) a wide distribution elsewhere may indicate high dispersal ability and ecological adaptability, so that species introduced >30 years previously and that had not yet spread markedly were considered likely to be poor invaders. That particular latency period reflected the availability of Galapagos baseline information. Large numbers of such naturalised species can occur in natural ecosystems, but most of the insects of greatest individual concern in conservation are higher level consumers that directly affect native species.

The above categorisation reflects wider attempts to explore correlates of vulnerability amongst species in the receiving environment, as a complement to the more commonly investigated theme of correlates of invasion success. In general, and other than in contexts of individual threatened species' susceptibility, few such potential generalities have emerged – although a widespread association between invertebrate body size and susceptibility to alien rodent predation seems likely (p. 181). Identifying 'at risk taxa' was attempted for 300 arthropod species in parts of Hawai'i being invaded by tramp ants (Krushelnycky and Gillespie 2010). Five middle to high elevation sites on Maui and Hawai'i, chosen so that each was undergoing invasion by an expanding invasive ant population (one site by *Pheidole megacephala*, four sites by *Linepithema humile*), were surveyed. Their arthropod assemblages were compared with those on adjacent non-invaded sites, using a combination of pitfall trapping, leaf litter extraction and beating the predominant shrub or small tree species. At each site, eight 5 × 5 m invaded plots and eight similar uninvaded plots yielded material that was categorised into 'rare species' (n = 172, characterised by density of <5 individuals/total sampling effort in combined uninvaded plots at a site, across all sites where the species occurred) and 'non-rare species' (n = 128). High variability occurred across all trends examined, but some potentially constructive findings related to vulnerability were (1) provenance was an important factor associated with absence of rare species from invaded plots, with losses especially found amongst endemic taxa; (2) Hawai'ian endemics amongst non-rare species were more reduced in invaded plots than were introduced species and, amongst these, less abundant species were more vulnerable than those found at high densities; (3) feeding role was important in combination with provenance, so that rare endemic carnivores were the most vulnerable group, followed by rare endemic detritivores; and (4) body size did not correlate with vulnerability amongst species in either category.

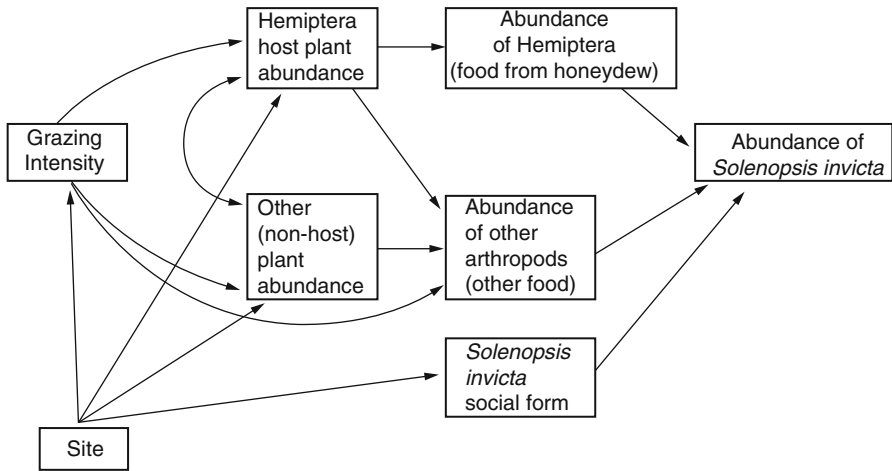
Interactions between invasive ants and Hemiptera on islands, involving the protection of the bugs from natural enemies and the ants gaining honeydew as a predominant carbohydrate resource, can lead to very high densities of these mutualists, as described on Christmas Island, Indian Ocean (Abbott and Green 2007). Further

west, high densities of Big-headed ant, *Pheidole megacephala*, occur on Cousine Island, Seychelles, where the Hemiptera (themselves alien cosmopolitan scale insects, notably *Pulvinaria urbicola* and *Dysmicoccus* sp.) cause severe damage to indigenous trees, notably *Pisonia grandis* (Gaigher et al. 2011). Increased scale insect abundance associated with increased ant abundance intensified damage to the host trees, implying gradual forest decline. The same broad *Pheidole* – scale insect mutualism has similar impacts on *P. grandis* forests elsewhere. These invasive insects and the mutualisms they then form are thus a clear threat to some key island ecosystems, and their control is an urgent conservation need (Gaigher et al. 2011). Even such apparently clearcut associations, however, are not universal. *Pheidole megacephala* and *Pulvinaria urbicola* occur together on some coral islets on Australia's Great Barrier Reef (Hoffman and Kay 2009), where the ant's distribution was limited to coastal fringes of the islands, and declined rapidly within the near-monoculture *Pisonia* forests of the interior zones. The ant was present in mixed-forest stands. This apparent anomaly was linked tentatively to the *Pisonia* forests having substantial deposits of guano, as they are important rookery sites for large numbers of seabirds. Modifications caused by that guano could possibly affect honeydew to render it unsuitable for the ants. Hoffman and Kay suggested that there might now be no carbohydrate source of adequate quality from *Pisonia* on these small islets.

Novel trophic interactions between invasive ants and alien Hemiptera are not uncommon, with both parties flourishing in part due to escape from the natural enemies of their native ranges. In the southern United States, honeydew produced by the invasive mealybug *Antonina graminis* has been estimated to supply 16–48% of the nutritional energy used by Red imported fire ant (*Solenopsis invicta*) colonies and facilitating colony growth substantially over that possible from arthropod prey alone (Helms and Vinson 2008). In grazing pastures in that region, Helms et al. (2011) hypothesised the interactions summarised in Fig. 4.4, also recognising that *S. invicta* occurs in both 'social' (multiple queens) and single queen colonies. The suggested relationship between grazing intensity and arthropod abundance reflects the likely importance of arthropods associated with dung and used as food by the ants. Association between mealybug abundance and *S. invicta* abundance was strong, with the bug's host plants having strong effects on ant abundance through their direct effects on *A. graminis*.

Simberloff and Von Holle (1999) suggested the term 'invasional meltdown', in which the presence of invasive species aids the invasion of further alien species. The most dramatic ecological impacts of invasive ants, as a well-studied context of 'invasional meltdown', are exemplified by the Yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island, Indian Ocean, where rapid increase of this omnivorous ant led to formation of enormous supercolonies. That invasion dramatically affected at least three trophic levels in the tropical rainforest ecosystem (O'Dowd et al. 2003). The island is famous for the enormous numbers of the ecologically dominant keystone terrestrial herbivore, the Red land crab (*Geocarcinus natalis*). The crabs undergo spectacular seasonal migrations and are killed in vast numbers by the ant. Consequently, seedling recruitment was released, plant species richness increased





**Fig. 4.4** Possible factors affecting the abundance of the invasive Red imported fire ant (*Solenopsis invicta*) in grazing pastures in Texas. The factors were hypothesised and tested for their importance, with the presumed relationship between grazing intensity and ‘abundance of other arthropods’ reflecting the potential importance of arthropods associated with dung (Helms et al. 2011)

and litter breakdown slowed. High foraging levels by the ant in forest canopy led to high populations of scale insects, with increased growth of sooty moulds on honeydew leading to canopy dieback and tree deaths. The ant invasion thereby led to markedly changed resource supply and habitat structure, which Davis et al. (2008) showed also to have impacts on endemic forest birds on Christmas Island. *A. gracilipes* reduced abundance and reproductive success of some birds, with the areas occupied by ant supercolonies extending those impacts over several tens of square kilometres. Ground-foraging birds, such as the Island thrush (*Turdus poliocephalus erythropleura*) and Emerald dove (*Chalcophleps indica natalis*) were especially affected. In contrast, the Island white-eye (*Zosterops natalis*), a generalist feeder on vegetation, increased in inland forest, reflecting increased scale insect prey from the enhanced ant-scale insect mutualism. Full consequences of this ‘meltdown’ are complex (Green et al. 2011), with the mutualism between the invasive ant and invasive scale insect enabling invasion by the African giant land snail (*Achatina fulica*) in ant supercolony areas, where large numbers of land crabs had been killed. Suggested future management may thus seek to restore ‘pre-meltdown’ interactions – in this scenario, suppression of the crazy ant-scale insect mutualism should lead to recovery of red crab populations and, in turn, their predation lead to reversal of the snail invasion potential.

A somewhat different mechanism, not involving ants, produced parallel cascade impacts on the Tristan da Cunha archipelago, where invasive scale insects infested the islands’ only native tree (*Phyllica arborea*, Rhamnaceae), on which associations with a resulting sooty honeydew mould led to reduction of fruit production (Ryan et al. 2014). Endemic finches (*Neospiza* spp.) use that fruit as a key resource, and

fruit losses may affect the finch populations, with wider ecological consequences as the finches are diverted progressively to feed by gleaning on native insect prey.

The widespread alien distributions of tramp ants and some other taxa raise the theme that important insights into alien insect impacts might come from comparing the trajectories and roles of the same taxon being invasive in different places. That approach necessarily incorporates a range of geographically discrete incursions and the study and analysis of their fates, so is relatively unusual. A recent comparative study, for the Spotted-wing drosophila fly (*Drosophila suzukii*, Drosophilidae), native to Asia but a major invasive pest of fruit-growing areas in Europe and the Americas over the last two decades, has illustrated some of the values of examining outcomes in different regions (Asplen et al. 2015). Not least, the difficulties of formulating sound general control programmes, rather than regionally-tailored exercises, were emphasised and the gaps in biological knowledge and in which research was needed to redress this became apparent. These fields reflected different host uses in different countries, and post-invasion detection intervals with surveillance intensity for new detections being well-founded in Europe and less so elsewhere. Recent, and believed genuine, first records of the fly for parts of Europe (such as Belgium, Switzerland: 2011; Hungary, United Kingdom: 2012) allow for rapid response. Research priorities noted by Asplen et al. included clarifying biology of *D. suzukii* at lower temperatures, diapause regimes and host plant effects on both fruit crop and non-crop hosts, and movement patterns – these simply indicating some of the more intrinsic factors that might influence invasion success. The alien North American Black cherry (*Prunus serotina*) is a notable resource for *D. suzukii* in Europe (Poyet et al. 2014), and could promote the fly's invasion in both Europe and North America.

Whatever its shortcomings may be, the approach of predicting the risks from a potentially invasive species based on its impacts elsewhere is a widespread tool, subject to connotations of alarmism in some cases but salutary in the warnings it may provide. Based on its record after introduction to Tasmania, Hingston (2007) projected the potential effects of the invasive bumble bee *Bombus terrestris* (p. 51) should it reach the Australian mainland – a region with many climatic and vegetation features in common with Tasmania. Kingston's concerns encompassed four themes: (1) although introduced for glasshouse crop pollination, escapes of the bee are highly likely and formation of feral populations then almost certain; (2) *B. terrestris* forages on a great variety of native and introduced flora, and spread rapidly across all major vegetation types in Tasmania; (3) there, it was able to reduce nectar supplies available to other consumers, in part by foraging at lower temperatures than other bees were able to do; and (4) affecting pollination efficiency by behaviour differing from that of co-evolved pollinators – for example by chewing into tubular flowers near the base of the corolla to gain nectar, thereby bypassing anthers and stigmas as a direct impact on plant reproduction. Wider ecological consequences noted by Hingston included facilitating spread of some competitive invasive plants, and reducing reproductive success in an endangered nectar-feeding bird.

Many different extinction threats from invasive insect herbivores are relatively localised, and relatively specific. The Erythrina gall wasp (*Quadrastichus erythrinae*, Eulophidae) is a dramatic exception in having undergone a rapid and extensive spread across much of the Pacific Basin, where it has caused severe damage to most species of Coral trees (*Erythrina* spp., Leguminosae). Both ornamental and native *Erythrina* are affected, with several species suffering complete defoliation and death in many different environments, and the wasp is believed likely to cause extinctions of native species. In Hawai'i, for example, the endemic *E. sandwicensis* has been 'devastated' (Rubinoff et al. 2010). One impact of this has been losses to Hawai'ian tourism, agriculture and native ecosystems, in a pattern that Rubinoff et al. declared to be 'typical everywhere the wasp has spread'. Possibility that the wasp might comprise a complex of species rather than a single entity across its range prompted extensive genetic surveys. These confirmed that only a single species is involved – but also that it exhibits a complete lack of significant genetic variation, implying recent rapid expansion from only a small founder population. Control of *Q. erythrinae* by insecticides and tree pruning have not been effective, and classical biological control may now be the only realistic option (Messing et al. 2009, Chap. 6).

Perhaps more commonly than causing extinctions, strongly competitive pressures from invasive species may induce various forms of decreased fitness as non-lethal effects in native species. High densities of the invasive wasp *Vespula vulgaris* in honeydew beech (*Fuscospora* spp.) forests of New Zealand are well documented as exploiters of honeydew produced by the endemic scale insect *Ultracoelostoma assimile*. The wasp's consumption of honeydew has become so great as to lead to declines in other native consumers as diverse as birds and insects (Moller and Tilley 1989; Moller et al. 1991). The native ant *Prolasius advenus* is the most abundant ant in those forests, and depends on honeydew as its predominant carbohydrate source. *V. vulgaris* does not directly eat *Prolasius* adults (but can consume early stages), but appears to be the major competitor with foraging worker ants for honeydew. Worker ants were collected at seven sites monitored for wasp density and measured to examine the hypothesis that worker sizes decreased as wasp density increased (Burne et al. 2015). A series of morphological features was also examined. Lower mean worker size in *Prolasius* with increased wasp density probably reflected restricted food resources. A related study (Duthie and Lester 2013) revealed substantially increased ant foraging where wasps were abundant in comparison to sites on which wasps had been experimentally controlled. Burne et al. doubted whether the decreased size of ants, although statistically significant, was biologically important - but nevertheless implied some form of ecological character displacement, as did the subtle morphological scaling differences found in six of the eight characters assessed. They, again, might reflect some subtle form of sublethal impact from the wasps.

The endemic scale insect *Coelostomidia waiorensis* (Coccoidea: Coelostomidiidae) is a major producer of honeydew in New Zealand's endemic Myrtaceae in the North Island, and provides a key food supply for a number of insects and birds (Gardner-Gee and Beggs 2012). The honeydew is exploited extensively by *Vespula germanica* and *V. vulgaris*, and no other diurnal consumers were

detected; the near monopoly may lead to increased wasp abundance. Possibly reflecting that abundance, no evidence of native birds exploiting honeydew was found, and ant activity (with five of the nine species detected alien) was also low.

Competition effects between native and alien species can be subtle and difficult to investigate and confirm. Understanding this process, especially between species that are closely related, is recognised widely as an important aspect of appraising invasiveness, with any dominance or displacement often attributed to some form of competitive asymmetry - most commonly with this favouring the invasive species. Social Hymenoptera are the most frequently studied insect group (Chap. 6), but a study on co-occurring subterranean termites in France (Perderau et al. 2011) showed many parallels in this other social insect group. The invasive American *Reticulotermes flavipes* is a destructive species in urban areas of France, and has also invaded forests in the west of the country. There, it co-occurs with the native *R. grassei*, found only in south western Europe. Samples collected from tree stumps and wood fragments in forests were studied, and encounters between the species examined in laboratory arenas, with mortality assessed after 24 h. The two species do not wholly overlap in the study area but, where they do co-occur, the introduced *R. flavipes* always prevailed over *R. grassei* and invariably won aggressive encounters. Its superior fighting ability implied that *R. flavipes* may progressively displace the native species.

Competition between invasive insect herbivores and native species using the same host species can become very intricate and transcend feeding guilds, with changes in food quality affecting the less competitively able species. An intriguing study in British Columbia of the consequences of an invasive gall-forming cynipoid wasp (*Neuroterus saltatorius*) for a native specialist butterfly (*Erynnis propertius*, Hesperidae) with larvae also feeding on oak foliage suggested an indirect plant-mediated competitive interaction (Prior and Hellmann 2010). The wasp occurred in higher densities in its invasive range than in its natural area, with this increased abundance useful in seeking to explore any competitive effects. Larvae from captive-held butterflies were released into enclosures on oak trees (*Quercus garryana*) on branches with different measured densities of leaf galls produced by the second (agamic) wasp generation; the amount of foliage in each enclosure was not limiting. Lowered butterfly performance (shown as smaller size and lower survival) occurred with increased gall wasp density. Prior and Hellmann attributed this to reduced plant quality, assessed as increased carbon and reduced nitrogen, with the increased carbon:nitrogen ratio providing a significant change in foliage nutritional quality. Such changes, although rarely documented amongst putative competitors, may prove to be frequent.

Sublethal impacts from alien species resulting from feeding by native species manifest in many ways of reduced development rates, fecundity, size and general 'performance'. All are common as differences amongst native food stuff effects on polyphagous consumers, but not as frequently observed amongst species regarded as dietary specialists. Simplistically, and at least in theory, selection of host plant (or other food) by ovipositing insects should optimise fitness by targeting those species that maximise opportunity to develop successfully and produce the fittest offspring.

Suboptimal relationships between oviposition choice/preference and later performance, however, are very common. Likewise, introduced species may become ecological traps more frequently than is commonly supposed (Schlaepfer et al. 2005).

## 4.4 Ecological Traps

Most demonstrated examples of ‘ecological traps’ or ‘evolutionary traps’ involving alien species focus on alien plants as population sinks for specialist herbivores for which the novel potential plant host is excessively attractive for oviposition. Female insects are thus lured or diverted from acceptable normal hosts to lay on them, but the alien plant is either toxic to larvae, or in some way reduces their survival rate, viability or performance. Some such alien plants pose significant threats to insects of conservation concern. The South American vine *Aristolochia elegans* (Aristolochiaceae) has been planted widely as an ornamental plant throughout the historical range of the Richmond birdwing butterfly (*Ornithoptera richmondia*, Papilionidae) in central eastern Australia (Sands and New 2013), over the same period that the usual native host vine (*Pararistolochia praevanosa*) has been reduced by forest clearing and urbanisation. *A. elegans* is attractive to female birdwings for oviposition, but the foliage is toxic to the emerging larvae, which die after feeding. The alien vine is a serious threat to the butterfly, in concert with habitat degradation and losses of the natural food plant, and removal of *A. elegans* and extensive plantings of *P. praevanosa* are continuing activities for its conservation throughout its limited range, essentially to increase availability of the natural host and reduce opportunities for the ecological trap to occur.

Parallel cases have been reported elsewhere, as a major component of novel plant-insect associations (Chap. 5). They are sometimes referred to as ‘oviposition mortality’ and have been noticed most among butterflies: Davis and Cipollini (2014) noted cases from among Papilionidae, Pieridae and Nymphalidae, for example. The pierid example they discussed explored the relationship between the European invasive garlic mustard (*Alliaria petiolata*) and two native butterflies (*Pieris oleracea*, *P. virginiensis*) in the United States. Both species oviposit occasionally on this novel host, and *P. oleracea* appears to be gradually adapting to it. Over more than a hundred generations this bivoltine butterfly had begun using this host, with larvae viable but with increased development time and leading to reduced pupal weight (Keeler and Chew 2008). Field study of *P. virginiensis* showed that it readily lays on *Alliaria* and actively prefers this to the native host examined (*Cardamine diphylla*). However, unlike *O. richmondia* in Australia, the pierid is not naturally monophagous or narrowly oligophagous, and this crucifer is simply one of many potential hosts, in this survey being the only long-lived co-occurring native mustard host found with *Alliaria*. At present, *A. petiolata* is a population sink for *P. virginiensis* (Davis and Cipollini 2014), and introduction of this plant into the butterfly’s range may accelerate its already evident decline. One butterfly population (in Morrow County, Ohio) was described as ‘robust’ in the late 1980s but is now thought to be

extinct, with the loss coinciding with introduction of *A. petiolata*. Current conservation efforts include removal of *Alliaria* from key areas, and Davis and Cipollini recommended that such removals be undertaken before the butterfly flight season commences, in order to reduce risks of wasteful oviposition. The complexities of the *P. oleracea* - *A. petiolata* interaction were explored more extensively by Morton et al. (2014), who considered also impacts of and on two alien braconid wasp parasitoids (*Cotesia glomerata*, *C. rubecula*), both released to control the invasive *Pieris rapae*. *C. rubecula* is dominant in competition with *C. glomerata*. *C. glomerata* was introduced in the 1880s and is a major contributor to the decline of *P. oleracea*, with its impacts exacerbated by the ecological trap of *Alliaria*. *C. rubecula* was introduced much more recently (1988), and does not attack *P. oleracea*, but greatly lowers abundance of *C. glomerata* to potentially create enemy-free space for the butterfly. The tendency seen for *P. oleracea* to progressively recruit *A. petiolata* into its diet might facilitate the butterfly's recovery, mainly by this reduction of an oppressive parasitoid and increasing its larval survival rates. Modelling a wide range of potential scenarios gave an equally wide range of possible outcomes, from extinction of the butterfly to high likelihood of persistence. In general, pressures of alien species, even at different trophic levels, interacting in complex ways, need greater understanding in many similar scenarios. Here, a top-down impact (from *C. glomerata*) and a bottom-up effect (from *A. petiolata*) were both negative, with another top-down effect (from *C. rubecula*) ameliorating those negative impacts to enhance survival of the focal butterfly species.

However, declines of *P. oleracea* have varied considerably across its range, and possible reasons for its decline in Massachusetts but continued abundance in more northerly Vermont included a combination of parasitoid (*C. glomerata*) attack and seasonal pattern of development along a north-south cline (Benson et al. 2003). The butterfly is normally bivoltine or trivoltine in the region, with the first generation occurring in woodland and later generation(s) in open meadow areas. Persistence in the northern region may be related to high parasitisation of the second generation in meadows in Massachusetts. Essentially, diapause regimes led to the northerly populations acting functionally as a univoltine species developing in a parasitoid-free woodland habitat, whilst southern populations constitute a functional bivoltine species highly susceptible to *C. glomerata* in meadows during the second generation.

Female Monarch butterflies (*Danaus plexippus*, Nymphalidae) given a choice between the introduced Black swallowwort (*Vincetoxicum nigrum*) and the native host *Asclepias syriaca* lay about a quarter of their eggs on the former, on which larvae are unable to develop (Tewksbury et al. 2002). Preference for the introduced toxic host was assessed by Schlaepfer et al. (2005) as an evolutionary trap rather than a more broadly defined population sink. That insects will oviposit on plants that cannot support larval development leaves no opportunity for any evolutionary host shift. If such plants are aliens, as in the above cases (and others, such as the Green-veined white butterfly, *Pieris napi*, laying on the introduced *Thlaspi arvense* in North America: Chew 1977), the colonist's traits include inherited ability to respond to oviposition stimulants shared by normal hosts, but not to cope with other plant traits that affect the larvae. Ecological stimuli that govern oviposition behav-

our here have wide implications for the species in novel environments. The ‘mother knows best’ principle (Jaenike 1978) that female insects should maximise fitness by laying eggs on plant species on which their offspring develop most successfully is attractive, but clearly not universal. That novel host plants can either (1) lack oviposition cues to reject oviposition or (2) possess oviposition stimulants even when unsuitable as food may both be a function of time for the consumer species to develop recognition cues to adapt to unfamiliar phytochemicals.

‘Preference’ for an alien plant host may not always occur, but its prevalence and availability sometimes render it the far more accessible resource. The saturniid moth *Hemileuca maia* (one of the ‘buck moths’) is relatively widespread in parts of the United States. However, an ecological variant designated by Gratton (2006) as ‘*Hemileuca* sp.’, with its precise taxonomic status unsettled, is of conservation concern in some areas. Larvae feed on the invasive Purple loosestrife (*Lythrum salicaria*, Lythraceae), causing significant defoliation and reducing seed production. In laboratory comparisons, however, fitness (much reduced survival, lower pupal weight) suffered in relation to feeding on a more natural host (a willow, *Salix* sp.). Larval mortality, for example, was more than seven times higher when fed on *Lythrum*, and in choice trials, this was also the less preferred host. The weed thus provides a substantial resource for *Hemileuca* in the field, but may also constitute an ecological sink on which average population growth and fitness may decline if it persists as predominant in the moth’s diet (Gratton 2006).

Plant examples are paralleled amongst alien invasive insects when they are accepted as prey or hosts by native predators or parasitoids but are then unsuitable to support those consumers. The pentatomid bug *Halyomorpha halys* is an Asian pest of orchard fruits that has now become very common in parts of North America and is expected to expand its range further and to continue to cause economic losses in Canada and the United States. Within that range the native *Telenomus podisi* (Hymenoptera: Scelionidae) is a widespread polyphagous parasitoid of pentatomid eggs, and trials showed that female wasps readily accepted newly laid eggs of *H. halys* for oviposition (Abram et al. 2014). Although some offspring reached their pupal stage within host eggs, none completed development. However, successful development has been reported elsewhere, confirming that development can sometimes occur. Rather than increasing vulnerability of the parasitoid, a possible outcome through diversion of the parasitoid to attack this sink host species is to reduce their pressure on native suitable hosts and facilitate their increase. As some other scelionids also do, *T. podisi* females ‘guard’ bug egg masses in which they have laid, so further diverting the wasps from native hosts by their spending time in this futile activity – a behaviour that Abram et al. termed a ‘time sink’. Parallel lack of development on the same host probably occurs with a different native parasitoid (*Telenomus chloropus*) in central Europe, where the bug is also a recent arrival.

In general, three categories of evidence demonstrate the existence of an ecological trap (Robertson and Hutto 2006), namely (1) individuals prefer one host (the ‘trap’) over another, or accept it as equal in quality to the normal host; (2) individual fitness differs between the hosts; and (3) individuals that select the trap habitat incur reduced fitness. In general, then, an ecological trap can be defined as a low quality

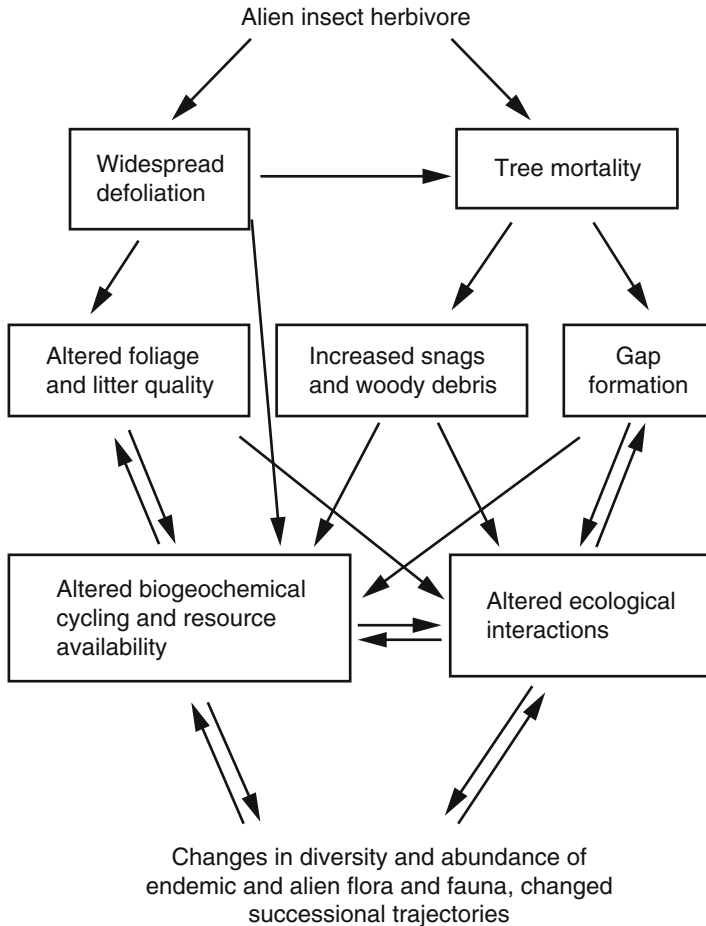
habitat/resource that cannot sustain a population of a species selecting it, but which is preferred over other, higher quality habitats/resources. As a further generality, it is likely that ecological traps have greater consequences for specialist species than for generalist exploiters, simply because the number of favourable host/resource patches may be far lower.

## 4.5 Ecological Specialisation

The concept and implications of ecological specialisation are universal themes in considering invasive species' impacts. In general, specialisation is most likely to occur in relatively stable environments in which a consumer's association with individual resources (such as host plants or prey) can persist and the species form intricate co-adapted associations. Those associations may be very susceptible to disturbance, and the vulnerability of ecological specialists to imposed changes is an ever-present concern. Declines of specialists lead to functional homogenisation, the extent of which may be a measure of the impact of disturbances on the communities (Clavel et al. 2011). The twin components of biotic homogenisation (taxonomic homogenisation, functional homogenisation) both result directly from replacement of local specialists by local to widespread generalists, and Clavel et al. distinguished three mechanisms that contribute to this through functional homogenisation: (1) global changes have direct negative effects on specialists, irrespective of the presence of generalists, because specialists can no longer use alternative resources available to generalists; (2) generalists, unlike less flexible specialists, may be able to colonise newly available situations as they arise and caused, for example, by climate changes; and (3) global changes may inflict the same changes, whether positive or negative, on both generalists and specialists, but to different extents so that competitive effects then influence their relative fates. The three mechanisms may combine in communities and generally promote wellbeing of generalists. Clavel et al. (2011) suggested that functional homogenisation measured as the proportion of specialist species in a community is a good indicator of the 'state' of biodiversity, as it is linked clearly to factors driving global change and occurs in all ecosystems.

Invasions by generalists cause widespread concern, and have been documented in many disruptions of ecological function, and changes to native assemblage composition and ecosystem structure. Many are not initially obvious. Figure 4.5, after Gandhi and Herms (2010), summarises how invasive insect herbivores have both direct and indirect impacts on forest trees in North America, with overall effects including changes to community composition and successions in the forest environment. Some features were highlighted as noted or characterised only infrequently: Gandhi and Herms noted, for example, that the ecological significance of canopy gaps formed by major pests such as the Gypsy moth is especially important in the eastern forests in which wildfires are infrequent, and can lead to major changes in microclimate and understorey vegetation dynamics, as well as changes in canopy composition. Some endemic trees can increase in dominance as alien insects kill off

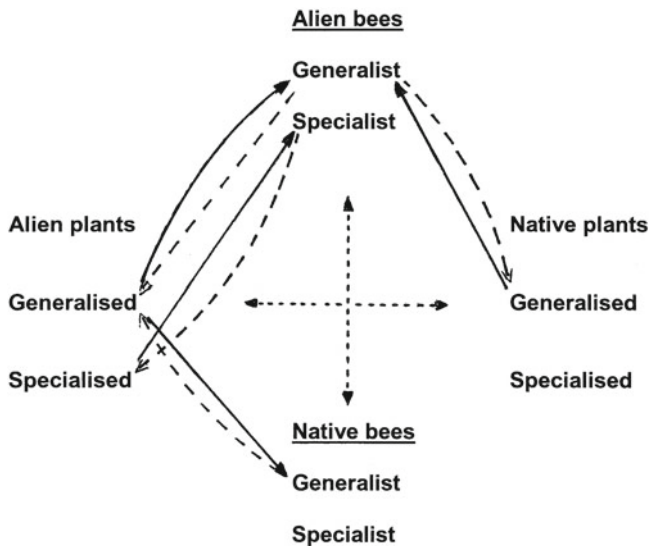




**Fig. 4.5** A generalised conceptual model that shows cascading direct and indirect effects of alien insect herbivores on ecological processes and interactions that ultimately affect community composition and successional trajectories in eastern North American forests (after Gandhi and Herms 2010)

their competitors – and in due course themselves become vulnerable to later alien herbivore invaders.

The wider context, of the relative roles of generalists and specialists in sustaining key ecological processes, incorporates assessing both positive and negative outcomes. For pollination, as one of the most extensively studied themes, the impacts of both alien bees and alien plants vary greatly. In general (Stout and Morales 2009), native specialist bees (with one or few host plants) and specialised plants (with one or few pollinators) do not benefit from alien invasions, whilst alien generalist bees and generalist plants gain greatest benefits. The mosaic of potential impacts (Fig. 4.6) may lead to formation of new invasion complexes. Invasive plants may



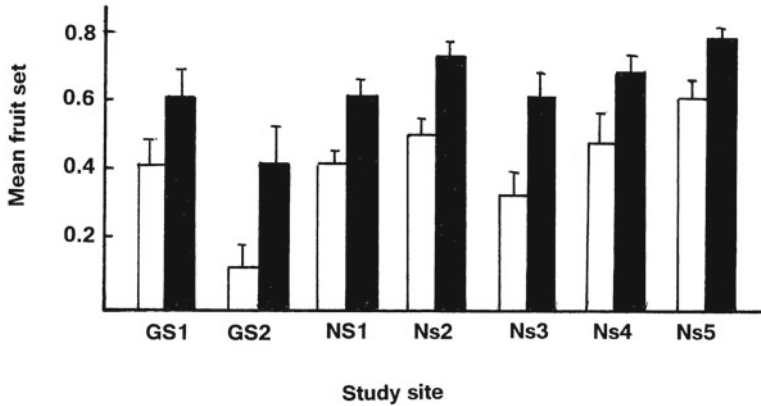
**Fig. 4.6** Scheme of potential interactions between native and alien plants and bees in invaded ecosystems. Note that native specialist bees and specialised plants do not benefit from alien invasion, whilst alien generalist bees and generalist plants benefit the most. *Solid black lines* indicate direct impacts of plants on bees (by providing a forage resource), and *broken lines* indicate direct impacts of bees on plants (by pollination services); the *dotted lines* represent resource competition among native and alien species (Stout and Morales 2009)

require specialised pollination mechanisms not provided by native bees in their invasion area – buzz pollination or need for heavy bees to expose the stamens or stigmas are possible examples: Goulson (2003) cited the latter scenario for the invasive alien *Lupinus arboreus* in Tasmania. In such cases, the invasive plants are avoided by the native bees and so do not contribute to their food supplies. More generally, Stout and Morales cited three main conditions for native bees to utilise alien invasive plants successfully, as (1) being morphologically accessible; (2) containing nutritionally valuable rewards; and (3) being accessible in time and space to the bee's activity and seasonal appearance. They also noted conditions under which invasive alien insects (including bees) might compete with native bees, namely (1) substantially overlapping floral resources; (2) the floral resources being limiting; and (3) decrease in resource gain leading to decreased fitness of the less competitive species, or of both species. Mass flowering invasive plants, as often associated with agricultural landscapes, may increase competition amongst pollinators.

The extent to which native host plants are affected directly by alien herbivores can affect co-feeding native species. At least 21 monophagous species of North American Lepidoptera feed on the ash trees being lost due to the Emerald ash borer (Wagner 2007), but such wider community impacts have scarcely been explored amongst many key invasive insect herbivores. Both direct competitive effects and indirect effects, such as changing food supply and accessibility across the landscape, occur.

Pollinating insects are an important focus in impact studies, with concerns over reduced pollen transfer and pollination efficacy linked with displacement of specialised native pollinators by introduced invasive generalists (Chap. 6). Far less is known of the impacts of more specialist invasives in new areas. The oil-collecting bee *Centris nitida* (Apidae) exemplifies this, as a recent naturalisation in southern Florida, extending from its natural range in tropical Mexico to South America. Southern Florida supports only one native mutualism between such a bee (*Centris errans*) and plant, *Byrsonima lucida* (Locust berry, Malpighiaceae). The closely related and newly arrived bee was considered to have potential to disrupt this intricate association in which the bees collect floral resins and nectar for nest building and larval food, and pollinate the flowers. Downing and Liu (2012) hypothesised that visitation rates of *C. errans* might be lower in sites where *C. nitida* occurs, that the latter (a smaller bee) may be a less efficient pollinator, and that sites with both bees present might suffer more pollen limitation than sites with only the native bee. Both in garden sites (where *C. nitida* was more abundant than in natural areas) and natural sites, impacts of the invasive bee were apparently insignificant in 2010 and 2011, following its arrival only a few years before. Both species contribute to pollination, with the native bee the more frequent visitor (Fig. 4.7). No direct physical interference between the species was observed, and exploitation competition may be reduced by the same flowers continually producing oil over several days. Implications of the bee's arrival in Florida are mixed – Downing and Liu noted its potential to boost fruit production of the endangered oil plant with minimal impact on the native bee, especially in urban areas.

Whilst harmful impacts of generalist invaders are often anticipated or predicted, they are often far more difficult to prove. The Asian paper wasp (*Polistes chinensis antennalis*, Vespidae) was first recorded in New Zealand in 1979, and has since raised concerns that its predation on native invertebrates, notably on larvae of Lepidoptera (Clapperton 1999) could pose a significant threat. Modelling the wasp's current and potential distribution (Ward and Morgan 2014) showed that the range of habitats is likely to remain restricted, with the wasp's greatest incidence in areas with herbaceous saline vegetation – a habitat in which a considerable diversity of Lepidoptera larvae are exploited (Ward and Ramon-Laca 2013) – followed by built-up areas and then woodland and scrub. Much of the country is climatically unsuitable for the wasp to establish at present. The estimated more than 1.5 million nests across New Zealand coupled with estimates of foraging activity and success implied that *Polistes* could eliminate three to four billion prey items over a single season. Its high nest densities and occupancy rates in the saline vegetation areas suggested that the wasp's impacts there might be especially significant, so those areas are an important focus for further investigations and for control of the wasp. Prey surveys were undertaken by collecting wasp nests from urban and saline marsh habitats and amplifying the CO1 unit of DNA from the gut of wasp larvae, using samples of one to six individuals from each nest, and from which species or near-species level recognition was possible (Ward and Ramon-Laca 2013). About 70% of the 299 larvae tested yielded sequences suitable for prey identification. Lepidoptera was by far the predominant prey group, with 39 taxa (of the total of 42



**Fig. 4.7** Comparison of mean (with standard errors shown) fruit set for control (*open bars*) and artificial pollen supplement (*black bars*) treatments on *Byrsonima lucida* (at least three plants each site) at two garden sites (G) and five natural pine sites (N) in Florida (see text, p. 87). Reduction in mean fruit set between control and supplement treatments suggests pollen limitation; both bee species present only at three left hand sites shown (GS1, GS2, NS1), sites Ns2-Ns5 with only one bee species (Downing and Liu 2012)

taxa) across 192 samples. Twenty four species were endemic, and 15 were aliens; none of the native species was of direct conservation concern, but this study confirmed that this wasp, although nominally a generalist predator, may have potential to harm threatened taxa if range and opportunity coincide.

## 4.6 Functional Equivalence

The major outcomes from a study involving removal of invasive wasps in Hawai'i (Hanna et al. 2013, see p. 164) emphasised the central need to incorporate ecological context and function into invasive species management. They demonstrated the major harmful impacts that invasive nectar thieves can have on reproduction of native plants, and that native pollinators can be effectively substituted by introduced pollinators – in this case by *A. mellifera* – as ‘taxon substitution’. This theme is debated strongly in conservation literature, from the viewpoint that emphasis on sustaining ecological functions may lead to preferences for encouraging alien generalist taxa over native species because they are more effective. From that viewpoint, the less effective native specialist insects become the more expendable: in an extreme (and hypothetical) case drawing from honeybees, *A. mellifera* could be deemed more worthy than the collective 25,000 or so other bee species because of its generalist pollinating capability and direct services to humanity through crop pollination, and demands for the conservation of this vast array of other bees decrease. Combining conservation and the maintenance and restoration of key ecological ‘services’ such as pollination is a continuing challenge in ecosystems

invaded by alien species that can fulfill those roles. Conservation benefits from non-native species are cited commonly. The examples of alien plant species becoming key food resources for Lepidoptera whose native food plants are diminishing (p. 166) perhaps represent a much wider scenario. Likewise, the purposeful establishment of alien ‘nectar plants’ (primarily ornamentals, but some achieving weed status) that provide food for numerous adult insects is widespread, and can lead to their promotion for use in ‘butterfly gardens’ and similar conservation-motivated exercises. The ‘butterfly bush’, *Buddleia davidii*, is a very widespread naturalised urban alien plant, for example. More broadly, Schlaepfer et al. (2011) noted three major categories of conservation contributions from alien species as (1) providing habitat or resources for rare species; (2) serving as functional substitutes for extinct or rare taxa; and (3) providing desirable ecosystem functions.

Extrapolation to the more general supposition that high native species richness is needed to assure ecological functions adds a further dilemma. Schwartz et al. (2000) found little support for ecosystem functioning to depend on the full complement of native species. If most rare species do not contribute materially to this integrity, or if the postulated link between species richness and ecological functions is otherwise weakened, a conservation perspective based largely on maintenance of function may lead to many native species being deemed redundant and the alien species more worthy of management to encourage their abundance and spread. Schwarz et al. also noted the widespread tendency to postulate ‘functional groups’, whereby species fulfilling similar roles are lumped together and individual species (even if threatened) are not actively considered. It follows that if alien species contribute largely to any functional role, to many observers the significance of native species may be relatively diminished.

## 4.7 Clarifying and Defining Impacts

The impacts of invasive species often appear clear, but the ways in which they interact with other processes – notably habitat change – are complex and often difficult to distinguish. Such changes are usually examined (and managed) separately, but Didham et al. (2007) noted that complex non-additive interactions between such major drivers of change occur. For example, losses of native habitat are often associated with proliferation of invasive or alien species, so confusing the real contributions of these to native species declines. Two major categories of interactions were distinguished, with fundamentally different pathways and different implications for management. These (Didham et al. 2007) are defined as (1) the ‘interaction chain effect’, the initial effects of habitat modification on native species declines by altering the numerical abundance or geographical range of an invasive species; and (2) the ‘interaction modification effect’, the direct moderating effect of habitat modification on the per capita impact of invasive species on native species. The outcomes may appear similar, but the processes differ. In the first case, habitat modification drives increased abundance of an invasive species but its per capita impacts remain

constant, in a process that is likely to be very common. It is shown by examples such as the abundance of an invasive ladybird beetle being far higher in grasslands within a cropland system than at control sites in more pasture grassland-dominated landscapes, leading to additional predation pressure on a native aphid by predator spillover from the surrounding matrix (Rand and Louda 2006). Interaction modification effects incorporate assessment of invasive impacts modifying per capita interaction strength between native and invasive species, so that impact depends both on invader abundance and the extent to which interactions are changed through habitat modification. Access to hosts, prey or food plants, for example, may be influenced strongly by the structure of the local environment.

Native herbivores may thereby suffer increased predation or parasitisation pressure in natural habitats because of such spillover of (both alien and native) generalist enemies from nearby cropping areas. In Rand and Louda's experiments, this rationale was supported by three themes: (1) there was substantial overlap in coccinellid assemblages between cropland and grassland habitats, with the same four ladybird species, all generalists, predominant in each; (2) coccinellids were more abundant on crop edges than on edges of adjacent grasslands, implying that the crops may generally support higher predator densities; and (3) coccinellids were by far (2.7–9.6 times) more abundant in aerial samples from grassland within cropland than in a grassland matrix, implying that the crops are the potential sources of predators.

Interaction effects are important considerations in conservation management, and Didham et al. (2007) noted that establishing the cause(s) of changes being assessed is 'crucial for achieving conservation goals'. They noted an example discussed by King and Tschinkel (2006), of the fire ant *Solenopsis invicta* (p. 150) widely reported to displace native ant species in its invasive range, but for which experiments on eliminating fire ant colonies did not induce increased abundance or diversity of native ants. In this case, conservation of the native ants needed remediation of habitat disturbances that simultaneously led to native insect declines and facilitated fire ant invasion. *S. invicta* colonies in 40×40 m square plots in Florida were killed with hot water, and ants were surveyed there and on untreated control plots by pitfall trapping. This treatment led to 60% reduction of fire ants relative to numbers on the control plots but, unlike other common fire ant treatments (such as use of insecticidal baits), was specific to this target. Apparent lack of impacts of *S. invicta* on other ants might reflect that the fire ant had been established for around 50 years, so that the initial impact of its arrival was long past (King and Tschinkel 2006). Lack of any influences on the remaining fauna implied strongly that other factors might now be more important. Those findings, however, do not diminish the reality that *S. invicta* has replaced its native ecological equivalent (*Solenopsis geminata*) in many disturbed habitats in the region, but led to implication that habitat disturbance may be a primary cause of the dominance of *S. invicta*. Conservation of native ants then depends increasingly on conservation and restoration of undisturbed habitats.

The range of interactions between invasive insects (or other species) with endemic taxa and with each other assures an almost infinite combination of possible

outcomes, each context-specific, and hampering attempts to explore generality. The alien European carabid *Trechus obtusus* and the Argentine ant (*Linepithema humile*) both occur on Maui (Hawai'i), in areas that harbour a suite of endemic flightless *Mecyclothorax* ground beetles (Liebherr and Kruschelnycky 2007). The latter are all brachypterous, and many species have very narrow distributions. They occur in native forest remnants now surrounded by alien conifer plantations – in which the alien *T. obtusus* was recorded first in 2001. Samples in later years showed (1) increased levels of brachyptery in *T. obtusus*, a trait that had been interpreted from other carabid studies as helping to stabilise the beetle populations in newly colonised areas by reducing opportunity for emigration by flight, and (2) coincidental relative reduction of native forest floor ground beetles, notably of *Mecyclothorax cordithorax*. Native beetles continued to decline in areas invaded by Argentine ant, in contrast to *T. obtusus* whose persistence could reflect four possible factors, listed by Liebherr and Kruschelnycky as (1) the higher competitive capability of *T. obtusus* when both beetles interacted with the predaceous ant; (2) avoidance of ants by temporal activity of *T. obtusus*; (3) avoidance of ants in space by the beetle; and (4) relatively greater reproduction or immigration of *Trechus* over *Mecyclothorax* as traits that sustained population levels when under predation. Liebherr and Kruschelnycky (2007) suggested that a combination of invasive ants and large numbers of *Trechus* competing with *Mecyclothorax* spp. for refuge habitats could eventually render that mechanism unsustainable for the latter.

In practice, the impacts of alien species vary widely, and devising some way of comparing impacts of different taxa as a basis for determining priority for possible management needs has attracted much attention. Approaches explore many different parameters and predictive measures based on a species' characteristics and published/recorded information on its trajectory if it is invasive elsewhere, and sometimes incorporating information on related taxa for comparison. Attempts to formulate standard 'scoring systems' are exemplified by that used for alien species in Europe (Kumschick et al. 2015) by collecting records of ecological and socio-economic impacts using the 12 separate impact categories proposed through the 'Generic Impact Scoring System' (Table 4.3). This scheme was devised initially for vertebrates but was expanded subsequently to compare mammals, birds, fish, terrestrial arthropods and plants. Collectively, terrestrial arthropods had the lowest environmental impacts, but Kumschick et al. recognised that inferences from this initial study across major groups should be interpreted with caution.

Difficulties of forming worthwhile generalities are apparent in any particular ecological context. The varied roles of invasive species in disrupting plant reproductive mutualisms are one such, widespread, context of concern reviewed by Traveset and Richardson (2006). These are – in their words - 'often documented, although the profound implications of such impacts are not widely recognised'. Examples they cited spanned alien pollinators, herbivores, seed dispersers, plants and predators, each with potential for numerous outcomes and disruptions to long-coevolved mutualisms. To clarify changes, they believed it necessary to examine the relevant networks of interactions and the influences of increasing abundance and distribution of generalist pollinator and seed dispersers, noting also that many such interactions

**Table 4.3** The twelve categories of impact considered as the foundation of a scoring system to assess overall impacts of alien plants and animals (Kumschick et al. 2015)

<u>Environmental impacts</u>	Competiton	Transmission of disease
	Predation	Herbivory
	Hybridisation	Ecosystem
<u>Socioeconomic impacts</u>	Agriculture	Human health
	Animal production	Infrastructure
	Forestry	Human social life

**Table 4.4** Hypotheses considered worthy of investigation to help clarify mutualistic interactions involving invasive species within plant-pollinator or plant-disperser networks, as listed by Traveset and Richardson (2006)

1.	Introduction of an invasive pollinator/disperser that can displace native equivalents is expected to affect specialist plants more than generalist ones, as the latter are more effectively buffered against loss of native mutualists
2.	Specialist pollinators/dispersers are more prone than are generalist ones to disruptions by invasive pollinators/dispersers, as generalists rely on a wider range of resources
3.	Invasive alien plants offer more floral/fruit resources than do native plants, allowing greater numbers of pollinators/seed dispersers, especially generalists; specialist plants are more likely to be affected than generalist plants
4.	Plants that depend on an array of pollinators/dispersers might be less vulnerable to (1) introduction of an invasive herbivore that decreases plant attractiveness to (some of) those mutualists, or (2) introduction of an invasive predator that causes declines in populations of (some of) those mutualists
5.	An invasive herbivore (generalist) poses a major risk to specialist pollinators/dispersers. An invasive predator is more likely to affect specialist pollinators/dispersers as more easily encountered on those plants
6.	Mutualistic interactions among native plants and pollinators/dispersers will be the least vulnerable to disruption by invasive pollinators/dispersers or by invasive plants. By definitions, specialist pollinators/dispersers are unlikely to share plants, and specialist plants are unlikely to share pollinators/dispersers

are functionally ‘asymmetrical’. Specialist pollinators or dispersers tend to visit plants that accept a wide range of those species, whilst specialist plants may be pollinated or dispersed by generalists, leading to a series of hypotheses amenable to testing – and some of which have been promoted more specifically in various studies. Those hypotheses (Table 4.4) encapsulate much relevant consideration of mutualistic interactions and the needs to maintain/restore these through management appropriate to each situation.

Considerations over fates of pollinators have tended to overshadow other mutualisms between native species, which may prove equally profound and also ‘key casualties of invasions’ (Traveset and Richardson 2011). Invasive flowering plants can divert pollinators from native plants and so reduce their fitness. One informative example is of the introduced Australian *Acacia saligna* (Mimosaceae) in the Cape



Floristic Region of South Africa (Gibson et al. 2013), for which flower visitation rates by bees and other insects were compared on a range of native flora at sites with or without the acacia, as well as on the acacia itself. Conclusions were tentative, but *A. saligna* appeared to have a strong effect on honeybee (the native subspecies *Apis mellifera capensis*) visitation rates to co-occurring native plants. At least one plant (*Roepera fulva*, Zygophyllaceae) showed significantly lowered bee visitation rates, and this was attributed to competition with *A. saligna* for honeybee visits. Invasive plants as nectar sources can disrupt long-coevolved pollinator-plant associations. The invasive flowering *Chromolaema odorata* (Asteraceae) became a predominant herb in the understorey of forests in Thailand, and substantially increased the supply of floral nectar for butterflies (Ghazoul 2004). The flowers attracted the butterfly pollinators of the forest tree *Dipterocarpus obtusifolius* (Dipterocarpaceae), which is pollinated by Lepidoptera and birds, and one outcome was much reduced diurnal pollinator activity on the tree.

The central roles of interactions between plants and insects, mirrored in their prominence in any listings of alien species, are equally prominent in conservation, and some ramifications are summarised in the next two chapters. Many workers have emphasised that the establishments of alien plants and the ways in which they then recruit and accumulate native insect herbivores, are key aspects of analysing the evolution of dietary breadth. One example (Fox et al. 1997) is of the seed-feeding beetle *Stator limbatus* (Bruchidae) and its exploitation of the introduced ornamental tree Texas ebony (*Chloroleucon ebano*, Fabaceae) in Arizona. Laboratory rearing trials showed that use of this host was facilitated by host plant-mediated maternal effects: parents reared on the native *Cercidium floridum* produced progeny with substantially higher survivorship on *C. ebano* than parents reared on another native host, *Acacia greggii*. Fox et al. suggested that such host-mediated effects are likely to be common, and significant for understanding insect-plant interactions in numerous cases in which host switching occurs. A further complication in the above example is the likely repeated colonisation of *Chloroleucon* by each generation of *Stator*, so that local adaptations to that host and subsequent evolution of host preferences are effectively prohibited.

It is perhaps pertinent to reflect that, whilst most alien insects have arrived in their new environments by accident, with deliberate introductions a very small proportion of the spectrum, historical introductions of most alien plants have been deliberate, many as horticultural, forestry or garden ornamental, hobbyist collection purposes. ‘Desirable’ plants substantially outnumber pest or nuisance species.

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